THRESHOLDS IN HABITAT SUPPLY: A REVIEW OF THE LITERATURE

by P. R. Dykstra

BRITISH
COLUMBIA

Ministry of Sustainable Resource Management
Ecosystem Conservation Section
Ministry of Water, Land and Air Protection
Biodiversity Branch
Victoria, B.C.

Wildlife Report No. R-27

September 2004

Wildlife reports are documents relevant to biodiversity and wildlife in British Columbia. Manuscripts submitted for publication in this series are generally reviewed by two or three referees. Copies of this document may be obtained, depending on supply, through Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, BC. http://wlapwww.gov.bc.ca/wld/pub/pub.htm.

Library and Archives Canada Cataloguing in Publication Data
Dykstra, Pamela.
Thresholds in habitat supply : a review of the literature.

(Wildlife report ; no. R-27)

Available on the Internet.
Issued also in printed format on demand.
ISBN 0-7726-5210-4

1. Forest fauna - Effect of habitat modification on.
2. Habitat (Ecology) - Modification. 3. Habitat (Ecology) - British Columbia - Management. 4. Ecosystem management - British Columbia. 5. Forest management - British Columbia. 6. Biological diversity conservation - British Columbia. I. British Columbia. Ministry of Sustainable Resource Management. II. British Columbia. Ecosystem Conservation Section. III. Title. IV. Series title: Wildlife report (Victoria, B.C.) ; no. R-27.

QH541.I5D94 2004 333.95’4 C2004-960108-3

Citation
Dykstra, P.R. 2004. Thresholds in Habitat Supply: A Review of the Literature. B.C. Minist. Sustainable Resour. Manage. Ecosystem Conserv. Section, and B.C. Minist. Water, Land and Air Protection Biodiversity Branch, Victoria, BC. Wildl. Rep. No. R-27.

ABSTRACT

Understanding how and when species respond to habitat change is relevant to sustaining viable populations in managed forest ecosystems. Because some ecosystem changes are irreversible, of particular interest is knowledge about non-linear or "threshold" change that may have rapid, drastic effects on species or ecosystems. Ecological thresholds involve a change in the rate of response to ecosystem change; a critical value of an ecosystem property at which previously linear or unobserved change becomes a drastic transformation. Around thresholds, change occurs suddenly. Paradoxically, the changed state may be long-lived or irreversible. Threshold change caused by habitat loss can result in small, unviable populations, or species extirpation or extinction. These threshold changes in species populations ultimately occur due to insufficient amounts of habitat, leading to the concept of minimum thresholds in habitat amount, or the "extinction threshold." Although thresholds can manifest in many aspects of ecosystem dynamics, the focus of this review was thresholds in the response of species to changes in the amount of habitat.

Theoretical studies demonstrating thresholds are many. These models provide valuable insight into the processes, such as reproduction and dispersal, which primarily influence species response to habitat change. The empirical forest studies, which are more valuable than are models as predictive tools, are relatively few, with none set in British Columbia. However, empirical evidence of threshold change in other regions describes the dynamics in some forest ecosystems found in British Columbia, for example, boreal mixedwood. Initiatives currently underway to systematically quantify thresholds in the boreal provide the most advanced approach to utilizing thresholds in forest management. Overall, empirical threshold studies primarily occur in forest-farmland mosaics, where the loss of habitat is genuine. Given that agriculture is one of the primary threats to species loss locally, findings from research in these pastoral habitats may also be particularly relevant to habitats that are spatially similar in British Columbia.

The literature on thresholds in habitat amount is currently inadequate to provide a general, quantitative, scientific basis for forest management. Although thresholds are pervasive, there is little in the literature to indicate universal thresholds in forested habitats; there is no general consistency to when thresholds occur numerically across species and ecosystems. Formal evidence for "threshold responses to linear habitat loss" thus remains limited. Rather, the literature shows that systems under management are capable of producing unexpectedly non-linear responses to management actions in surprising circumstances.

The range of threshold behaviour demonstrated by the literature can inform a working hypothesis for managing ecosystems and conducting research. However, thresholds are relevant primarily in systems with similar disturbance regimes and ecologies. This emphasis on landscape context suggests the need for local work to characterize and integrate thresholds into the management of ecosystems in British Columbia. Overall, the literature suggests that an appropriate management direction with regard to thresholds is a commitment to monitoring and experimentation in local ecosystems, and a readiness with mitigating policies and actions.

Keywords: *thresholds, forests, non-linear, extirpation, extinction, habitat loss, fragmentation*

ACKNOWLEDGEMENTS

This paper began as a collaborative effort between students at Simon Fraser University's School of Resource and Environmental Management, and the University of British Columbia's Centre for Conservation Biology. I appreciate contributions to an earlier draft from Richard Feldman (UBC), Laurel Brewster (SFU), Dan Buffett (SFU), Pamela Dykstra (SFU), Sarb Mann (SFU), Marcella Olguin (SFU), Volker Michelfelder (SFU), Jason Smith (SFU), and Andres Valle-Domenech (SFU). Jason Smith also greatly helped with the bibliographic database. Alton Harestad (Biology Department, SFU) contributed to Section 3.1. Andy MacKinnon (Forests, Lands and Marine Branch, B.C. Ministry of Sustainable Resource Management) initiated the project, and provided direction and advice. Funding for compilation and editing of the report was provided by the B.C. Ministry of Sustainable Resource Management. Audrey Roburn (Ecosystem Conservation Branch, MSRM), and Gail Harcombe (MWLAP) assisted with project completion. Review comments on an early draft from Marvin Eng (Research Branch, B.C. Ministry of Forests) helped focus the project. Thoughtful review comments from Ken Lertzman (School of Resource and Environmental Management, SFU) and John Innes (Centre for Conservation Ecology, UBC) greatly improved the final manuscript. Warm thanks to Tom Braumandl for many discussions about thresholds, and for support and advice throughout the project.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

1.1 Background

Thresholds have a long and pervasive history in the ecological literature. The concept of thresholds has evolved in part from the debate about ecological stability. Historically, ecological stability from the perspective of the "balance of nature," considered only a single, static configuration toward which ecosystems would progress (Egerton 1973; Pimm 1991; Wu and Loucks 1995; Perry 2002). Since the late 1960s, discussions about ecosystem stability have undergone a paradigm shift, and expanded to consider the concept of multiple stable states in ecosystems, and by extension, thresholds of change (Lewontin 1969; Holling 1973; May 1973, 1977; Wissel 1984).

The importance of threshold responses to habitat change has more recently emerged as a resource management issue (Lande 1987, 1988a; Kareiva and Wennergren 1995; Eiswerth and Haney 2001). Habitat loss and degradation are widely considered to be the most important factors causing environmental change regionally and globally (Brown 1985; Wilson 1985; Meyer and Turner 1992; British Columbia Ministry of Water, Land and Air Protection 2002); exotic species introductions, and resource and urban development, result in the greatest changes to forest habitat in British Columbia (B.C. Ministry of Water, Land and Air Protection 2002). Changes in forest habitat result in the reduction in habitat area, isolation and fragmentation of habitat patches, and reduction in habitat quality. A predominant effect of habitat change is species decline and loss.

Species and ecosystem response to environmental change is complex. The timing and magnitude of the effects of change on natural systems are particularly difficult to predict. Species response to habitat change is often non-linear; evidence is emerging for thresholds of change in species tolerance to habitat alteration (e.g., Swift and Hannon 2002). Understanding the magnitude and the timing of species response to habitat change is therefore a desirable component of predicting the effects of such change. Additionally, once populations have become small, factors other than habitat loss — factors related to demographic, genetic, and environmental stochasticity — act on them to increase the probability of extinction (Frankel and Soulé 1981). Due to the higher risk of species extinction once population numbers are lower, maintaining functioning landscapes above critical habitat requirements is necessary to maintain viable populations. However, because species differ in their need for habitat amount, connectivity, and quality, characterization of what comprises landscape function can vary. The characteristics of threshold-sensitive species are therefore of interest, as are the habitat levels where threshold changes are known occur.

I reviewed the literature on habitat thresholds to help provide a scientific rationale for incorporating species threshold responses to habitat change into resource management planning in British Columbia. The broad objective of this review was to present the scientific literature pertinent to the concept of thresholds in terrestrial ecosystems. I approached the literature to answer the question: is there sufficient evidence of thresholds to support science-based forest management? To present the thresholds most relevant to conditions in British Columbia, I primarily concentrated on thresholds in habitat amount that cause rapid species (or population) decline, or extinction/extirpation.

1.1.1 Key Concepts and Definitions

Definitions and characteristics of thresholds

The term "threshold"[1] is present in the common lexicon, defined variously as: "any place or point of entering or beginning" (Nichols 2001, p. 1976); "the point at which a stimulus is of sufficient intensity to begin to produce an effect" (Nichols 2001, p. 1976); or "a level, point, or value above which something is true or will take place and below which it is not or will not" (Merriam-Webster online[2]).

---

[1] The etymology of the term threshold is Middle English, where threshold refers to 'the plank, stone, or piece of timber that lies under a door' (Gove 1961); the purpose of a threshold was to contain in a dwelling the 'thresh' or straw used as insulation against

[2] http://www.meriamwebster.com/cgi-bin/dictionary?book=Dictionary&va=threshold&x=21&y=18

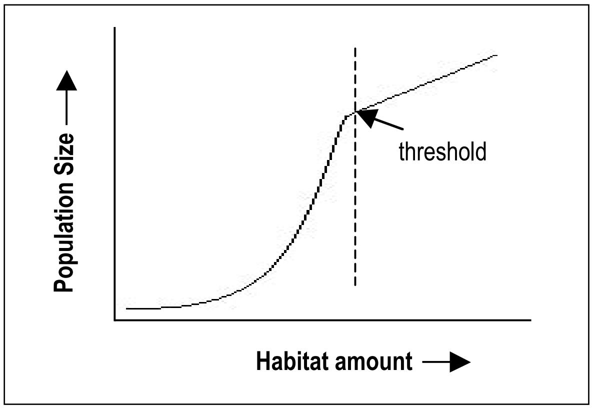
Please Note: some URLs link only to the home page of an organization - the path shown may be the result of a search feature within the site, which must be followed each time the site is visited.

Within the ecological literature, a set of conditions characterizes thresholds (May 1973, 1977; Wissel 1984). The presence of thresholds implies a critical region or value of a control variable, around which the response variable or system flips from one state to another (Muradian 2001). Ecological thresholds thus involve a change in the “rate of change” in the response of an ecosystem property — a critical value of habitat alteration at which previously linear or unobserved response in an ecosystem property (e.g., a species’ population size) causes drastic transformations. Around thresholds, change occurs suddenly. Paradoxically, the changed state may be long-lived; return to the previous state, if it occurs at all, might require long return times after a threshold is crossed (May 1977; Ludwig *et al.* 1997). The affected variable may fail to respond to the return of the control variable to the pre-threshold level, and begin to recover only when the control variable is returned to a significantly lower level (Holling 1973; May 1977). In some cases, the changed state may be irreversible (Wissel 1984). Additionally, ecosystems are more vulnerable to disturbance around thresholds (Wissel 1984). A disturbed ecosystem may require relatively more time to recover the nearer it is perturbed toward a threshold.

Types of thresholds

Thresholds occur at multiple levels, affecting all elements of biodiversity (i.e., affecting diversity at the ecological, genetic, and organism levels) (Heywood and Baste 1995). The first type of threshold I define is that present at the ecosystem level. Thresholds present at the ecological level have implications for ecosystem function (Chapin *et al.* 2000). Thresholds in ecosystem function may involve a critical level or composition of species diversity necessary for ecosystem functioning. The overall effect of an individual species’ loss on an ecosystem varies, depending on its interactions with other species and its ecosystem role. Thresholds in ecosystem function may thus accompany population decline in a keystone species, or decline in a species that has a cascade effect on other species due to trophic interactions or energy flows (see Chapin *et al.* 2000). McNaughton (1993) suggests there is a “…threshold of change that will overcome the damping effect of biodiversity, with an associated break point of ecosystem function to quite different levels…” Other authors (Tilman and Downing 1994), suggest a saturation point along a logistic curve, beyond which the system destabilizes rapidly as species diversity decreases. Alternatively, following disturbance, thresholds in community assembly may occur, whereby rapid change results in a long-lived, drastic change to the community composition (Frelich and Reich 1998; Lomolino and Perault 2000). Properties at the ecosystem level present a complex research problem; hence, understanding of ecosystem dynamics is poor, constraining the characterization of thresholds at the ecosystem level (Muradian 2001).

A second type of threshold affects genetic and organism diversity at the level of species (and subspecies) and populations. The removal of a seemingly insignificant amount of additional habitat may result in accelerated population declines not predicted from previous population trends (Pimm 1986). So called “extinction thresholds” (Lande 1987) result from species response to habitat loss based on minimum requirements for habitat. Thus, thresholds in habitat amount occur when an organism tends to extinction or extirpation beyond a minimum specified level of suitable habitat. For example, a species or population may exhibit a linear relationship between the proportion of habitat in the landscape and population size, across a range of habitat loss. However, at some threshold level of habitat loss or degradation, change may cause disproportionate declines. Where thresholds in habitat amount occur, the threshold value of habitat loss that precipitates rapid decline varies by species (or population) and by landscape, depending on resource availability and quality, and species habitat



Reprinted with permission

Figure 1. Hypothetical extinction threshold.

needs. One may observe the effect of crossing a habitat amount threshold as a rapid decline in species (or population) size, or a rapid or drastic change in the response of life history traits, particularly reproductive parameters (e.g., Swift and Hannon 2002).

A third type of threshold may occur, also affecting genetic and organism diversity at the species or population level, as a result of the spatial arrangement of habitat. The spatial effects of habitat loss — isolation of patches, reduced patch size, and an increase in the number of patches — result in a particular case of the habitat loss threshold, termed the "fragmentation threshold" (Andrén 1996). Thresholds in habitat amount are primarily quantitative phenomena, whereas spatial thresholds occur due to a qualitative shift from pure habitat amount effects to the spatial effects caused by the structural arrangement of habitat. However, the spatial effects of fragmentation are more prevalent with increasing habitat loss (Fahrig 2002, 2003). As habitat loss increases, the dominant influence in a landscape shifts from pure habitat amount effects to spatial effects; fragmentation of habitat, and subsequently fragmentation thresholds, are therefore increasingly important along the habitat loss gradient.

Thresholds reviewed in this paper

In this review, I concentrated on two types of thresholds: thresholds in habitat amount, and fragmentation thresholds. Although thresholds at the ecosystem level are ultimately relevant to ecosystem change in British Columbia, thresholds in habitat amount are a more immediate concern (Angelstam 1999). Angelstam (1999) describes phases of habitat change, and for each phase, the associated features of habitat change that are the focus for action to mitigate the negative aspects of habitat change. A recent literature survey (Muradian 2001) addresses the literature related to thresholds that occur at the ecosystem level; that is, threshold effects expected in ecosystems in an advanced state of degradation (Angelstam 1999). On a global scale, British Columbia is in a relatively early stage of habitat change (Angelstam 1999). To present the thresholds most relevant to conditions in this province, I therefore concentrated on the literature related to the influence of habitat loss and fragmentation on thresholds in species (or population) decline or extinction/extirpation. My goal was primarily to determine the degree to which the existing literature was sufficient to support using the concept of thresholds as a scientific basis for forest management.

2 RESEARCH METHODS AND DOCUMENT STRUCTURE

2.1 Research Methods

In this review, I initially hoped to focus on empirical data from British Columbia landscapes. Because of a paucity of local data, the scope broadened to incorporate studies from North American and European grassland and temperate and boreal forest habitats. I reviewed the development of threshold theory to place the current literature in context. I also reviewed methods for identifying thresholds. Although thresholds have a long history in the ecological literature, researchers have rarely approached the question of thresholds in a management context. To the contrary, because thresholds can manifest in many aspects of ecosystem dynamics, research about thresholds is spread over many ecological disciplines. The literature encompasses habitat characteristics such spatial structure and habitat amount, and species traits such as dispersal and reproduction. The broad scope of this literature review reflects the diffuse nature of the literature. Although not exhaustive across all disciplines, in this review I sought a degree of depth that provided a representative picture in relevant topic areas, with an emphasis on those subjects most relevant to habitat change in British Columbia (e.g., habitat loss and fragmentation).

Bibliographic database searches generated approximately half of the literature reviewed. Search terms included combinations of "threshold," "forest," "ecosystem," "fragmentation," "extinction," "habitat," and others. To minimize gaps in the literature search, names of key authors, bibliographies of key papers, and poorly covered taxonomic groups were also searched. In several instances, a topic's literature genealogy was traced back chronologically through the bibliographies of relevant papers. Databases searched included the following:

BIOSIS (1969-present[3])
Digital Dissertations (1980-present)
Web of Science (1985-present)
Zoological Record (1993-present)
Current Index to Statistics (1994-present)

The literature review has three components. The literature is presented firstly in this paper, secondly in table format (Appendix Table 1), and thirdly in an Endnote 5.0 database (Niles & Associates 1996). The structure of this paper is described below in Section 2.2. Appendix Table 1 summarizes numerical results of the core thresholds work. Because the literature covers such diverse aspects of ecology, readers should be cautious about using Appendix Table 1 to generalize across topics. In Appendix Table 1, for each paper in the table, I recorded the citation (author and date), the research setting (theoretical or empirical), the type of model (for theoretical studies), the keywords (based on the topics in this paper), the threshold (amount of habitat remaining), the taxa, and a brief description of the study location, methods, and main results.

The Endnote database contains all citations and annotations for many of the publications. In addition to the citation (*author*, *date published*, *title*, *journal*, *volume*, *issue*, *pages,* and *abstract* where possible), annotations addressed what the article said, how useful the article was, and what information was missing.

2.2 Document Structure

The literature review was structured into three main topic areas:

- background, history, and evolution of the habitat threshold concept (Section 3);
- characteristics of habitat alteration related to species decline, such as habitat loss and fragmentation (Section 4); and
- characteristics of species that cause them to respond in a threshold-like manner to habitat change, such as reproductive traits or inter-specific relationships (e.g., plant-pollinator) (Section 5).

A reader's guide is found in Table 1. This table contains a synopsis of the major points, arranged according to the Table of Contents. Section 3 contains a considerable amount of background material on theoretical ecology, and is intended to provide the ecological context for studying the literature on thresholds. While germane to the topic of thresholds, Section 3 may not be required reading for many readers with a background in ecology. These readers should refer to Section 3 for definition and elaboration of the technical terms and concepts used throughout the document. Section 3 can thus be used to refresh the experienced reader's memory for uncommon concepts and terms, or to provide a context for readers less familiar with theoretical ecology. Sections 4 and 5 and contain the core thresholds literature. Section 6 contains conclusions and recommendations. Within each section and sub-section, the literature is generally arranged to examine the theoretical and modeling studies first, followed by the empirical evidence. Each section ends with a short summary.

3 REVIEW OF RELATED ECOLOGICAL THEORY

A significant body of ecological theory and empirical evidence spanning many ecological disciplines over 30 years addresses threshold dynamics in landscapes fragmented by habitat loss. Dominant themes relevant to the question of ecological thresholds are many: scale, keystone processes and biotic entrainment, the equilibrium theory of island biogeography (TIB), metapopulation theory, percolation theory, non-equilibrium and stability theory, threshold properties, the Allee effect, and extinction debt. I discuss each of the themes in detail in the sections below.

3.1 Habitat[4]

In this review of over 400 references related to habitat thresholds, there was abundant use, but no definition, of the term "habitat." I define habitat here to explicitly link the discussion of habitat thresholds to the way in which organisms use the composite of resource attributes collectively known as "habitat." Habitat is the suite of abiotic and biotic resources in an organisms

---

[3] Present = December 2003

[4] Alton Harestad, Department of Biology, Simon Fraser University, contributed to this section.

Table 1. Reader's guide. Section numbers and headings parallel the Table of Contents.

SECTION	SECTION HEADING	CONTENT
1.	INTRODUCTION	
1.1	Background	Context of literature review, problem statement, definitions
2.	RESEARCH METHODS AND DOCUMENT STRUCTURE	
2.1	Research Methods	Methods for literature review, lists databases searched and search terms, provides overview of the products stemming from the literature review (e.g., synthesis document, table of core literature, EndNote database).
2.2	Document Structure	Organization of the literature in the synthesis document; includes this table.
3.	REVIEW OF RELATED ECOLOGICAL THEORY	
3.1	Habitat	Habitat is the suite of abiotic and biotic resources in an organism's environment, which the organism uses to meet its requirements for energy, nutrients, shelter, security, and social partners.
3.2	Landscape Structure, Process, and Scale	Key processes operating at different scales structures landscape pattern. The distribution of organisms across landscapes reflects this pattern. Species respond to landscape change at a scale consistent with their size and trophic level.
3.3	Systems with Multiple Stable States	Mathematical and empirical evidence demonstrates that more than one stable state occurs in ecosystems, the transition between states is characterized by rapid, sudden (threshold) change.
3.4	Island Biogeography and Related Theory	Species richness is a function of colonization and extinction processes, limited by habitat isolation and size.
3.5	Metapopulation Theory	Population size is a function of colonization and extinction processes of sub-populations between patches in a landscape.
3.6	Percolation Theory	Modeling demonstrates that rapid changes (thresholds) occur in the size, number and shape of habitat patches at a critical amount of habitat. Percolation theory is a modeling analogue for fragmentation effects.
3.7	Effects on Small Populations	Once populations have become small, factors external to changes in habitat quantity or quality in effect drive populations toward extinction, including environmental, genetic, and demographic factors.
3.8	Extinction Debt	Time lags occur between landscape change and species response, therefore the results of habitat loss and fragmentation are unlikely to appear until some undetermined and possibly long time afterwards.
4.	HABITAT CHARACTERISTICS INFLUENCING THRESHOLD RESPONSES	
4.1	Effects of Habitat Loss	Habitat loss is the single most significant factor affecting species decline. Habitat amount thresholds occur at the stand and landscape level.

Table 1. Continued.

SECTION	SECTION HEADING	CONTENT
4.2	Spatial Effects of Habitat Loss	Simulation modeling demonstrates fragmentation thresholds. However, the concept of fragmentation thresholds derived from percolation theory is a poor analogue for the process of fragmentation in forests. Nonetheless, spatial modeling shows that, in landscapes with dispersed habitat, occupancy in remaining habitat declines with habitat loss, necessitating a greater habitat amount for species persistence in such landscapes. Accordingly, habitat aggregation results in a lower habitat amount threshold. Evidence of thresholds in fragmentation from EMSs is equivocal. Empirical evidence initially considered to clearly demonstrate fragmentation thresholds across landscapes is significant in landscapes comprised of forest / farmland, but not in forested landscapes. Empirical evidence of thresholds in fragmentation is often measured directly as habitat loss or a variable related to habitat loss. Model inadequacy and sampling issues constrain empirical demonstrations of theoretical thresholds in fragmentation.
4.3	Physical and Biological Effects of Habitat Loss	Modeling suggests thresholds in species tolerance to habitat loss, depending on edge sensitivity. Edge sensitivity can be more important to thresholds in habitat than sensitivity to area. Models also predict catastrophic loss of ecosystem function when edges are abundant in landscapes. Edge density shows threshold changes around critical shapes and sizes of patches. Through their influence on the amount of edge in a landscape, the rate, amount, and pattern of habitat loss may cause secondary thresholds in edges.
4.4	Matrix Effects	Incorporating the influence of the matrix is difficult, due to the complexity of modeling movement, and does not always significantly improve model predictions. If high-quality matrices reduce mortality in the matrix, improvements to matrix quality may result in a lower threshold in habitat amount. Several studies suggest that the relative influence of matrix quality on thresholds in habitat depends on patch isolation (i.e., landscape context), implying that the importance of the quality of the matrix is most pronounced in landscapes with high habitat loss.
4.5	Landscape Context	Discussions of landscape context in the literature reflect three different usages of the term. First, landscape context can refer to the degree of isolation of a patch in the landscape. Second, landscape context can refer to the landscape type that occurs in the matrix. Third, landscape context can refer to the natural landscape pattern. Each of these usages implies that thresholds differ in different landscapes.
5.	SPECIES CHARACTERISTICS INFLUENCING THRESHOLD RESPONSES	
5.1	Dispersal	A species' dispersal capability determines, in part, its perception of landscape connectivity. Habitat aggregation appears to mitigate some of the effects of habitat loss, particularly at high levels of habitat loss. Poor dispersers appear to be affected more detrimentally than are good dispersers by thresholds in habitat amount, requiring greater aggregation at lower levels of habitat loss. Species may respond more to the quality of habitat patches and to barriers such as openings than they do to the configuration of patches. However, the details of the relative importance of movement choices of patch size and isolation are inconclusive from the threshold literature. Because the critical connectivity threshold varies by species relative to their perception of the landscape, a single connectivity threshold for an entire community is very unlikely.

Table 1. Continued.

SECTION	SECTION HEADING	CONTENT
5.2	Reproductive Traits	Reproductive measures have the greatest influence on extinction, are early indicators of habitat thresholds, and are also the most relevant to evaluating habitat suitability. Reproductive measures are thus the best means to determine species persistence probability in a landscape.
5.3	Rarity	Rarity affects both the location of species-specific thresholds and the nature of species response to habitat loss and fragmentation. Rare species disappear at lower levels of habitat loss than do generalists species, and rare species show threshold responses, even when generalist species do not.
5.4	Geographic Range	Variation in species density across a geographic range and vulnerability to habitat change at range margins suggest that we should treat a single species as a separate ecological entity at various points along its range.
5.5	Metapopulation Structure	The threshold amount of habitat loss tolerated by a metapopulation varies as a result of patch arrangement, life-history characteristics of individual populations, and stochastic influences on extinction and colonization rates. Metapopulation models now incorporate the physical aspect of the patch network, complex dynamics arising from migration patterns, environmental and demographic stochasticity, environmental correlation, and non-equilibrium dynamics. Several tools exist to calculate the threshold conditions required for metapopulation persistence and the metapopulation capacity of landscapes.
5.6	Inter-specific Dynamics	
5.6.1	Competition	The effect of species competitive traits on the habitat threshold depends on assumptions about the rules governing species co-existence. Models that assume that community structure is based on competition-colonization trade-offs show that habitat loss and fragmentation result in the extinction of the superior competitor first. Models that incorporate details about species relative dispersal capability, and about landscape structure, find that these specifics can influence extinction probabilities, and, in certain cases, inferior competitors are most vulnerable. Whether abundant or rare, and under different assumptions about the spatial pattern of habitat loss, competitors with poor dispersal suffer the highest extinction thresholds.
5.6.2	Plant-pollinator systems	Allee effects in plant-pollinator systems are important because they lead to patch extinctions, thereby increasing extinction probabilities for populations at low densities. Empirical data show links between patch area and Allee thresholds; isolation of patches exacerbates the detrimental effects of patch size. The vulnerability of plants to Allee thresholds depends on the degree to which reproduction depends on pollinators and seed production. Ranking criteria exist to aid assessment of plant vulnerability to extinction, incorporating the species traits that lead to Allee thresholds in plant-pollinator mutualisms.
5.6.3	Keystone species	Keystone species are those whose impact on the community or ecosystems is disproportionately large relative to their abundance. Keystones may interact with other species based on predation, mutualisms such as plant-pollinator relationships, or through habitat modification (e.g., primary excavators). The loss of keystone species implies ecosystem-level effects of habitat thresholds.
6.	Summary, Conclusions, and Recommendations	

Table 1. Continued.

SECTION	SECTION HEADING	CONTENT
6.1	Summary	Habitat loss has the greatest influence on habitat thresholds. Fragmenting habitat results in more habitat required for persistence; however, the evidence is weak for ubiquitous fragmentation thresholds in forests. Threshold changes appear to occur at low levels of habitat loss for rare species, poor dispersers, and habitat specialists. Thresholds are increasingly important to other species in forested habitats as habitat loss progresses. Reproductive traits appear to be the life-history traits most sensitive to habitat change, and are appropriate as an early indicator of threshold response.
6.2	Conclusions	Habitat loss is the primary cause of the threshold response of species to habitat change. However, there is little in the literature to indicate universal thresholds in habitat; there is no general consistency to when thresholds occur numerically across species and ecosystems. The literature on thresholds in habitat amount is currently inadequate to provide a quantitative, scientific basis for forest management. This result suggests that an appropriate management direction with regard to thresholds is a commitment to monitoring and experimentation, and a readiness with mitigating policies and actions. The range of threshold behaviour demonstrated by the literature can inform a working hypothesis for managing ecosystems and conducting research.
6.3	Recommendations to improve science concerning thresholds	1. Retention of sufficient habitat and habitat elements is the primary means of maintaining species above habitat thresholds. 2. In the short term, the range of risk demonstrated by the literature can inform a working hypothesis for managing ecosystems and conducting research. 3. In the long term, research would determine habitat thresholds in regional systems. 4. Research would increase understanding about habitat suitability, patch dynamics, species tolerance for matrix habitat, and the efficacy of maintaining habitat elements. 5. Research would increase knowledge about the threshold responses of taxa other than birds and insects. 6. Research and monitoring of species focused on reproductive traits would provide the most useful information. 7. Monitoring programs that include the concept of time lags in species response to habitat change would provide the most useful information for management. 8. Provincially consistent interpretation and application of the term “fragmentation” would be the most useful to support management. Studies examining fragmentation effects would be most useful if they use experimental or statistical methods to control for the effects of habitat loss.

environment, which the organism uses to meet its requirements for energy, nutrients, shelter, security, and social partners. These broad requirements are common among all organisms. However, the particular structures, elements, and environmental conditions that provide the resources to meet an organism's requirements vary greatly among species; plants, animals and other organisms use habitat in different ways. For all species, habitat incorporates seasonal ranges, life stages (e.g., reproduction), and habitat elements (e.g., food source or nesting site) (Jones *et al.* 2002).

Habitat is temporally (e.g., Jones *et al.* 1994; Waterhouse *et al.* 2002) and spatially (e.g., Weir and Harestad 2003) variable. At shorter temporal scales, seasonal environmental changes impose variation in energy availability and energy expenditures. At longer temporal scales, natural and human-caused forest dynamics create a shifting tableau of habitat availability across the landscape. Changes to forest structure mediated by succession at the stand level alter the resources available over time (Waterhouse *et al.* 2002). Spatially, an organism accesses its requirements for energy, nutrients, and cover within its home range. The size of the home range is a function of an organism's body size and trophic level; heavier organisms with higher trophic levels use larger home ranges (Harestad and Bunnell 1979). Within the home range, an organism may preferentially use specific stands, patches, and habitat elements (structures) distributed throughout the range (Weir and Harestad 2003).

An organism's needs vary seasonally and over its life; seasonal movements may result in multiple home ranges, and the repeated use of intermediate habitat between seasonal ranges. At larger temporal and spatial scales, animals can place themselves in suitable habitats by making relatively long dispersal movements and then establishing home ranges in areas that fulfill their habitat requirements. These post-juvenile dispersal movements increase the spatial extent of an organism's range. For birds and mammals, these one-time, long-distance movements are a function of body size, trophic level, and taxa; heavier organisms with higher trophic levels disperse farthest, and birds disperse farther than mammals (Sutherland *et al.* 2000).

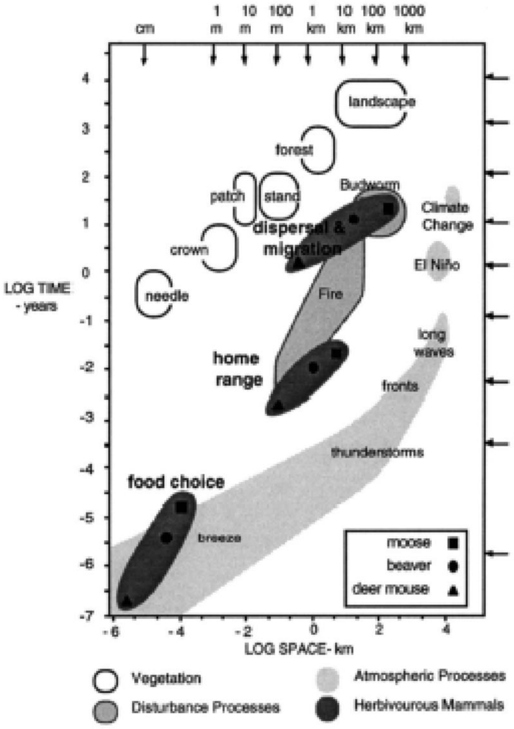
The spatial and temporal distribution of habitat and the differential use of habitat by different organisms suggest that habitat supply is specific to organisms or groups of organisms, and consequently, specific to scale. Accordingly, thresholds in amount of habitat are organism- and scale-specific (Angelstam *et al.* 2001a, 2003).

3.2 Landscape Structure, Process, and Scale

Ecological processes shape ecosystem pattern (Turner 1989; Wiens 1989; Kotliar and Wiens 1990). Ecosystem pattern is organized by a few abiotic and biotic keystone structuring processes that occur at different scales (Figure 2) (Holling 1992). Faster processes operating at smaller scales are constrained by and linked to slower processes at larger scales (Urban *et al.* 1987). This nested hierarchy of processes corresponds to a patchy hierarchy of structure (Kotliar and Wiens 1990; O'Neill *et al.* 1991). Energetics operating across scales create distinct breaks in structural patterns across landscapes (Figure 2). As a result, pattern-and-process based discontinuities form threshold changes in landscape structure.

Landscape patterns and processes aggregate over space and time (O'Neill *et al.* 1991), and within this structure (read "habitat"), organisms have evolved and adapted. Patterns of species distributions reflect scale-dependent patterns in landscape structure. For example, patterns of species size (weight) distributions mirror structural aggregation in landscapes (Holling 1992). Holling (1992) performed an elegant test, demonstrating a discontinuous distribution in animal body-mass that holds across biomes (e.g., boreal forest and grasslands) and body plans (birds and mammals). More recent work has confirmed discontinuous body mass patterns (Restrepo *et al.* 1997; Lambert and Holling 1998; Allen *et al.* 1999; Raffaelli *et al.* 2000; Havlicek and Carpenter 2001). Similarly, home range area and migration and dispersal distances are related to trophic level and body size (Harestad and Bunnell 1979; Sutherland *et al.* 2000). Species thus perceive the landscape at a scale consistent with their size, body plan, and trophic level (Figure 2) (Harestad and Bunnell 1979; Sutherland *et al.* 2000). As a result, species respond differently to resource distribution at different levels within the hierarchical patch structure of the landscape (Kotliar and Wiens 1990). Changes in vegetation structure will have a different effect on population processes at different scales (e.g., Doak *et al.* 1992; Pither and Taylor 1998).

Habitat loss and fragmentation and an organism's interaction with its environment are both scale-specific phenomena — the degree to which a landscape is perceived as fragmented depends on the scale of perception, and at broad scales, is related to dispersal ability (Kotliar and Wiens 1990). Movement by individuals therefore determines the scale at which they respond to patchiness and spatial heterogeneity (Fahrig and Paloheimo 1988; Gardner and O'Neill 1991). Accordingly, vegetation structure differentially affects the movement patterns of animals (Crist *et al.* 1992; Wiens *et al.* 1997; Pither and Taylor 1998). Because movements occur at different spatial and temporal scales (e.g., daily movements, seasonal migration patterns, and single, within-generation dispersal movements), changes in landscape structure can affect individual and population-level processes in different ways at different temporal and spatial scales. Accordingly, the World Conservation Union (IUCN) identifies scale as a critical problem for resolution with respect to thresholds (Keith *et al.* 2000), while Angelstam *et al.* (2003) observe thresholds at multiple scales.



Reprinted with permission

Figure 2. Time and space scales of the boreal forest and their relationship to some of the processes that structure the forest. These processes include insect outbreaks, fire, atmospheric processes, and the rapid carbon dioxide increase in modern times. Contagious mesoscale disturbance processes provide a linkage between macroscale atmospheric processes and microscale landscape process. Scales at which deer mouse, beaver, and moose choose food items, occupy a home range, and disperse to locate suitable home ranges vary with their body size. (Figure 8 in Peterson et al. (1998). Caption from Figure 1 in Allen and Holling 2002).

3.3 Systems with Multiple Stable States

The concept of thresholds is closely linked to, and to some extent has evolved from, the debate about ecological stability. Historically, the perspective on ecological stability, from the "balance of nature" paradigm, considered only a single, static configuration toward which ecosystems would progress (Egerton 1973; Pimm 1991; Wu and Loucks 1995; Perry 2002). Although deeply embedded in ecological thinking, this paradigm had a theological, rather than a theoretical or empirical basis, and dissenting perspectives are centuries old (see Egerton 1973). In particular, since the late 1960s, discussions about ecosystem stability have expanded to consider the concept of multiple stable states in ecosystems, and by extension, thresholds of change.

Lewontin (1969) distinguishes between two perspectives of stability. The first, the "balance of nature" perspective, sees the structure of all ecological communities as a consequence of certain fixed forces, with the assumption that only one stable point exists, which he terms "globally stable." An analogue for this perspective in forested systems is Clements' theory of successional dynamics, in which macroclimate over a broad region results in a stable endpoint, determined by the climax vegetation (Turner 1989). In an example from British Columbia, the globally stable, Clementian perspective forms the basis for the ecosystem classification scheme (Meidinger and Pojar 1991). The second stability perspective sees communities with different structures, or populations with different abundances, as a consequence of two alternate stable states. In this perspective, the present state is a consequence of the community or population history. Lewontin terms the alternate equilibria model "globally unstable," but "locally stable" in the vicinity of either of the states. Insect outbreaks are an example of alternate stable-state systems (Holling 1973). Similarly, population dynamics of other organisms can fluctuate between relatively high and relatively low occupation in the landscape. Low landscape occupancy levels are in this case synonymous with small, unviable populations (Frankel and Soulé 1981). In both the "balance of nature" and the alternate equilibria model, stability is synonymous with constancy.

Theoretical and empirical attempts to describe ecological stability led to the conjecture that multiple stable states exist in ecosystems (Lewontin 1969; Holling 1973; Sutherland 1974). Instability and long return times or irreversibility characterize the behaviour of systems around thresholds (Wissel 1984). During the 1970s, theoretical (Holling 1973; May 1973, 1977; Peterman *et al.* 1979), and empirical (e.g., Sutherland 1974; Diamond 1975; Gilpin and Diamond 1982) demonstrations of rapid changes in ecosystems, leading to altered species composition or change in species abundance, led ecologists to adopt the notion of ecological thresholds associated with multiple stability domains as an explanation for discontinuous change in communities and ecosystems.

Accompanying the shift to the multiple-stability state perspective was a shift in thinking about the importance of constancy (Holling 1973). Whereas in the single-state paradigm, constancy is a measure of stability, the multiple-state paradigm embraces the dynamic nature of ecosystems. In the multiple-state perspective, the ecological system is "profoundly affected by changes external to it, and continually confronted by the unexpected, [therefore] the constancy of its behaviour becomes less important than the persistence of the relationships" (Holling 1973, p. 1). Our attention shifts from the equilibrium states to the conditions required for persistence, and from stability to resilience. The probabilities of extinction of ecosystem elements are a measure of the resilience of the system, and the ability of the system to return to an equilibrium state after a disturbance is a measure of stability. The system persists in its current form within a "domain of attraction" (range of persistence), which replaces the narrowly defined stable state of previous models.

In this view, the focus should be at the boundary of the system's domain(s) of stability (Holling 1973). Instability occurs at domain boundaries, and thresholds of change characterize this instability. Stability domains are dynamic, and the effect of random events on the persistence of the system will vary as the deterministic forces shaping the domains' size and characteristics vary (Holling 1973). In systems managed for a stable maximum sustained yield, for instance, we fix our attention on the constancy of the system at a single point, and the "sustainable" yield is determined from the properties of the system in this state. Because harvesting itself is a novel and additional disturbance, it alters the shape and characteristics of the previous range of persistence in the system. Under harvesting pressure, system resilience changes (Holling 1973). Ecosystems also become more vulnerable to disturbance around thresholds (Wissel 1984). A random event that may have been previously absorbed, or even the harvesting pressure alone, can thus trigger rapid change in the integrity of the system (Holling 1973). Hence, the boundary of the stability domains that characterize an ecosystem, in part determine the ecosystem's response to human perturbation.

Much ambiguity, and even dichotomy, is found in the ecological stability literature (e.g., Pimm 1984). Several authors suggest that much of the ambiguity is in the terminology (e.g., Orians 1975; Connell and Sousa 1983; Pimm 1984; Grimm and Wissel 1997), or the experimental setting (Connell and Sousa 1983), rather than in research results *per se*. Connell and Sousa (1983) conclude that there is ambiguity in the "accepted" empirical evidence (i.e., Sutherland 1974; Diamond 1975; Gilpin and Diamond 1982) for ecosystem stability in both the traditional sense of a single equilibrium state, and the more recent perspective of multiple stable domains. Using strict criteria, Connell and Sousa (1983) reject virtually all previous empirical examples of stability and persistence,[5] on one or more of

---

[5] □
area, o□
place (Connell and Sousa 1983, p. 791).

three grounds. First, they consider evidence inapplicable since the physical environment was different in the different various alternate states. Second, either one or both of the alternate states persisted only when "artificial" controls (e.g., anthropogenic perturbations) were maintained; and/or third, the evidence was simply inadequate. In addition to these three grounds, the authors cite inappropriate spatial or temporal scale as the main barrier to the observation of multiple states. In many of the studies cited by Connell and Sousa (1983) as inconclusive evidence of single or multiple states of stability or persistence, the existence of thresholds of discontinuous change are not debated. In their conclusion, the authors propose that ecological systems should be conceptually regarded as persisting within stochastically defined bounds (*sensu* Holling 1973). More recently, one study provided further evidence against the hypothesis that a particular intertidal system exhibited multiple equilibria (Bertness *et al.* 2002, and references therein).

In a more recent literature review, two authors found 163 definitions of 70 different stability concepts (Grimm and Wissel 1997). They attribute the terminological confusion to the inappropriate projection onto complex ecological systems, of concepts derived from simple, dynamic systems in mathematics and physics. The classic stability analogues borrowed from physics — the pendulum and the rolling ball — are unambiguous in their state variables, reference states, and disturbances. In an ecological system such as a forest, on the other hand, many variables can be described (e.g., species richness, diversity, biomass, trophic partitioning, nutrient cycling rate); and a disturbance/perturbation can affect each variable differently (Grimm and Wissel 1997).

An inventory of the terminology enabled Grimm and Wissel (1997) to propose a systematic method for communicating and interpreting stability statements (Appendix Table 2). They find that the majority of the references to stability described one of three properties: (1) staying essentially unchanged (constancy), (2) returning to the reference state (or dynamic) after a temporary disturbance (resilience), and (3) persistence through time of an ecological system (persistence). They propose dispensing with the notion that "stability" is itself a property of ecological systems, and instead, communicating about the three stability properties: constancy, resilience, and persistence. To bring further refinement to the portrayal of the stability properties of a system, they suggest thorough characterization of the ecological situation, and strict limits to generalizations about stability properties: "the domain of validity of a stability statement is delimited by the ecological situation under observation" (Grimm and Wissel 1997, p.328). From the conservative, but thoughtful perspectives of critical authors (e.g., Connell and Sousa 1983; Grimm and Wissel 1997), it is apparent that providing unequivocal evidence of alternate stable states and stability requires clear articulation about the system in question, careful planning, and, in the case of forests, large spatial and temporal scales.

There is currently insufficient empirical data to prompt conclusive generalizations about ecological stability. While Connell and Sousa (1983) make a case against the "accepted" evidence for multiple stable states (e.g., Holling 1973; Sutherland 1974; Diamond 1975; Gilpin and Diamond 1982), their perspective has been largely ignored in the literature. In fact, authors more frequently cite the empirical studies rejected by Connell and Sousa (1983) as conclusive evidence of alternate stable states (e.g., Ward and Thornton 1998), demonstrating that the strength of the conviction may not be synonymous with the strength of the evidence. However, there are several, more recent studies that demonstrate the existence of multiple stable states; for example, in grassland/savannah (van Langevelde *et al.* 2003) and ungulate grazing (Augustine *et al.* 1998) systems (See the Resilience Alliance website for a review of thresholds in ecosystem states: http://resalliance.org/ev_en.php? ID=2797_201&ID2=DO_TOPIC). These differing views about the strength of evidence for multiple stable states represent different degrees of conservatism with respect to a paradigm shift in ecological thinking. The "balance of nature" perspective survived millennia without evidence, providing a context to understand and describe the natural world. Similarly, the alternate stable state perspective is not conclusively demonstrated, but this does not preclude gaining a greater understanding of ecological systems via this perspective. Perhaps most importantly for this review, it is also clear that empirical evidence of alternate stable states and stability, or complete characterization of a system with respect to these properties, are not necessarily prerequisites to examining a system for threshold behaviour.

3.4 Island Biogeography and Related Theory

The conceptual framework of the theory of island biogeography (TIB) posits that there are limits to species diversity on islands, influenced by island size and isolation from the mainland (Preston 1962; MacArthur and Wilson 1967). According to the TIB, the equilibrium number of species in island habitats is a function of colonization and extinction rates, as determined by distance from a mainland habitat (isolation), and island size (area) (Figure 3). The TIB predicts that smaller and more isolated islands will support fewer species than larger islands that are in closer proximity to the mainland. The TIB corollary in fragmented forested landscapes is that patches are analogous to islands. Therefore, as habitat loss increases, colonization rates decrease and the number of species within a patch declines.

The analogy between oceanic and habitat islands is not entirely transferable to forest patches; forest patches are analogous to islands only in certain circumstances, and for certain species or species groups. The ecotone between habitats (edge) and the intervening habitat (matrix) exhibit complex mitigating and/or exacerbating effects on species, depending on matrix quality, individual species level of habitat specificity, and natural landscape heterogeneity (Margules *et al.* 1982; Saunders *et al.* 1991; Doak and Mills 1994; Schieck *et al.* 1995; Gustafson and Gardner 1996; Norton *et al.* 2000). Where habitat loss and forest fragmentation are genuine (i.e., the forest is replaced by a different habitat type, or habitat loss is permanent), the island analogy is appropriate for species that can neither disperse through nor utilize the matrix. However, where the removed forest is replanted, creating a pattern of different seral stages, the TIB is of little use for many species. Nonetheless, the TIB signalled a change in ecological thinking about terrestrial habitats, distinguishing the spatial configuration of habitats as an important component of population and community dynamics (Harrison and Bruna 1999).

The TIB raises questions about how organisms that evolved in either a continuous or a naturally disturbed landscape will respond to human-caused discontinuity in their habitat, or to the spatial dilution of preferred habitat with less preferred types. If insensitivity to the spatial arrangement of their habitat characterizes species response to habitat alteration, then a continuous decrease in the abundance of a single species would be concomitant with a decrease in amount of habitat. However, island biogeography also considers the arrangement of islands, or habitat patches, by showing a negative correlation between the degree of isolation of an island and its species richness (MacArthur and Wilson 1967). These relationships between the species richness of an island and its size and degree of isolation are key to most fragmentation studies in the literature (e.g., Robbins *et al.* 1989).

The random sample hypothesis is a method based on the theory of island biogeography, and is used to examine declines in species richness resulting from

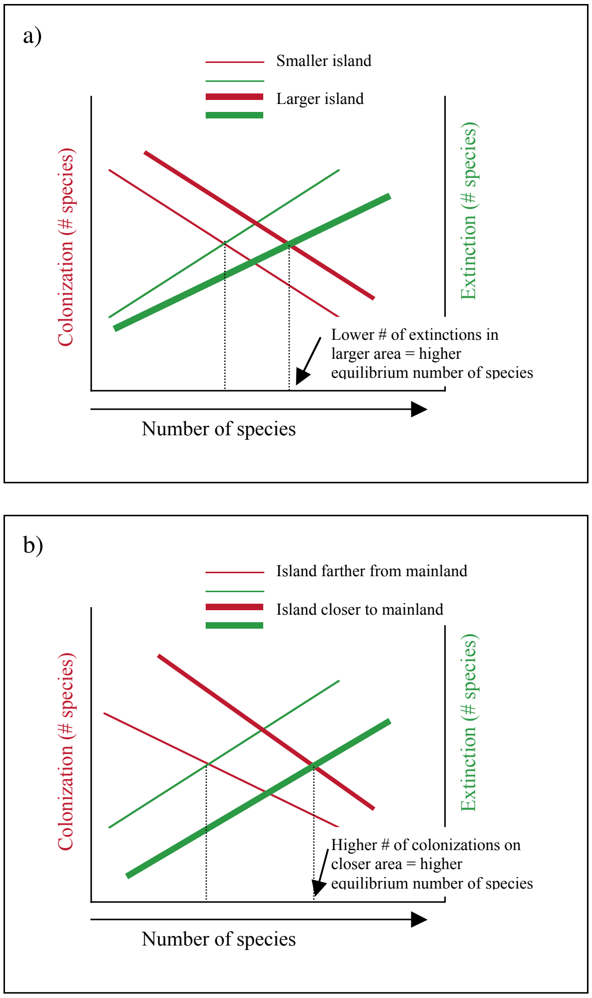


Figure 3. Species area curves showing the influence of a) area and b) distance from mainland, on the equilibrium number of species.

Reprinted with permission

declines in island size (Conner and McCoy 1979; Haila *et al.* 1983). The random sample hypothesis also extends to single species to describe declines in population size. The random sample hypothesis has a simple premise: there should be a simple one-to-one linear relationship between changes in the proportion of suitable habitat in the landscape and changes in the species diversity or population size in the landscape. There are two relevant, theoretical interpretations of the random sample hypothesis. First, if species numbers in communities and population density in patches appear not to be randomly drawn from a source pool of species and individuals, respectively, then factors related to patch size and isolation are operating; that is, the spatial aspects of habitat loss are operating (Andrén 1994, 1996; Rodríguez and Andrén 1999). This method is therefore used in the literature to detect fragmentation thresholds — declines in species numbers or population size attributed to the spatial effects of habitat loss (Andrén 1994; 1996; see Section 4.2, Spatial Effects of Habitat Loss). Secondly, the random sample hypothesis predicts that rare species will be the first to disappear as the proportion of suitable habitat declines in the landscape, due to chance alone (Conner and McCoy 1979).

A general criticism of the TIB, which would also apply to the random sample hypothesis, is that, while the explanatory power of these models is reasonable for species numbers and extinction rates, they are poor tools for predicting what species are most likely to go extinct and in what sequence (Doak and Mills 1994, and references therein). Another method for studying species diversity — nested subset analysis — addresses the patterns of species presence, and in particular, whether species-poor islands' assemblages are merely subsets of species rich-islands' assemblages (Patterson and Atmar 1986). In nested subset analysis, monitoring occurs of species numbers and identities in different habitats. If the "nestedness" is a result of extinctions (or extirpations) resulting from faunal relaxation (see below), then a deterministic sequence of extinctions is inferred (Doak and Mills 1994; Andrén 1997). However, expected and observed results from nested subset analysis are complex and equivocal, partly due to the mitigating effects of the matrix, and because different ecological processes can generate similar nestedness scores (Simberloff and Martin 1991; Doak and Mills 1994; Andrén 1997). Nonetheless, if a significant species-area relationship exists, and knowledge exists about the nested subset structure, prediction of community composition with respect to fragmentation and habitat loss is possible (e.g., Bolger *et al.* 1991; Andrén 1997; Edenius and Elmberg 1997, and references therein; Hager 1998; Schmieglow and Monkkonnen 2002). Nested subset analysis and the random sample hypothesis may enable identification of risk-prone species (Worthen 1996, cited by Andrén 1997), or of the threshold habitat size below which species loss is predicted by sampling effects (habitat loss) alone. The latter can be used as a basis to elucidate the presence of spatial fragmentation effects (Schmiegelow and Mönkkönen 2002).

3.5 Metapopulation Theory

Metapopulation theory is a specialized case of the TIB, resembling the TIB in focusing on extinction and colonization, but differing in assuming a network of small patches with no persistent mainland habitat, and in focusing on the dynamics of a single species (Harrison and Bruna 1999). Hence, the "classic" metapopulation is a "population of populations," distributed throughout a patch network (Hanski and Gilpin 1991). Although difficult, if the following conditions are met, one can demonstrate that species persistence in a fragmented landscape is due to classic metapopulation dynamics; that is, population turnover is attributed to stochastic local extinction and recolonization events. Classic metapopulation conditions are: (1) habitat patches support local breeding populations; (2) no single population is large enough to ensure long-term survival; (3) patches are not so isolated as to prevent recolonization; and (4) local population dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely (Hanski *et al.* 1995).

The metapopulation concept extends far back into the ecological literature. Ideas that can be seen to represent metapopulation concepts are evident in Andrewartha and Birch's (1954, cited by Hanski and Gilpin 1991) discussion of local extinctions and re-populations in patchy habitats due to resource competition. However, Levins' (1969) seminal work became the real starting point for metapopulation theory. Levins (1969) distinguished between the dynamics of a single population and a set of local populations. He developed a model in a regional pest control context, within which local populations would fluctuate asynchronously. The simple metapopulation model was analogous to the logistic model for local population growth. Levins realized that regional pest population abundance was reduced by increasing extinction rate, and therefore recommended pest control be implemented synchronously throughout a large region (Hanski and Gilpin 1991). The metapopulation model did not receive much attention between 1969 and 1987, when Lande modified the model and established the idea of minimum habitat requirements (the "extinction threshold") for a territorial species (Lande 1987; 1988a).

For metapopulations, increasing frequency of species extirpation in local patches increases extinction risk at the landscape or metapopulation scale (Levins 1969; Hanski 1994a). Authors have used the metapopulation model to show that threshold conditions exist for metapopulation persistence, characterized by patch density and area at the point where extinction rates exceed colonization rates (Lande 1987; Nee 1994; Bascompte and Solé 1996; Hanski *et al.* 1996; Hanski and Ovaskainen 2000). The threshold coincides with the minimum amount of suitable habitat required for a particular species to persist in a landscape (Hanski *et al.* 1996): the "extinction threshold" (herein referred to as the "habitat threshold"). Beyond this threshold, a metapopulation will tend towards extirpation from the landscape.

Debate exists as to whether patch occupancy represents "classic" metapopulation dynamics, or if "mega-population" (Hanski 1999b), "mainland-island," "single patch" (Harrison 1991, 1994), "source-sink," or "pseudo-sink" (Pulliam 1988; Watkinson and Sutherland 1995) models better describe population dynamics. This debate is non-trivial, because applied conservation biology has embraced classic metapopulation theory (Fiedler and Jain 1992). The notable distinction between classic metapopulation dynamics and other forms of patch-based metapopulation dynamics is the relative importance of local extinction events to the overall metapopulation persistence. If classic metapopulation structure is not the case, persistence of the metapopulation should be relatively unaffected by population turnover on small patches, and will more likely be affected by population dynamics in one or a few large patches (Harrison 1991).

Brown and Kodric-Brown (1977) present the concept of the "rescue effect" — the idea that it is more likely that a small number of immigrants can successfully rescue an extant population than colonize a new area. The rescue effect is central to the theory of metapopulation dynamics, which posits that population equilibrium is a landscape-level phenomenon — a function of colonization and extinction in patches. Demonstrating the importance of considering populations as open rather than as closed systems, Burkey (1989) showed that the rescue effect can greatly affect the extinction probability of species in fragmented reserves. Metapopulation modeling has also shown that, where relevant (in the case of sub-populations spatially close enough to see regular exchange of organisms), the rescue effect should be incorporated into models used to determine minimum habitat requirements (i.e., models that determine the "extinction threshold" or habitat threshold) (Hanski *et al.* 1996). Failure to account for rescue effects results in an underestimation of the habitat threshold.

More recently, one author has reformulated and expanded the concept central to the rescue effect in terms of source-sink dynamics in highly variable habitats (Pulliam 1988). Landscape heterogeneity generates a mosaic of habitats of differing quality to different species; human activity adds another component to this heterogeneity. Within a species, habitat use may include highly variable habitats, with associated differential impacts on individual survival and population dynamics. "Sink" habitats are characterized by within-habitat reproduction that is insufficient to balance local mortality (Pulliam 1988). Populations may persist in sinks, because of continued immigration from "source" habitats, which are more productive and characterized by greater reproduction than mortality (Pulliam 1988). Examples of source-sink populations include, among others: Beaver (*Castor canadensis*) (Fryxell 2001), grassland sparrows (Curnutt *et al.* 1996), and American Pika (*Ochotona princeps*) (Kreuzer and Huntly 2003), although a separate study reports on a metapopulation dynamics in a different pika population (Moilanen *et al.* 1998).

The concepts of the rescue effect and source-sink dynamics are important, because the presence of individuals in sub-optimal habitat may mask the actual influence of such habitat on population dynamics; an organism's *presence* in a habitat is not necessarily the same as its *persistence* in a habitat. Additionally, overall population vulnerability may be high in a source-sink population, because of the relatively high importance of the source habitat; the fate of the entire population hinges on the persistence of the source habitat population. Demographic or environmental stochasticity in what is essentially a single-source habitat could threaten the population. Note that source-sink populations are not classic metapopulations, because sink habitats cannot support a sub-population. The difference in the pika studies discussed above illustrates this (Moilanen *et al.* 1998; Kreuzer and Huntly 2003). Variation in population dynamics in different landscapes is interesting because it contrasts a landscape with a habitat distribution that supports colonizing individuals (the metapopulation landscape) with a landscape in which the habitat distribution results in sink populations (the source-sink landscape). This illustrates the importance of discerning patch-scale dynamics in different landscapes.

Research in British Columbia underscores the need to consider complex landscape-level and within-patch population dynamics such as source-sink habitats and the rescue effect, to discern the true population trends occurring in managed forest landscapes. In a survey of birds in remnant patches of old-growth (>300 years old) montane forests on Vancouver Island, several authors examined species richness and abundance of non-old-growth and old-growth species (defined as species found by previous research to have higher abundance within old-growth forest than they have in other habitats) in small and large patches following harvesting (Schieck *et al.* 1995). The authors hypothesized that non-old-growth species would be more abundant in small-patch centres, than in large-patch centres, and, conversely, that old-growth species would be more abundant in large old-growth patches than in small. The results supported the first hypothesis, but not the second; the authors did not detect a strong relationship between old-growth species numbers and patch size. They suggested that a rescue effect may occur with respect to the relative proximity of extensive old-growth forests; immigration from the nearby old-growth forests may have maintained populations within the small patches studied. The authors also recognized that, since they did not evaluate population productivity or viability, the relations between these variables and patch size might demonstrate different patterns than those they observed for species distributions, such as extinction debt due to sink dynamics in small patches. They suggested cautious interpretation of their results, until further work addresses population viability in remnant patches (Schieck *et al.* 1995), but no other published research from coastal British Columbia is available to refute or corroborate their results.

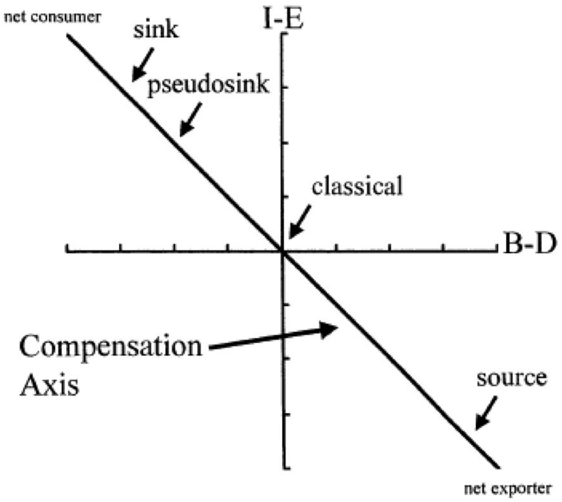
There are many sub-categories of spatial dynamics in populations that do not necessarily fit the metapopulation criteria. Thomas and Kunin (1999) suggest that the various definitions are confusing, and do not effectively categorize all populations. Many populations may exhibit characteristics from more than one category, and some populations may exhibit characteristics that are intermediate between categories (Thomas and Kunin 1999). Populations may also exhibit scale-dependent population dynamics. For example, because of immigration from a distant habitat, a habitat network observed to support a classic metapopulation at one scale may actually exhibit mainland-island characteristics at a coarser scale (Pagel and Payne 1996; Thomas and Kunin 1999; Wilson *et al.* 2002). Additionally, population dynamics might change over time in one place (e.g., as succession progresses), or populations of the same species may exhibit different population dynamics in different landscapes, reflecting the local disturbance history and the resulting habitat network (Moilanen *et al.* 1998; Thomas and Kunin 1999; Kreuzer and Huntly 2003).

Given the critiques of "classic" metapopulation theory that find the theory insufficient to describe real populations (Harrison 1991, 1994; Harrison and Taylor 1997; Hanski 1999b; Thomas and Kunin 1999), emphasis should shift toward understanding the relative importance of individual patches to regional population persistence (Thomas and Kunin 1999). From this perspective, it is more appropriate to perceive population dynamics and patches within a network as falling along a continuum (Figure 4 and 5). In proposing a continuum-based approach, Thomas and Kunin (1999) suggest shifting focus — from interpreting patterns to interpreting the compensating processes driving population numbers within a patch; that is, "internal" process (birth and death) and "external" processes (immigration and emigration) (Figure 4). This type of graphic representation allows consideration of the effect of removing, for example, the patch containing the source of immigrants, and emphasizes the identification of the highest quality and/or largest patches for protection. Thomas and Kunin (1999) also propose a graphic representation of the spatial structure of populations ("mobility"), portraying the relative importance of the process of dispersal (i.e., the importance of the external processes of immigration and emigration) to population structure and persistence (Figure 5). Because perception of population structure is scale-dependent , the identification of critical patches in the network also relies on a multi-scale approach to studying patch- and network-level occupancy. (Thomas and Kunin 1999; Wilson *et al.* 2002).

In summary, metapopulation theory is an inherently spatial perspective of population persistence. Metapopulation theory links the size, quality, and arrangement of habitat patches with the dispersal characteristics of a species. This perspective enables recognition and conservation of those habitat patches most critical to population survival. Metapopulation theory predicts minimum (i.e., threshold) conditions for metapopulation persistence. The development of theory and modeling to estimate habitat thresholds in the context of metapopulations is presented in Section 5.5 Metapopulation Structure. Forest harvesting alters landscapes by way of habitat loss, fragmentation, and changing habitat quality, hence altering the landscape from the metapopulation perspective. Fragmentation (or connectivity) thresholds are one component of the threshold landscape characteristics required for metapopulation persistence. To explore the link between metapopulation persistence and connectivity thresholds, in the next section I present a theory concerned with spatial threshold effects caused by fragmentation-percolation theory.

3.6 Percolation Theory

The prevailing theory about the effects of spatial fragmentation threshold predicts threshold declines in species numbers or population size at critical levels of habitat loss (Andrén 1996). This perspective is entrenched in the idea that landscape connectivity is important for species persistence. Landscape connectivity is "…the degree to which a landscape facilitates or impedes movement of organisms among resource patches…" (Taylor *et al.* 1993). Percolation theory (Stauffer 1985; Stauffer and Aharony 1992), used as an analogue for the processes of habitat loss and fragmentation (e.g., Franklin and Forman 1987), predicts threshold changes in connectivity as habitat is lost. Fragmentation in the narrowest sense is the breaking apart of habitat (Fahrig 1997), although traditional definitions of fragmentation consider other spatial effects of habitat loss, such as patch isolation (Wiens 1989). Based on the idea that populations have evolved in patchy environments, or may exist in human-caused patchy environments, in the metapopulation perspective, habitat discontinuity has a large effect on how species function (Harrison and Taylor 1997). Regardless of the specific metapopulation dynamics (e.g., source-sink, classic metapopulation; see Section 3.5, Metapopulation Theory), colonization



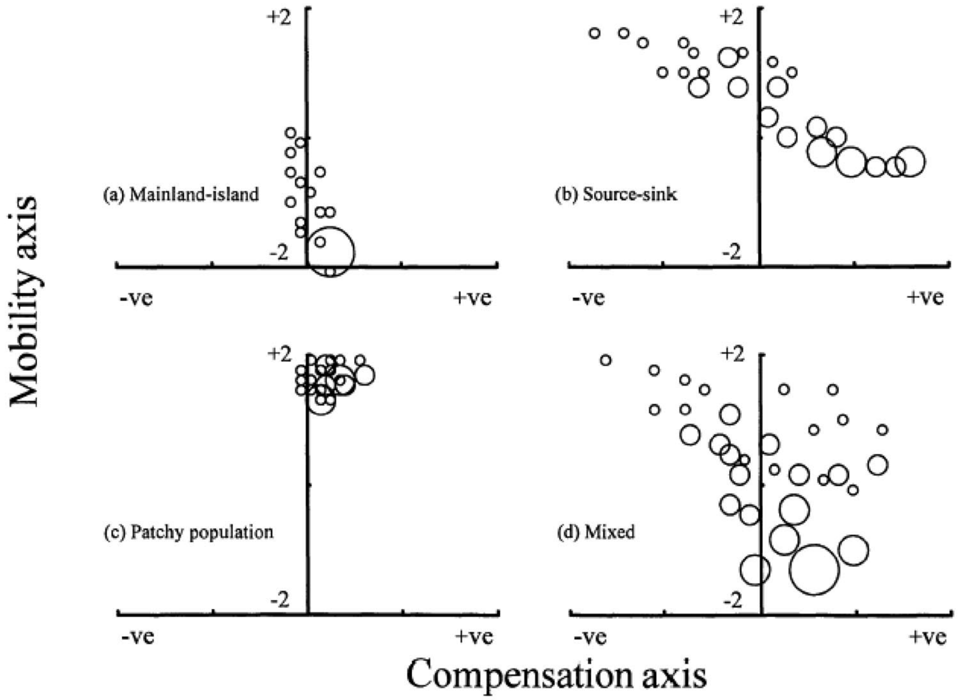
Reprinted with permission

Figure 4. The Compensation Axis. B = birth; D = death; I = immigration; E = emigration; per capita rates. The "Compensation Axis" captures much of the variation between population categories, with net demographic generators of individuals on one side and net consumers on the other. The compensation axis serves as an attractor in demographic space; assuming even weak density-dependence, any population unit that is temporarily away from this line will return towards it" (Thomas and Kunin 1999, p. 648). (Figure 1 in Thomas and Kunin 1999.)

(dispersal between patches) is therefore critical to metapopulation persistence. Habitat loss that results in a hostile matrix and/or increasing patch isolation may have detrimental effects on species persistence. For organisms vulnerable to the conditions in the area between patches (the matrix), landscape connectivity may be important.

The study of fragmentation-related threshold behaviour is demonstrated by percolation theory, using cellular automaton models (Stauffer 1985; Stauffer and Aharony 1992) to investigate the idea that fragmentation influences the extinction threshold. In these grid-based models, connectivity indices are used to measure the effect on the remaining landscape of cell (habitat) removal. According to percolation theory, rapid changes in the size, number, and shape of clusters (habitat patches) occur around a critical probability "p_c" (proportion of habitat), wherein the largest cluster (patch) just "percolates" (i.e., extends from one edge of the map to another) (Stauffer 1985; Gardner and O'Neill 1991). In landscape-level ecological applications, these critical percolation values imply that a sudden change in connectivity of the landscape may be expected at a critical density of clusters — the "percolation threshold" (Gardner *et al.* 1987; Turner *et al.* 1989; Gardner and O'Neill 1991; Gustafson and Parker 1992; With 1997). Below the percolation threshold, there is no longer a contiguous cluster (patch) extending across the landscape (Gardner *et al.* 1987; Turner *et al.* 1989; Gardner and O'Neill 1991; Gustafson and Parker 1992).

Although the exact amount of "habitat loss" at which this connectivity threshold occurs depends upon the assumptions of individual models, its existence has been numerically demonstrated in several different simulation and GIS studies (Gardner *et al.* 1987; Gustafson and Parker 1992; Stauffer and Aharony 1992; Lavorel *et al.* 1993; Keitt *et al.* 1997). The p_c of 0.5928 refers to clusters defined by contacts with the nearest neighbour (four adjacent sites), while additionally taking into account the four diagonal sites results in a p_c of 0.4072 (Stauffer 1985). For species capable of crossing unsuitable habitat (gaps), the p_c is between 0.25 and 0.30 (Plotnick *et al.* 1993). In landscapes with a low



Reprinted with permission

Figure 5. Hypothetical distribution of population (size of symbol proportional to population size) on compensation and mobility axes. (a) mainland-island metapopulation system; (b) source-sink system; (c) patchy population system; and (d) mixed system with a range of compensation and mobility values. On the compensation axis, +ve indicates relatively high importance of migration, -ve indicates relatively low importance of migration. (Figure 3 in Thomas and Kunin 1999).

proportion of suitable habitat (<20%), ongoing habitat loss results in an exponential increase in distances between patches (Gustafson and Parker 1992), creating thresholds in habitat gap (opening) measures (observed at 20% remaining habitat) (With and King 1999a), or complete isolation of patches (observed at 30% remaining habitat; Franklin and Forman 1987). Hence, the loss of connectivity associated with percolation thresholds may relate to a loss of landscape function and influence population dynamics (Taylor *et al.* 1993; With and Crist 1995; Keitt *et al.* 1997; Wiens *et al.* 1997; With *et al.* 1997).

3.7 Effects on Small Populations

Small populations are subject to a variety of factors other than changes in habitat quantity or quality that can drive populations toward extinction, including environmental, genetic, and demographic factors (Frankel and Soulé 1981). Small-population demographics are relevant because a great number of populations can persist at low levels for long periods of time, particularly in the absence of environmental perturbation (Lande 1993), resulting in an overabundance of rare species in a landscape — the "signature of extinction debt" (Hanski and Ovaskainen 2002) (see Section 3.8, Extinction Debt, for more discussion about this concept). Small-population demographics fall into three main categories: environmental influences (including environmental stochasticity and natural catastrophes); genetic stochasticity (generally leading to genetic deterioration); and demographic influences (including demographic stochasticity and social dysfunction — so-called "Allee" effects) (Shaffer 1981; Wilcove 1987; Lande 1993, 1994). Natural catastrophes, such as fire, storms, and disease epidemics may occur infrequently, but may be devastating to a small population, whereas a larger population would more likely survive such an event (Lande 1993). Small populations are also vulnerable to environmental effects in the absence of catastrophes, arising from temporal or spatial variation in habitat parameters (e.g., temporary food shortages). Small, isolated populations draw from a restricted gene pool, leading to the "establishment of deleterious traits within a population, or the inability to adapt to sudden environmental changes" (Wilcove 1987); for empirical examples see Buza *et al.* (2000), Hildner *et al.* (2003), Reed and Frankham (2003), and Saccheri *et al.* (1998).

The Allee effect suggests that there is a positive relationship between individual fitness and either the number or density of a species (Allee 1938; Stephens and Sutherland 1999; Stephens *et al.* 1999). Only processes or mechanisms that lead to reduced individual fitness at low population size or density are classed as Allee effects; these are distinct from other effects that might lead to extinction, such as environmental stochasticity (Stephens and Sutherland 1999; Stephens *et al.* 1999). Reported Allee effects commonly involve behavioural interactions related to reproduction (Berec *et al.* 2001, and references therein; also see review in Dennis 1989). Fitness reduction may occur due to the inability of an individual to find a mate; or, in social species, because a necessary, critical mass of individuals does not occur to trigger an individual process such as mating. Dysfunctional social behaviour may occur as population reduction occurs or as the habitat patches become smaller and more isolated, and individuals experience difficulty finding either suitable mating habitat or a mate, or both (Lande 1988a). Alternatively, an imbalance in the age, size, or sex structure (e.g., too few reproducing females) may reduce reproductive fitness (Berec *et al.* 2001). Plant-pollinator systems represent a distinctive form of the difficulty in finding a mate (see Section 5.6.2).

Allee effects related to reproduction also occur in species that require a threshold number of individuals to trigger some process, such as reproduction. One author theorized that the Passenger Pigeon (*Ectopistes migratorius*) might have exhibited this behaviour (Halliday 1978, cited by Wilcove 1987). Breeding in a small number of massive colonies, the social facilitation provided by sheer numbers may have induced the birds to breed, while reduced numbers below some threshold may have been insufficient to stimulate mating. Beyond reproductive effects, other mechanisms result in improved fitness with increasing numbers or density. For example, reduced densities decrease western hemlock's ability to acidify soil and sequester water (Ferson and Burgman 1990). The Allee effect ultimately implies threshold abundances or densities, below which populations tend toward extirpation, even in the absence of random bad luck.

3.8 Extinction Debt

Field research often occurs over short time scales, relative to the time span of ecological response to habitat alteration (Saunders *et al.* 1991; Kattan *et al.* 1994; Eriksson 1996a, 1996b, 1997; Eriksson and Kiviniemi 1999; Renjifo 1999; Debinski and Holt 2000; Hanski and Ovaskainen 2002). Complex responses to habitat alteration may result in a time delay between cause and effect (MacArthur and Wilson 1967; Brown 1971; Tilman *et al.* 1994; Hanski and Ovaskainen 2002). Where habitat alteration results in populations that are unviable, relic species are considered "extinction debt" (Tilman *et al.* 1994; Hanski and Ovaskainen 2002; Ovaskainen and Hanski 2002). Extinction debt refers to situations of habitat loss in which the threshold condition for survival is no longer met, but the species have not yet gone extinct due to the time delay in their response to environmental change. Additionally, human-caused habitat loss may have occurred over a short time-span, relative to the response time of many affected organisms (Eriksson 1996a, 1996b, 1997; Eriksson and Kiviniemi 1999; Carlson 2000). As a result, short-term research may capture only transient results, ignoring responses that occur over long time scales due to complex population dynamics, or, alternatively, results may reflect the delayed response of previous habitat alteration, and not capture response to recent changes. This section outlines the processes that cause delayed reponse, and presents empirical examples.

Island biogeography theory (MacArthur and Wilson 1967) recognizes that a system undergoing change (i.e., at non-equilibrium) experiences a species decline and a time delay between initial colonization and attaining equilibrium species richness; they term this process "faunal relaxation." However, rates of extirpation or extinction associated with faunal relaxation are poorly understood (but see Karr 1982). Brown (1971) discusses relaxation or mammalian "community collapse" following faunal relaxation in terrestrial habitats such as mountaintops. The continuation from faunal relaxation to community collapse in montane islands occurs because colonization does not augment extinction to maintain equilibrium in this type of isolated habitat. The delayed response in species richness or population size initially proposed by MacArthur and Wilson (1967) and Brown (1971) was recently reformulated, expanded, and termed the "extinction debt" (Tilman *et al.* 1994).

Quantitatively, extinction debt at a given time is the number of species expected to go extinct eventually because their threshold condition is no longer satisfied (e.g., Hanski 2000). Modeling has demonstrated that the length of the time delay increases as metapopulations near the extinction threshold (Hanski and Ovaskainen 2002). Furthermore, there is positive correlation between the length of the time delay, and both the strength of the perturbation and the characteristic turnover time of the metapopulation (Ovaskainen and Hanski 2002). As a result, an overabundance of rare species will occur in the transient time between habitat loss and extinction (Hanski 2000; Hanski and Ovaskainen 2002). Other research demonstrates that, at high levels of habitat loss, the rate at which species become rare and are added to the extinction debt is an accelerating curve (Figure 6) (Tilman *et al.* 1994). The shift to a high number of rare species is a general but "previously overlooked signature of extinction debt" (Hanski and Ovaskainen 2002).

Few studies have explicitly examined long-term extinction rates following fragmentation, but a number demonstrate trends that reveal the effects of faunal relaxation and extinction debt (Kattan *et al.* 1994; Petit and Burel 1998; Brooks *et al.* 1999; Renjifo 1999; Hanski 2000; citations in Hanski and Ovaskainen 2002). Two studies examined different regions of fragmented sub-Andean forest (Kattan *et al.* 1994; Renjifo 1999). Both studies found that 30% of the original forest bird species (41 species) were extinct. In one region, over 90 years, continuous forest cover was reduced from 80% to 20%. One author speculates that the relatively high proportion of species still present there (70% remaining), is largely due to the rescue effect (Renjifo 1999). The presence of large forest fragments and one large tract of continuous forest may provide a source for continual recolonization of smaller, sink habitat. In a third study of extinction debt, Brooks *et al.* (1999) created an exponential decay rate function to model the extinction rate in 1000-ha patches in a fragmented tropical forest. The authors estimate that only half of the expected extinctions occurred within the first 50 years following fragmentation.

Incorporating non-equilibrium dynamics (ongoing timber harvest) into a study of the extinction threshold for Spotted Owl (*Strix occidentalis caurina*) shows that extinction can take place long after (> 100 years) landscape change has occurred and ceased (Lamberson *et al.* 1992). Metapopulation modeling for the Glanville Fritillary (*Melitaea cinzia*) similarly showed a time lag between habitat change and extinction (Hanski *et al.* 1996).

Two extinction debt studies examined beetles (Petit and Burel 1998; Hanski and Ovaskainen 2002). In one study, a time lag in response to environmental change was demonstrated for the ground beetle *Abax parallelepipedus* in northern France (Petit and Burel 1998). The connectivity of the study landscape from the perspective of the beetle was reduced 28% over a 41-year period (1952-1993). The connectivity of the landscape in 1952 is a better predictor of the 1993 beetle distribution than the 1993 connectivity, suggesting a delayed response to loss of habitat and connectivity. In a final example of extinction debt, data from multiple studies on forest beetles in Finnish boreal forests demonstrate that in regions with similar remnant forest at the time of the studies, there are large differences in the number of extirpated populations (Hanski and Ovaskainen 2002, and references therein). In the southwestern coastal forests, where human impacts are long term and severe, >50% of specialist beetle species in the coniferous boreal are extirpated. In the northeastern forests, where habitat alteration has a relatively short history (beginning after World War II), but similarly severe effects, only 10-20% of species are regionally extinct. The authors speculate that the remaining endangered species in the northeastern forests represent the extinction debt resulting from massive habitat loss (Hanski and Ovaskainen 2002).

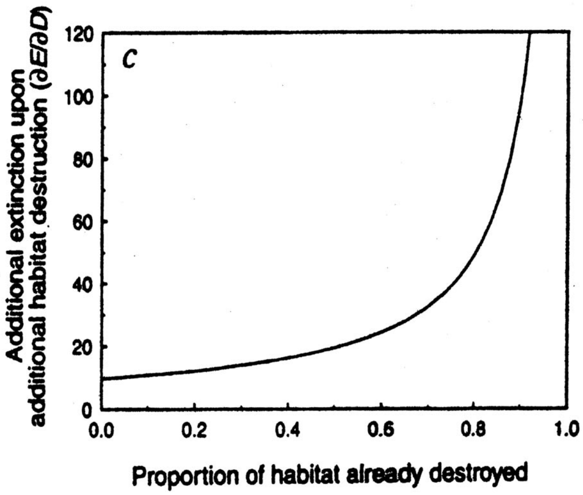


Figure 6. The more habitat already destroyed, the greater the effect of additional destruction on extinction. Units on y-axis ($\partial E/\partial D$) represent the change in extinction debt/ change in unit proportion of sites permanently destroyed. (Figure 1c in Tilman *et al.* 1994.)

Reprinted with permission

Many short-term empirical studies also report delayed effects of habitat loss and fragmentation. Gonzalez (2000) showed a delayed effect of fragmentation on grasshopper species richness in experimentally fragmented moss patches. Specifically, significant ($p<0.05$) differences in species richness between continuous and fragmented landscapes were not apparent until months after the initial fragmentation event. Similarly, Hagan *et al.* (1996) observed “packing” of ovenbirds into forest fragments after harvesting. While ovenbird abundance was greater in fragmented landscapes, mating and nesting success was lower than in unfragmented landscapes, suggesting that the higher population levels were only temporary. Several other studies have also shown crowding of individuals in patches immediately following fragmentation, followed by a shift to lower abundances in subsequent years (e.g., Bierregaard and Lovejoy 1989; Darveau *et al.* 1995).

Time lags may additionally occur where human-caused habitat loss has occurred over a short time-span, relative to the response time or life history traits of many affected organisms. Extinction debt may exist in the form of “living dead” species (Hanski and Ovaskainen 2002), whose presence may superficially indicate no detrimental response to habitat change, but whose viability is in fact doomed. For example, several studies have found that even after habitat loss and fragmentation hinder reproduction and recruitment, several Scandinavian plants persist by way of long-lived life cycle stages, such as dormant seeds and clonal propagules (Eriksson 1996a, 1996b, 1997; Eriksson and Kiviniemi 1999). Other authors studying the White-backed Woodpecker (*Dendrocopos leucotos*) (an old-growth specialist) found a time lag in population declines that was attributed to species longevity and territoriality (Carlson 2000). In the woodpecker study, long-term habitat availability and population data demonstrated that between 1950 and 1970, woodpeckers were found in significantly ($p<0.05$) higher abundance than expected from the amount of remnant habitat. Woodpeckers tend to remain on a territory despite the removal of suitable habitat; coupled with species longevity (up to 11 years), territoriality likely resulted in higher than expected population numbers (Carlson and Stenberg 1995, cited by Carlson 2000). Significantly ($p<0.05$) greater declines than predicted by habitat loss between 1970 and 1980 were interpreted to reflect two factors: a delayed response to previous habitat loss and a threshold-type response to the decrease of suitable habitat below the minimum required for population viability (i.e., below the habitat threshold) (see Section 4.1, Effects of Habitat Loss, for further discussion of this study and the habitat threshold).

In summary, time-lag concepts are important to ecological thresholds because they mean we cannot expect the results of habitat loss and fragmentation to be apparent until some undetermined and possibly long time afterwards. Time lags in response to a changing environment may be due to organisms adapting to new conditions (Brown 1971). Alternatively, delayed response to habitat loss and fragmentation may express as an accelerated or threshold-like ecosystem-level response in the future. Maintenance of viable populations under changing habitat conditions depends on traits that influence species ability to adapt to the overall rate, quantity, and quality of habitat loss and recovery (Henle *et al.* 2004). In either case of adaptation or trend toward extinction in response to environmental change, the notion of delayed response imposes serious constraints on our ability to interpret what we see in the present landscape. Where extant species represent an extinction debt, extinction is likely under the current or decreasing habitat conditions. Alternatively, habitat improvement may enable the species to recover sufficiently (Hanski 2000; Hanski and Ovaskainen 2002). Trying to determine threshold response of species to habitat loss and fragmentation should take into account time lags, to prevent habitat targets from being set at artificially low levels, exacerbating extinction risk.

4 HABITAT CHARACTERISTICS INFLUENCING THRESHOLD RESPONSES

In managed forest landscapes, declines in biodiversity associated with habitat change have four primary components:[6] 1) reduction in the area original habitat, 2) reduction in the size of habitat patches, 3) increase in the number of habitat patches (literally, "fragmentation" of habitat), and 4) increase in the isolation of patches (reviewed by Fahrig 2003). However, researchers often study fragmentation as a broader phenomenon than that defined by Fahrig (2003), by measuring either the amount of habitat remaining on the landscape (habitat loss), or by measuring the change in habitat configuration — the collective effects of some combination of the latter three components: reduction in the size of habitat patches, and increases in the number and isolation of patches. However, these different components are interrelated, and do not have the same effects on biodiversity (reviewed by Fahrig 2003); it is often unclear which process has a greater impact, or if the effects of habitat loss and spatial effects might have differential impacts at different levels of overall habitat loss (Haila and Hanski 1984). The effects of strict habitat loss and the effects of changes to habitat configuration are confounded in many studies (Haila and Hanski 1984; Saunders *et al.* 1991; Fahrig 1997, 2003; Kremsater and Bunnell 1999; Debinski and Holt 2000). This lack of distinction has resulted in contradictory conclusions found in the literature about the influence of fragmentation on biodiversity (Fahrig 2003), leading Wiens (1993) to describe fragmentation as an ecological sub-discipline based on a body of literature that is more "descriptive than predictive." Additionally, most of the effects of habitat configuration, such as patch isolation (Fahrig 2003) and reductions in patch size (Bender *et al.* 2003), are caused by increasing habitat loss; small and/or isolated patches are generally found in landscapes with small amounts of habitat. The relative effects of habitat loss and the effects of changes to habitat configuration have nonetheless been shown to be two separate processes acting on landscapes (Andrén 1994; Fahrig 1997; With *et al.* 1997).

---

[6] No☐
biodiversity.

Habitat change has two other effects associated with habitat loss and configuration: physical and biological effects related to an increase in the amount of edge in the landscape (Laurance and Yensen 1991; Saunders *et al.* 1991; Kremsater and Bunnell 1999), and increases to the area covered by the matrix (Wilcove *et al.* 1986). Edge effects can be positive or negative (Kremsater and Bunnell 1999; Fahrig 2003), and many of the negative effects associated with fragmentation are ultimately related to edge effects caused by the increase in the number of habitat fragments (Harrison and Bruna 1999; Fahrig 2003). The matrix exerts similarly complex mitigating or exacerbating effects on species, depending on matrix quality, the individual species level of habitat specificity, and natural landscape heterogeneity (Margules *et al.* 1982; Saunders *et al.* 1991; Doak and Mills 1994; Schieck *et al.* 1995; Gustafson and Gardner 1996; Norton *et al.* 2000; Henle *et al.* 2004).

In the following sections, I present the literature arising from investigations of threshold responses related to each of the components of habitat loss. The section begins with studies about habitat loss (Section 4.1), followed by studies examining spatial configuration effects (Section 4.2), physical and biological edge effects (Section 4.3), and the matrix (Section 4.4). I conclude the discussion of threshold responses related to habitat characteristics with a section on landscape context (Section 4.5), which explores the interrelationships of the components of habitat change.

4.1 Effects of Habitat Loss

Destruction of habitat in a landscape can result in the loss of populations of organisms that depend on that habitat. Different species may disappear at different points on the habitat loss gradient (e.g., Gibbs 1998; Hager 1998), but all species have a "minimum suitable habitat" requirement — a threshold amount of habitat that they require for persistence. Minimum habitat requirements may be relevant at the landscape or patch level, and may involve minimum area and spatial (connectivity) components. Habitat thresholds are implicit in minimum viable population analysis (Shaffer 1981). Habitat thresholds — particularly the "extinction threshold" — are also rooted in Lande's (1987, 1988a) groundbreaking work. Lande popularized Levins' (1969) original metapopulation model, which, since Lande's work, has become the jumping-off point for other studies of terrestrial and aquatic metapopulations and of territorial organisms (e.g., Sjögren 1991; Bascompte and Solé 1996; Hanski *et al.* 1996; Carlson 2000). Early models of habitat thresholds (e.g., Shaffer 1980) emphasize the amount of habitat. Later models added a spatial component, showing that spatial effects change habitat threshold predictions (e.g., Bascompte and Solé 1996). However, recent research and literature reviews re-emphasize the overriding importance of loss in the amount of habitat alone (e.g., Fahrig 1997, 2003).

In this section, I first review the evidence in the debate about the relative effects of habitat loss and fragmentation, and present the small body of empirical landscape-level literature that examines this question in the context of threshold responses (Edenius and Sjöberg 1997; Drolet *et al.* 1999; Villard *et al.* 1999; Schmiegelow and Mönkkönen 2002). Following the discussion of habitat loss vs. fragmentation studies, I present Lande's (1987; 1988a) original work introducing the idea of the habitat threshold, together with a recent empirical study that assesses observed change against model predictions (Lande 1987) of habitat thresholds (Carlson 2000). I then present studies on habitat thresholds using minimum population viability analysis (Shaffer 1981; Beier 1993; Thompson and Harestad 1994; Wielgus 2002), followed by empirical demonstrations of habitat amount thresholds at the landscape scale (Hager 1998; Drolet *et al.* 1999; Villard *et al.* 1999; Swift and Hannon 2002). The section concludes with patch-level studies that examine thresholds in forest cover (Thompson and Harestad 1994; Saari *et al.* 1998; Burke and Nol 2000; Penteriani and Faivre 2001). Although the section begins with the literature on the debate about the relative importance of the effects of habitat loss and fragmentation, I otherwise restrict this section to the review of habitat amount threshold studies; fragmentation threshold studies follow in Section 4.2.

Research on fragmentation thresholds has led to the conjecture that habitat amount effects are more important *overall* to habitat thresholds than are fragmentation effects (e.g., Fahrig 1997, 2003).

The effects of habitat loss outweigh the effects of fragmentation as the primary cause of species decline.

Simulation studies that independently assess the effects of habitat loss and fragmentation find that habitat loss generally better predicts species abundance than does fragmentation (Fahrig 1997, 1998, 2002; Flather and Bevers 2002). Modeling research further suggests that the spatial arrangement of habitat contributes to extinction risk primarily at low levels of habitat (e.g., Fahrig 1997). Recent empirical research, particularly on birds, that has attempted to distinguish species response to the separate effects of habitat loss and spatial factors (reviewed by Fahrig 2003) also demonstrates the overwhelming influence of habitat amount. Studies that investigated both components find a stronger effect of habitat loss than the effects of fragmentation for forest-dwelling birds (seven of eight studies), insects (two of three studies), corals (one study), and a virus (one study on Hanta virus); but a stronger (positive) effect of fragmentation than habitat for Gray-tailed Voles (*Microtus canicaudus*) (reviewed by Fahrig 2003). Only one study finds approximately equivalent influence of fragmentation and habitat loss effects (Villard *et al.* 1999), and Fahrig (2003) finds that the relative importance of the effects of habitat loss and fragmentation, while controlled for, cannot be inferred from a further four studies in which habitat amount was held constant, and only fragmentation was varied. Two of the studies (Drolet *et al.* 1999; Villard *et al.* 1999) presented by Fahrig (2003) examine threshold responses at the landscape level. Drolet *et al.* (1999), in a study set in Canadian boreal mixedwood forests, find that habitat amount is the factor most relevant to predictions of bird species distribution, with an inconsistent effect of fragmentation. Villard *et al.* (1999) in a survey of 15 forest bird species in Canadian boreal mixedwood forests, find that spatial configuration and habitat amount are both important predictors of species presence (see below, *Empirical evidence at the landscape level*, for more discussion about these studies). Several other studies have examined both habitat loss and fragmentation parameters (although not controlling for either) and found that habitat amount better predicts species composition (Drapeau *et al.* 2000; Schmiegelow and Mönkkönen 2002), species presence (Schmiegelow and Mönkkönen 2002), and reproductive parameters (Tjernberg *et al.* 1993).

Overall, it appears that habitat loss outweighs fragmentation as a factor contributing to the decline of some species (Fahrig 2003). Thus, the spatial arrangement of habitat cannot necessarily mitigate the negative effects of habitat loss. Discerning the relative importance of the different aspects of habitat loss to species persistence is non-trivial; mitigating the relative effects of habitat loss and spatial factors on species persistence requires different conservation strategies.

Lande numerically derives the extinction threshold.

The foregoing models and empirical studies are compelling evidence that habitat loss alone exerts the greatest influence on some species. In fact, habitat thresholds were first demonstrated in the absence of spatial effects as a consequence of species requirements for a minimum proportion of suitable habitat (Lande 1987, 1988a). Modifications to the metapopulation model (Levins 1969) enabled Lande (1987, 1988a) to determine the minimum proportion of suitable habitat in the landscape required for population persistence of the Northern Spotted Owl (*Strix occidentalis caurina*) (see also Section 4.2 Spatial Effects of Habitat Loss for further discussion of the Spotted Owl viability analyses). The model incorporates life history traits and the behaviour of dispersing individuals searching for a territory. When the modeled population is at equilibrium in the landscape, Lande (1987, 1988a) shows the habitat threshold to be equal to the proportion of suitable, but unoccupied, patches in the landscape. Lande (1987) termed this critical amount of habitat the "extinction threshold." Later work derived from models of epidemiology (Anderson and May 1991; Lawton *et al.* 1994) demonstrate the same result — that the extinction threshold is equal to the proportion of suitable but unoccupied patches in the landscape at equilibrium occupancy (vulnerable but not infected hosts in the population), and present a model in which "seemingly important details of movement rates and demographic parameters cancel out" (Lawton *et al.* 1994, p. 54). However, later work improves the Spotted Owl habitat threshold analysis and shifts the location of the habitat threshold by improving modeling of dispersal parameters and small-population dynamics (i.e., the Allee effect), and incorporating the spatial characteristics of habitat, and nonequilibrium dynamics (to account for ongoing harvesting in the landscape) (Boyce 1987, cited by Lamberson *et al.* 1994; Lamberson *et al.* 1992; Carroll and Lamberson 1993; Lamberson *et al.* 1994). Although later modified, Lande's (1987, 1988a) original model was nonetheless significant because it focused attention on the concept of habitat thresholds.

Species threshold responses to habitat amount can be examined using minimum viable population analyses.

In an elegant demonstration of the habitat threshold, one study parameterized Lande's (1987, 1988a) model for a territorial species, with data for a rare, old-growth specialist: the White-backed Woodpecker (*Dendrocopos leucotos*) (Carlson 2000). Carlson (2000) modeled predictions of the threshold amount of suitable habitat (old broad-leaved forest in this case), and examined whether declines below the threshold were non-linear. Of four populations studied, one Swedish sub-population is extinct: it was in a landscape with habitat below the predicted threshold. Two other Swedish sub-populations in landscapes below the habitat threshold are declining. The fourth, a Finnish sub-population, persists in a landscape below the habitat threshold, but its decline is non-linear, and appears to show a delayed response, relative to landscape change (Carlson 2000) (see Section 3.8, Extinction Debt, for a discussion about time lags). Habitat loss and fragmentation effects are confounded in this study; it is discussed here under habitat loss, primarily because the analysis is based on Lande's aspatial model, an analytical framework primarily concerned with habitat amount thresholds (Lande 1987).

Thresholds in habitat amount have also been estimated using other methods of population viability analysis (e.g., Shaffer 1981; Beier 1993; Thompson and Harestad 1994), although little of this work is published in academic journals (Boyce 1992). Long before empirical evidence was available, ecologists questioned the size of the minimum population required for long-term species persistence (Allee 1938, cited by Dennis 1989). As the phenomenon of extinction became increasingly recognized, researchers began to use population viability analysis to resolve the question of the size of the minimum viable population (MVP) (the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes [Shaffer 1981, p. 132]). The basis for MVP analysis is that population size and expected population lifetime are positively related, and the corollary: very small populations are likely to become extinct rapidly (see references in Hanski *et al.* 1995). MVP analysis has more recently incorporated habitat area (e.g., Shaffer 1980; Beier 1993) and/or habitat elements (e.g., Thompson and Harestad 1994) to incorporate the idea of minimum area requirements for conservation (Shaffer 1981; Wilcove *et al.* 1986; Soulé 1987).

Several papers examine habitat thresholds with respect to the minimum habitat required to maintain the MVP (e.g., Shaffer 1980; Beier 1993; Thompson and Harestad 1994). American Marten (*Martes americana*) were the focus of a paper that synthesized existing data on habitat use to generate guidelines in habitat amount for management of minimum viable populations in boreal mixedwood forests (Thompson and Harestad 1994). Based on known demographic data, the authors estimate a minimum viable population size (MVP) (threshold population size = 237 individuals), and minimum habitat size for this population (600 km^2 mature and old-growth habitat). Based on data on habitat use, the authors also modeled carrying capacity across successional stages, and from these data, they estimated the proportion of maximum carrying capacity provided by each successional stage. The authors estimated a threshold range of carrying capacity (between 40% and 60%) necessary to maintain the MVP. They were thus able to elucidate the successional stages that would provide suitable habitat for marten (mature and older). From these and other data, Thompson and Harestad (1994) developed management prescriptions at the stand and ecosystem level for harvesting in boreal forests.

Other analyses of minimum amounts of habitat (e.g., Shaffer 1980; Beier 1993; Grimm and Storch 2000; Wielgus 2002) generally provide less detail about habitat elements than the presentation of Thompson and Harestad (1994). Modeling of demographic data on Grizzly Bears (*Ursus arctos*) in Yellowstone National Park results in an estimate of between 700 and 10,000 km^2 as a minimum amount of habitat to support a minimum viable population of 35-70 individuals (Shaffer 1980). In this case, the threshold area size range supports the smallest population with a 95%

probability of surviving at least 100 years (Shaffer 1980). Similar modeling for Grizzly Bears in British Columbia results in an estimate of between 8556 and 17,843 km^2 to support a minimum viable population of 200-250 bears with a small probability (p<0.05) of decline to a population at a quasi-extinction threshold (i.e., to a level that would be classed as threatened) within 20 years (Wielgus 2002). Another MVP analysis was performed for Cougars (Mountain Lion) (*Felis concolor*) in the Santa Ana mountain range of southern California (Beier 1993). A model simulating population dynamics of Cougars determines that a minimum area of 2200 km^2 is required to maintain a viable population with very low extinction risk. This prediction represents a threshold area, above which occasional emigration (from other populations) results in a marked increase in the probability of persistence (Beier 1993). These studies are examples of the use of demographic models to predict habitat amount thresholds. Many other MVP studies exist (e.g., Grimm and Storch 2000), but I do not exhaustively review these here.

Generating reliable estimates of thresholds in habitat amount is problematic. Although empirical modeling studies of MVP sizes abound (e.g., Reed *et al.* 2003), studies examining explicitly the habitat amount requirements to support MVPs are less common (but see, for example, Thompson and Harestad 1994; Grimm and Storch 2000; Wielgus 2002). Precise habitat requirements are difficult to quantify, in part, because species may associate more with elements of habitat quality than habitat quantity *per se* (Venier and Fahrig 1996; Donovan and Lamberson 2001; Summerville and Crist 2001). Very few studies on MVPs and habitat requirements quantify habitat quality based on habitat elements (but see Thompson and Harestad 1994). Modeled estimates of area requirements for MVPs are also constrained by a poor understanding of, or lack of information about the influence of environmental stochasticity (i.e., changes to habitat quality) on demographic traits (e.g., Wielgus 2002).

Empirical evidence shows that species exhibit threshold responses to the amount of habitat at the landscape level.

Empirical studies of thresholds at the landscape level are few. Most dispense with modeling the habitat threshold, and simply perform field tests for species response to different amounts of habitat. Three Canadian studies set in the boreal forest explore thresholds using this method (Drolet *et al.* 1999; Villard *et al.* 1999; Swift and Hannon 2002). Swift and Hannon (2002) examined avian species presence and/or relative abundance and pairing success, on fifty 100-ha landscapes ranging from 5% to 80% forest cover, set in the boreal mixedwood forest in east-central Alberta. The probability of occurrence of three species, Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*Sitta carolinensis*), and Hairy Woodpecker (*Picoides villosis*) declines sharply and disproportionately relative to forest cover losses. The threshold occurs between 20 and 40% of remaining forest, depending on the species. White-breasted Nuthatches also exhibit thresholds in the establishment of breeding pairs, at a higher level of forest cover — between 40% and 60%. A fourth species, Downy Woodpecker (*Picoides pubescens*), shows no change in occupancy with forest cover, but displays a threshold decrease in mated pair occurrence between 20-30% forest cover. The threshold response in reproductive parameters, which occurs at an earlier stage of habitat loss than the threshold response in presence, indicates that detrimental levels of habitat loss and fragmentation affect populations earlier than indicated by species presence. These effects on reproductive measures indicate that they are a more sensitive indicator of threshold response to habitat loss than are measures of presence.

Two other Canadian studies were set in boreal mixedwood forests near Québec City (Drolet *et al.* 1999) and Ottawa (Villard *et al.* 1999). Both of these studies examined the relative effects of habitat loss and configuration on bird species presence. Drolet *et al.* (1999) examined species presence in harvested areas where landscape-level (100 ha) forest cover ranged from <10% to 90%. They found that the Bay-breasted Warbler (*Dendroica castanea*) is absent from landscapes with <55% forest cover, an effect of habitat amount with no discernable effects of fragmentation, and that Solitary Vireo (*Vireo solitarius*) is also significantly (p<0.05) associated with landscapes with >58% average cover (Drolet *et al.* 1999). Villard *et al.* (1999) found that habitat loss and fragmentation each significantly predicted the presence of six species in habitats covering 6.25 km^2. Although threshold responses do not generally characterize presence and distributions in this study, the occurrence of two species (Black-and-White Warbler [*Mniotilta varia*] and Ovenbird [Seiurus aurocapillus]) declines rapidly beyond approximately 10% and 20% forest cover, respectively (Villard *et al.* 1999).

Hager (1998) demonstrates clear habitat amount thresholds that affect species presence in her empirical study examining amphibians and reptiles at the landscape level. Amphibians and reptiles are of particular interest to studies of habitat loss and fragmentation. Because of the wide fluctuation in their population dynamics, many researchers consider these taxa particularly sensitive to environmental change (see references in Gibbs 1998). Hager (1998) used an inventory of amphibians and reptiles in three island archipelagos in Ontario to examine sensitivity to insularization (i.e., area sensitivity). Communities occur in nested subsets (see Section 3.4, Island Biogeography and Related Theory), and species drop out along a gradient of habitat area, highlighting area thresholds. Species such as Red-spotted Newt (*Notophthalmus v. viridescens*), Ringneck Snake (*Diadophis punctatus edwarsii*), and Gray Treefrog (*Hyla versicolor*) are absent from smaller islands. The absence of these species indicates habitat amount thresholds below which they cannot persist.

Some species exhibit threshold responses to habitat loss at the stand level.

Although the habitat threshold (extinction threshold as defined by Lande 1987, 1988a) is inherently a landscape-level concept, habitat amount thresholds also characterize species response to habitat loss at other scales (e.g., Thompson and Harestad 1994; Saari *et al.* 1998; Penteriani and Faivre 2001; Angelstam *et al.* 2003 and citations therein). Angelstam *et al.* (2003) nicely demonstrate the link between the stand and landscape scale, in their review of recent work (Bütler *et al.* 2003a, 2003b, cited by Angelstam *et al.* 2003) characterizing habitat thresholds for woodpeckers based on dead wood amounts in forests. Using empirical and modeling data, Bütler *et al.* (2003a) suggest conservative threshold targets at the stand level for snags, of 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) or 14 ≥ 21 cm dbh snags/ha, over an area of 100 ha to maintain habitat for the Three-toed Woodpecker (*Picoides tridactylus*) in sub-alpine forests dominated by spruce (*Picea abies*) in Switzerland. In a comparison of the habitat occupancy threshold for the amount of dead wood in the Swiss forests studied by Bütler *et al.* (2003a), to Swedish boreal forests, threshold declines occur for probability of occupancy, from 0.95 to 0.10, when snag basal area decreases from 1.3 to 0.6 m^2 ha^{-1} in the Swiss forests, and from 0.5 to 0.3 m^2 ha^{-1} in Swedish forests (Bütler *et al.* 2003b, cited by Angelstam *et al.* 2003).

Penteriani and Faivre (2001) examined Goshawk (*Accipiter gentiles*) nesting patterns at the stand level in two European areas, focusing on the effects of harvesting activity and reduction in forest cover on occupancy rate, productivity, and number of young per breeding pair. The authors were interested in whether thresholds in nesting patterns would occur as a result of progressive thinning of the forest (removal of 10%, 20%, 20%, 20% in four passes) and clearcutting activities (removing the final 30% of stand) spaced over 10-15 years. In this study, site fidelity is strong if the harvest level does not exceed 30%. By the third pass (i.e., after removal of 50% of the stand), no nesting pairs remain. The authors therefore conclude that Goshawks in these habitats can tolerate some degree of timber harvesting within nesting stands, up to a threshold of 30% removal (the level of removal at which nesting pairs are last observed) (Penteriani and Faivre 2001).

Other studies also examine patch-level thresholds (Thompson and Harestad 1994; Edenius and Sjöberg 1997; Saari *et al.* 1998; Rodríguez and Andrén 1999; Burke and Nol 2000). Thompson and Harestad (1994) used the response of American Marten to changes in forest cover at the stand level to predict a threshold in habitat. Marten are absent from stands with <30% cover, and prefer stands with 50-70% cover (see references in Thompson and Harestad 1994). Saari *et al.* (1998) studied Hazel Grouse (*Bonasa bonasia*) in Finland and investigated the effects of patch size and isolation on patch extinction and recolonization. A threshold patch size of 10 ha results in marked improvement in Hazel Grouse occurrence and brood presence. Isolation effects are significant, but small and secondary to patch area effects (Saari *et al.* 1998). Burke and Nol (2000) studied forest-breeding songbirds and examined the influence of patch size on reproductive success in fragmented upland deciduous forests in south-central Ontario. The focus of this study was to determine the threshold size required for a patch to function as a source (as opposed to a sink) habitat. A source habitat is defined as one in which recruitment of young is sufficient to compensate for adult and juvenile mortality (Pulliam 1988; also see Section 3.5, Metapopulation Theory, for a review of source-sink habitats). To maintain sufficient core habitat, the most area-sensitive species, Ovenbird (*Seiurus aurocapillus*), requires a 500-ha fragment in order for the patch to function as a source habitat in this landscape. Patch size thresholds are also reported for species richness in the boreal (Edenius and Sjöberg 1997), and Eurasian Red Squirrel (*Scurius vulgaris*) occupancy (Rodríguez and Andrén 1999); see Section 4.2, Spatial Effects of Habitat Loss for more discussion about these studies.

Summary

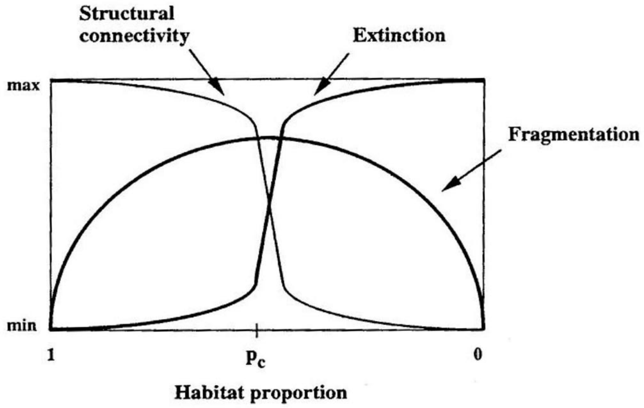
Because species have minimum requirements for the amount of habitat needed to survive and reproduce, habitat loss causes the decline and loss of species populations. Species differ in their requirements for minimum habitat; hence, species loss occurs along a gradient of habitat loss. Although data are scarce about the rate of species loss, modeling suggests that the gradient of species loss appears to be an accelerating curve; species loss per unit area lost increases along the habitat loss gradient (Figure 6) (Tilman *et al.* 1994). In Tilman *et al.*'s (1994) model, as habitat loss increases, the greater is the effect of additional habitat loss. Furthermore, although the spatial effects of habitat loss influence species' minimum habitat amount requirements, habitat loss alone accounts for the greatest declines in species abundance and presence. Studies on the effect of habitat loss on species presence indicate that species may temporarily persist in sub-optimal habitat. Although such sink habitats might contribute to population persistence at the landscape scale by augmenting resources in higher-quality patches, populations within these habitats are below replacement levels, therefore presence in these habitats is a poor indicator of population response to habitat change. Reproductive and juvenile survival parameters are thus better gauges than are presence parameters of the effects of habitat loss on species and of threshold habitat requirements. Although thresholds in habitat requirements are inherently landscape-level phenomena, some species also exhibit threshold tolerances at the level of stand cover or patch area.

4.2 Spatial Effects of Habitat Loss

The spatial effects of habitat loss refer to changes in the configuration and connectivity of landscapes, such as the size, number, and isolation of habitat fragments. The dominant hypothesis from percolation theory (Stauffer 1985; Orbach 1986; Stauffer and Aharony 1992) is that the spatial effects of habitat loss should result in threshold declines in response parameters such as population size, implying a "structural connectivity threshold" (Figure 7; see Section 3.6, Percolation Theory, for a detailed discussion of this topic; Metzger and Décamps 1997). At the landscape level, spatial models predict non-linear relationships between the amount of habitat in the landscape, and the size, number, and isolation of habitat fragments-the percolation threshold (Figure 8; Franklin and Forman 1987; Gardner *et al.* 1987; Turner *et al.* 1989; Gardner and O'Neill 1991; Gustafson and Parker 1992; Spies *et al.* 1994; Andrén 1996, 1997). Other models predict a critical level of habitat loss at which the spatial effects of habitat loss exert their strongest influence; a qualitative shift from habitat loss effects to spatial effects (Andrén 1996, 1999; Flather and Bevers 2002).

Applied to real landscapes, the term "fragmentation threshold" (Andrén 1996) is used to describe the non-linear responses of ecosystem variables to changes in the spatial arrangement of habitat. The fragmentation threshold is conceptually akin to the percolation threshold; that is, the point beyond which the spatial characteristics of habitat exert their strongest influence. There is considerable evidence of the fragmentation threshold from models derived from percolation theory (e.g, Franklin and Foreman 1987) and from simulation models examining generic species (e.g., Fahrig 2002). At the fragmentation threshold, rapid changes occur in the size and isolation of patches at critical proportions of habitat in the landscape; these changes correspond to precipitous declines in modeled species abundance (Andrén 1996, 1997).

These predictions raise two questions. First, as habitat loss increases, do real forest landscapes exhibit thresholds for indices of landscape structure, or a qualitative shift from habitat loss to spatial effects as the



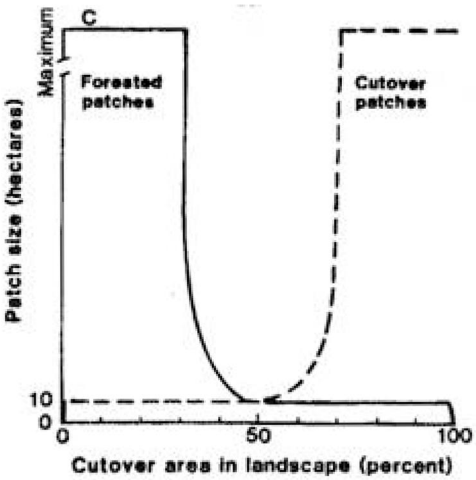
Reprinted with permission

Figure 7. Theoretical relations between proportion of habitat, structural connectivity, habitat fragmentation (measured by the proportion of boundaries between habitat and non-habitat units in landscape), and global species extinction. There are critical levels of habitat proportion where fragmentation (i.e., local extinction risk) becomes high, and connectivity (i.e., local colonization probability) becomes low, producing a rapid increase in global species extinction. (Figure 1 in Metzger and Décamps 1997.)

mechanisms influencing species response? Second, are threshold changes in landscape structure or qualitative shifts accompanied by threshold changes in biological parameters, such as population size? Next, I consider the literature that addresses fragmentation thresholds, beginning with some caveats about the application of models to ecological systems and a description and review of the simulation modeling studies demonstrating fragmentation thresholds. Discussion of empirical percolation studies in forested landscapes and empirical studies from experimental model systems and landscapes follows the modeling discussion. The section concludes with empirical, landscape-level forest studies that examine fragmentation thresholds in the absence of percolation theory.

"All models are wrong. Some are useful" (Box 1979). Hypotheses generated from (percolation) modeling form the premise for considering thresholds in fragmentation. Additionally, evidence of spatial fragmentation thresholds is primarily in the form of models. While these models make quantitative predictions about fragmentation effects and, hence, habitat loss thresholds, literal interpretation of these predictions may be inappropriate (With and King 1997). Depending on the rigour of model evaluation, the most appropriate use of models may be to help explain processes rather than to make predictions (Grant *et al.* 1997). Although the term "model evaluation" has multiple definitions, some of which conflict (see Rykiel 1996 for a review), "model validation" and "credibility" are the components of model evaluation that primarily relate to model application. Model validation is primarily a quantitative process, and generally means that a model met certain performance requirements; hence, the model is appropriate for its intended use (Rykiel 1996). Model validation also extends to conceptual validity, or the justification of cause and effect relationships in the model. Model credibility is a subjective, qualitative judgement about the degree of belief in the validity of a model for its intended use (Rykiel 1996). Particularly in the absence of model validation with empirical data, or model corroboration through hypothesis testing, and provided that the test of model credibility is met, models are most useful for explaining the processes and

Models are most useful for explaining the processes and mechanisms causing change in a system.



Reprinted with permission

Figure 8. Changes in landscape characteristics along a landscape cutting gradient, based on the regularly distributed dispersed patch cutting or checkerboard model, with respect to forest and cutover patch sizes. (Figure 3c in Franklin and Forman 1987.)

mechanisms forcing change in a system (Rykiel 1996, and references therein; With and King 1997).

Simulation modeling demonstrates fragmentation thresholds.

Models derived from percolation theory are used to predict the level of habitat loss at which the fragmentation threshold becomes apparent (e.g., Gardner *et al.* 1987; Gardner and O'Neill 1991; With and Crist 1995; Bascompte and Solé 1996; Fahrig 1997, 1998, 2001, 2002; With 1997; With and King 1997, 1999a, 1999b; With *et al.* 1997; Boswell *et al.* 1998). Modeling methods include reaction-diffusion models and spatially explicit population models (SEPMs). SEPMs are comprised of population models coupled with spatially explicit, "neutral" landscapes (With 1997). The models are generally "neutral" with respect to topography and habitat arrangement, and simple rules of movement behaviour commonly describe the dispersal process. The SEPMs generally examine a binary grid where the modeler assigns each cell a habitat or non-habitat value, and cells are occupied or empty, hence their description as "patch occupancy" models. This design allows the modeler to vary habitat amount and fragmentation independently of one another. The models use algorithms to adjust the degree of fragmentation by changing the spatial pattern or aggregation of habitat in the landscape (With 1997). Upon randomly removing habitat from these "null" models, modelers interpret "no effect" of fragmentation, so long as individuals remain dispersed on the landscape. The level of habitat at which "aggregation" occurs (clumping of individuals around remaining habitat) is interpreted to indicate a qualitative shift in the process driving population dynamics (e.g., With and Crist 1995; With *et al.* 1997). Alternatively, the level of aggregation or "clumpiness" of the landscape at which population dynamics exhibit threshold behaviour is the metric used to report results (e.g., Flather and Bevers 2002). In both cases, "level of aggregation" indicates the fragmentation threshold, the level of habitat loss beyond which spatial configuration matters most.

The increasing effects of habitat loss (patch isolation) result in a reduction in patch occupancy as habitat loss increases.

Several authors demonstrate that accounting for the spatial arrangement of habitat causes the habitat threshold to occur at a lower level of habitat loss than demonstrated by Lande's (1987) spatially uniform model (Lamberson *et al.* 1992; Dytham 1995a, 1995b; Moilanen and Hanski 1995; Bascompte and Solé 1996; With and King 1999b). The spatially explicit models show that the predictions of spatially implicit models (e.g., constant patch occupancy throughout habitat destruction), are not observed, but rather that the increasing effects of habitat loss (patch isolation) result in a reduction in patch occupancy as habitat loss increases — a secondary effect of habitat loss. As patches become more isolated in the landscape, colonization is increasingly unlikely. As a result, the amount of habitat required to maintain populations above the extinction threshold increases with dispersed habitat removal (Dytham 1995b).

A number of studies have used spatially explicit population models to test the hypothesis that the spatial effects of habitat loss cause the habitat threshold (e.g., Fahrig 1997, 2001, 2002; Hill and Caswell 1999; With and King 1999b; Flather and Bevers 2002). Flather and Bevers (2002) are clearest in showing the relationship between fragmentation and extinction. They show that, in scenarios with less than a 30-50% threshold of habitat loss, the amount of habitat in the landscape is overwhelmingly the best predictor of population size and persistence, accounting for 96% of the total variation in the model. When habitat loss exceeds 30-50%, the effect of spatial arrangement increases, predicting between 33% and 39% of the variation in population size. The qualitative change in process corresponds to a persistence threshold, at which they observe a rapid decline in the probability of the landscape to maintain viable populations (Flather and Bevers 2002). Many other models are clear in showing that the fragmentation threshold represents a qualitative change, from pure habitat loss effects, to spatial effects, as the primary mechanism driving species behaviour (e.g., With and Crist 1995; Bascompte and Solé 1996).

Fahrig (2002) synthesized results from four spatially explicit population models (Fahrig 1997, 1998, 2001; Hill and Caswell 1999; With and King 1999b; Flather and Bevers 2002) that differ in the predicted effect of spatial landscape configuration on the habitat threshold. The models all show that greater amounts of fragmentation decrease the level of habitat loss at which the habitat threshold occurs. In addition, they all show that the fragmentation effect is greatest when suitable habitat is already low in the unfragmented landscape. However, the models differ in the influence they predict fragmentation to have on the amount of habitat remaining at the habitat threshold. Two models predict large potential effects of fragmentation on the habitat threshold; that is, the amount of habitat required for persistence shifts from less than 5% of the landscape to more than 80% of the landscape, with a shift from completely clumped to completely fragmented habitat (Hill and Caswell 1999; With and King 1999b). These models are based solely on colonization and extinction rates (CE models). The other two models (Fahrig 1997, 1998, 2001; Flather and Bevers 2002) consider birth, immigration, death, and emigration rates (BIDE models). BIDE models predict a more modest fragmentation effect on the amount of habitat remaining at the habitat threshold, with the shift from clumped to fragmented habitat increasing the habitat amount threshold only up to 17%.

Fahrig (2002) concludes that the different predictions in the two types of models result from model assumptions, each set of which represents different but realistic ecological conditions. The CE models are variations of Lande's (1987) model, and do not consider factors such as birth and death rates within cells and mortality in the matrix, which are included in the BIDE models. In the CE models, habitat aggregation increases colonization rates, ameliorating the effects of fragmentation. For BIDE models, high amounts of habitat loss, even if aggregated, increase the time individuals spend in the matrix where mortality is high. Fahrig (2002) concludes that via its influence on dispersal, matrix quality affects the extent to which habitat aggregation, and, hence, fragmentation, influences the habitat threshold. Matrix quality is primarily relevant to non-specialist species, therefore the comparison of these models nicely demonstrates that the habitat threshold varies greatly depending on species traits.

The spatial effects of habitat loss in real forested landscapes differ from the predictions of percolation theory.

In a few cases, researchers have tested model results in empirical landscapes (e.g., With and Crist 1995). For simplicity, the empirical landscapes are generally grassland mosaics. However, the results of one early, simplistic, grid-based simulation study (Franklin and Forman 1987) were compared to forested landscapes in the Pacific Northwest (Oregon's Willamette National Forest and adjacent private land) to determine if actual landscape conditions reflected simulated thresholds (Spies *et al.* 1994). Franklin and Forman's (1987) simulation study was designed to examine the impact of the "staggered setting" clearcutting system used in the Pacific Northwest — a system of progressive 10- to 20-ha patch cutting, interspersed with uncut forest of equal or greater size. A threshold change occurs in remaining patch size and patch density at 30% habitat removal, and complete isolation of remaining patches occurs at 70% habitat removal. Edge density peaks at 50% removal, and no interior forest (based on edge effects permeating two tree lengths [160 m] into patches) remains at 50% removal (Franklin and Forman 1987). In an empirical study, Spies *et al.* (1994) examined all of these metrics in a 2,589 km^2 landscape, for which Landsat imagery was used to classify landscape into two classes — less than and greater than 60% conifer cover.

Spies *et al.* (1994) find different results in their real landscape from those predicted by the Franklin and Forman (1987). Their empirical analyses show that edge density peaks at 40% removal, somewhat lower than the 50% prediction, and there is approximately 30% interior forest remaining at 50% habitat removal, versus none in the simulated landscape (Spies *et al.* 1994). Patch size and density thresholds that appear at 30% and 70% removal in the model do not appear in the forested landscape. Spies *et al.* (1994) attribute the lack of patch thresholds to the scale of their sampling and the non-uniform application of staggered cutting, suggesting that investigation at a finer scale, where relatively rapid cutting occurs, may reveal thresholds. Spies *et al.* (1994) also point out that forest regrowth is not incorporated into the simulation model (a point also acknowledged by Franklin and Forman), whereas regrowth occurs in the empirical landscape. Second-growth forest mitigates edge effects, thereby reducing edge width and increasing forest interior over time. Forest regrowth also limits the maximum amount of cutover forest on the landscape, given harvest rates based on a rotation length of 80 years. Although the cutting pattern in the empirical landscape does not exhibit the patch size and density thresholds suggested by the model, a higher cutting rate in some landscapes resulted in higher amounts of edge and lower amounts of interior habitat than occur in landscapes with lower cutting rates. This difference demonstrates that cutting rate can have a greater influence than cutting pattern on the amount of edge and interior habitat (Spies *et al*. 1994).

Gardner *et al*. (1987) also compared spatial metrics in real, forested landscapes in the eastern United States to predictions from percolation theory. They examined three empirical landscapes with varying levels of forest cover, and determined the number, size, and fractal dimension of patches for each landscape. They also derived these values for neutral landscape maps (modeled maps), and compared the results of real to modeled landscapes. Gardner *et al*. (1987) find significantly ($p<0.05$) fewer patches in empirical than in modeled landscapes. They suggest that fragmentation in real landscapes results in greater aggregation of remaining habitat than predicted by neutral maps. However, they do observe critical thresholds in the number of patches in real landscapes, but at lower levels than they observe in the neutral maps. The non-forest landscape type is not specified in this study, nor is the forest type defined.

Although not a percolation study, Gibbs' (1998) landscape-level study demonstrates weak parallels between thresholds in landscape indices and thresholds in species response. Gibbs (1998) examined the presence / absence of amphibians along a fragmentation and forest cover gradient in Connecticut. Gibbs (1998) finds that one species, Red-spotted Newt, drops out along the habitat loss gradient near the threshold point at which fragmentation shifts from being uniformly low to uniformly high. The fragmentation threshold corresponds to ~ 50% forest habitat. Wood Frogs (*Rana sylvatica*) and Spotted Salamanders (*Ambystoma maculatum*) do not occur below ~ 30% forest habitat. Furthermore, because Wood Frogs and Spotted Salamanders decline at the fragmentation threshold (from ~ 90% each, to ~ 60% and ~ 80% occurrence in suitable habitat, respectively), but precipitous declines do not occur until farther along the habitat loss gradient (30% remaining), either the relative effect of habitat loss was still important below the fragmentation threshold, or the author observed an example of extinction debt.

Evidence of thresholds in fragmentation from EMSs is equivocal.

Although researchers are ultimately interested in landscape-level patterns in their exploration of fragmentation thresholds, experiments conducted at the landscape scale are prohibitively expensive and intractable (Saunders *et al*. 1991; Wiens *et al*. 1993; Debinski and Holt 2000). As a compromise, experimental model systems (EMSs) embedded in natural conditions, can represent "micro landscapes" (Wiens *et al*. 1993). Therein, researchers stage experiments to test theories that are of interest at the landscape scale (e.g., Wiens *et al*. 1993; With and Crist 1995; Parker and MacNally 2002). Scaling up from EMSs requires a balance between "judicious reductionism" and meaningless generalization; however, EMSs are a reasonable means to explore patterns of interest at the landscape scale (Wiens *et al*. 1993).

I report findings from five studies in four EMSs here (With and Crist 1995; Wiens *et al*. 1997; McIntyre and Wiens 1999; Summerville and Crist 2001; Parker and Mac Nally 2002). With and Crist (1995) developed landscape models and identified critical thresholds of habitat loss with respect to dispersal and habitat specificity (this study is also discussed in Section 5.1 Dispersal, and Section 5.3 Rarity). With and Crist (1995) find that limited dispersal ability results in a requirement for aggregated habitat at a lower level of habitat removal, compared to the connectivity requirements of generalist dispersers. Their modeling results are corroborated by an empirical test examining the distribution of two grasshopper species (*Psoloessa delicatula* and *Xanthippus corallipes*), which encountered different amounts of their preferred habitat and responded as the model predicted, based on habitat specificity and dispersal ability (see Section 5.3, Rarity, for further discussion of this study).

Summerville and Crist (2001) also examined rare species response to habitat fragmentation. They considered the effects of fragmentation on butterflies' (Lepidoptera spp.) patch use for five levels of vegetation cover (20, 40, 60, 80, and 100%). Common species (defined by >10 patch visits) display no effect of fragmentation; declines are proportional to the amount of habitat lost, and habitat quality is also a significant factor. However, fragmentation disproportionately affects rare species (defined by <10 patch visits). No rare species occur in patches with less than 40% habitat remaining, and over half of the total species pool of Lepidoptera are never observed in plots with less than 60% habitat remaining (Summerville and Crist 2001). Summerville and Crist (2001) suggest that evidence for threshold response to habitat fragmentation might be difficult to establish, due to the need for many (e.g., 10-15) replicates. Furthermore, since they use habitat amount as a measure of fragmentation, there is no independent accounting for the effects of habitat loss. In fact, this method of measuring fragmentation is more appropriately a test of the effect of habitat loss (Fahrig 2003).

Wiens *et al.* (1997) and McIntyre and Wiens (1999) conducted two studies on fragmentation thresholds in the same EMS. In the first study in this EMS, the authors examined tenebrionid beetle (*Eleodes obsoleta*) movement patterns in a mosaic of buffalograss (*Buchloë dactyloides*) and bare ground in which grass coverage varied between 0% and 80% in 20% increments, in a random pattern (Wiens *et al.* 1997). Three out of four investigated parameters of beetle movement pathways all display significant (p<0.05) non-linearity below the 20% grass cover treatment.

In a separate study in this same EMS, McIntyre and Wiens (1999) tested the separate effects of spatial pattern and habitat amount in an experimentally fragmented landscape, investigating the hypothesis that sparse but contagious habitat was functionally equivalent to a greater amount of randomly distributed habitat (*sensu* With and King 1997; McIntyre and Wiens 1999). They compared two levels of habitat loss (80% and 90%) combined with two levels of habitat arrangement (randomly distributed and contagious). Only 80% and 90% of habitat loss were investigated, based on results from the previous study in this experimental model system (Wiens *et al.* 1997), which indicates that grass-sand landscapes with ≥20% grass are functional with respect to movement, and significantly (p<0.05) different from homogeneous sand landscapes.

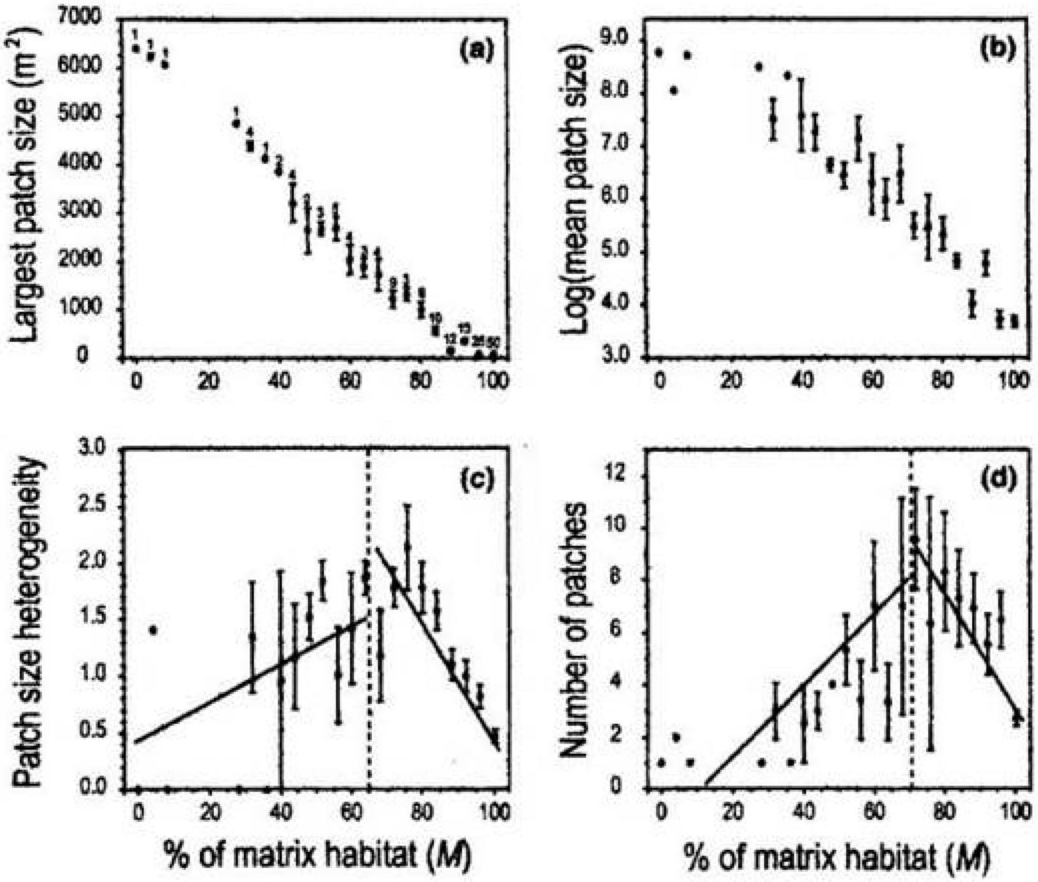
McIntyre and Wiens (1999) find that the comparison between the habitat amount treatments exhibit greater differences than the comparison between the spatial pattern treatments. However, the two parameters interact such that spatial pattern matters at higher amounts (i.e., 20%) of habitat. Interestingly, two of four landscape parameters (average patch size and average interpatch distance) exhibit greater differences between clumped and random landscapes in the 20% habitat treatment than they do in the 10% habitat treatment. These two parameters are better predictors of movement responses than the other two parameters, explaining the interaction between habitat loss and fragmentation. McIntyre and Wiens (1999) attribute the apparent anomaly (i.e., fragmentation more often appears to matter at lower levels of habitat loss) to the organisms' behavioural traits — insensitivity to environmental heterogeneity such as number of patches or patch edge (the other two landscape parameters) would disadvantage the beetles. Furthermore, they suggest that the anomalous result might be because "the effects of habitat configuration may emerge only after some minimal habitat needs are met" (McIntyre and Wiens 1999).

In the fifth and final EMS study reported here, Parker and MacNally (2002) investigated *Elodes* species richness and abundance at two levels of habitat loss (60% and 90%) and three levels (arrangements) of spatial configuration. In this study, no fragmentation threshold occurs in the EMS, although *post-hoc* power tests are low (<0.50) for all abundance measures, and the study duration is short (1 season). Additionally, Parker and Mac Nally (2002) propose that 90% habitat loss might not have been sufficient to precipitate threshold declines.

Taken together, the results from EMSs are equivocal. Four studies report that species respond to fragmentation thresholds (With and Crist 1995; Wiens *et al.* 1997; McIntyre and Wiens 1999; Summerville and Crist 2001), although the studies of McIntyre and Wiens (1999) and Summerville and Crist (2001) could be interpreted to indicate a habitat amount threshold. Parker and Mac Nally (2002) report that species do not respond to fragmentation thresholds within the studied levels of habitat loss (Parker and Mac Nally 2002) and Summerville and Crist (2001) similarly report no effect of thresholds in fragmentation on generalist species. However, Parker and Mac Nally (2002) and Summerville and Crist (2001) suggest that power may have been too low in their studies to detect a fragmentation effect. Where reported, thresholds occur at different levels for different species, ranging from 20% to 60% of habitat remaining. These differences in response are due to the influence of the matrix, the shape and connectivity of the remaining habitat, habitat quality, habitat specificity, and the spatial perception of the studied species (Summerville and Crist 2001). The EMS studies indicate that poor dispersal and rarity result in greater sensitivity to thresholds.

A study set in tallgrass prairie at the Konza Prairie Biological Station in Kansas is intermediate in scale between EMSs and large forested systems (Bascompte and Rodríguez 2001). For woody plants in a prairie matrix, Bascompte and Rodríguez (2001) examined how thresholds predicted by percolation theory applied to semi-natural landscape patterns and species richness. They investigated the relationship between increases in matrix habitat and correspondingly in woody species richness and variables describing habitat configuration, seeking evidence of non-linearity in response and distinct threshold effects. They examined the effects of increasing matrix habitat on species richness, and correspondingly on largest patch size, mean patch size, patch size heterogeneity, and number of patches.

Bascompte and Rodríguez (2001) find that threshold values between 65% and 71% of matrix habitat in the landscape significantly ($p<0.05$) correspond with rapid declines in species richness for three of the configuration parameters tested (Figures 9 and 10). Controlling for the effects of other configuration variables, patch size heterogeneity and the number of patches increase up to thresholds of 35% and 29% remaining woody vegetation habitat respectively (Figure 9). Conversely, decrease in the largest patch size as habitat loss occurs as habitat is lost (Figure 9). These opposing changes correspond to non-significant (p=0.45) fluctuations in species

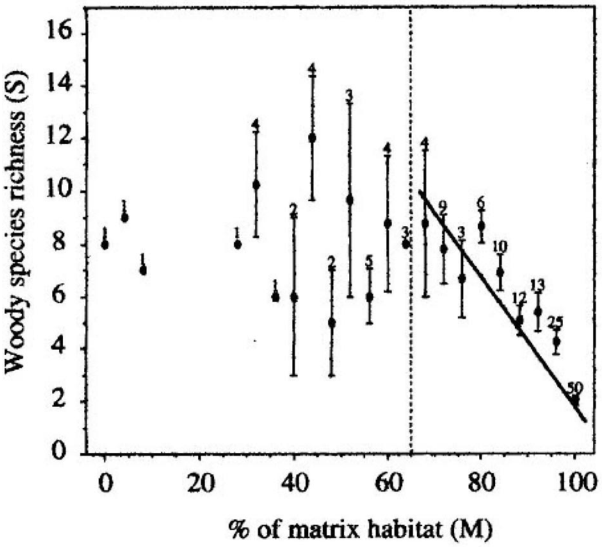


Reprinted with permission

Figure 9. Largest patch size, mean patch size, patch size heterogeneity, and number of patches plotted against the proportion of matrix habitat (M). Critical points in the relationships of patch size heterogeneity and number of patches with matrix habitat (split line regression results) are indicated with broken lines. In each case, the lines fitted to the data to the left and to the right of this point were obtained with linear regression. For representation purposes, the data were divided into 26 categories of percentage of matrix habitat (namely 0, >0-4, >4-8, >8-12,…,>96-100). Error bars represent one SE. (Figure 2 in Bascompte and Rodriguez 2001.)

richness. Thus, at low to intermediate values of habitat loss, these opposing forces result in no overall change in species richness (Figure 10). When woody vegetation habitat decreases from the 35% threshold (i.e., matrix covers >65% of the landscape), patch size heterogeneity and the number of patches peaks and declines (Figure 9). Beyond the 35% threshold, all landscape variables change in the same direction as the matrix increases, with corresponding, significant ($p<0.05$), threshold declines in species as the matrix increases (Figures 9 and 10).

Bascompte and Rodríguez's (2001) result agrees with the model proposed by Tilman *et al.* (1994; Figure 6), which suggests that species loss is an accelerating curve at higher levels of habitat loss. Bascompte and Rodríguez (2001) elegantly demonstrate correlations in thresholds between species richness and habitat loss, and between habitat loss and habitat configuration, showing that species richness declines at the same level of habitat loss as spatial variables alter rapidly (Figures 9 and 10). However, although Bascompte and Rodríguez (2001) control for the effects of the configuration variables on each other, the effect of habitat loss confounds their results.



Reprinted with permission

Figure 10. Woody species richness (S) plotted as a function of the percentage of matrix habitat (M). The broken line indicates the critical value of M (65%) beyond which species richness starts to decrease. This critical point was obtained with split line regression routines. The line fitted to the data on the right of the critical point was obtained with linear regression. There is no significant relationship between S and M to the left of this point (p=0.45). For conventions see Figure 9. Numbers at the top of the error bars are the numbers of quadrats. (Figure 1 in Bascompte and Rodriguez 2001.)

Empirical evidence initially considered to clearly demonstrate fragmentation thresholds across landscapes is significant in landscapes comprised of forest/farmland, but not in forested landscapes.

A synthesis of 35 bird and mammal studies by Andrén (1994) is the empirical study most frequently cited as evidence of fragmentation thresholds. Andrén (1994) hypothesized a null effect of fragmentation; that is, that the random sample hypothesis (small habitat fragments are random samples from large ones) would be sufficient to explain the relationship between habitat loss and species abundance (see Section 3.4, Island Biogeography and Related Theory, about the random sample hypothesis). Species abundance or diversity that is significantly different ($p<0.05$) from that predicted by the random sample hypothesis provides evidence for the alternate hypothesis (fragmentation effects; Andrén 1994). For values less than approximately 70% habitat loss, population size or species richness is proportional to the amount of habitat in the landscape (i.e., the random sample hypothesis). For values of habitat loss greater than this threshold value, species richness or population is disproportionately less than predicted by habitat loss alone. Most study results indicate that the level of fragmentation, as indicated by average patch size and distance between patches, became a better predictor of species richness and population size than the amount of habitat in the landscape (Andrén 1994).

Two studies dispute Andrén's (1994) findings as evidence for fragmentation thresholds in forests (Bender *et al.* 1998; Mönkkönen and Reunanen 1999). In re-evaluating Andrén's (1994) data, Mönkkönen and Ruenanen (1999) argue that the evidence for generalized thresholds is weak, and that extrapolating the 30% proportion of suitable habitat threshold to forest landscapes might underestimate the needs of many species. Mönkkönen and Ruenanen (1999) find that the effect of proportion of suitable habitat in the landscape on the probability to reject the random sample hypothesis is not as strong as the effect of landscape type. Also, when they considered only the forest datasets from Andrén's (1994) study, it appeared that the random sample hypothesis was sufficient to explain species abundance. There were no demonstrated fragmentation effects; habitat loss alone was sufficient to explain declines in species abundance (Mönkkönen and Reunanen 1999). Andrén (1999) agrees with Mönkkönen and Ruenanen (1999) in his own re-analysis of Andrén's (1994) data. Andrén (1999) emphasizes that the effect of landscape type is entirely due to the forest data set; removing the forest dataset causes the influence of proportion of suitable habitat on the fragmentation threshold to become stronger in other landscape types (e.g., forest/farmland). However, Mönkkönen and Ruenanen (1999) do not discount the fragmentation threshold theory. To the contrary, they argue that the 30% threshold for proportion of suitable habitat is quite possibly an underestimate for many species.

As evidence for higher thresholds, Mönkkönen and Ruenanen (1999) cite several studies (Raivio 1992; Edenius and Sjöberg 1997; Reunanen and Nikula 1998), one of which was available (Edenius and Sjöberg 1997) (see Section 4.1, Effects of Habitat Loss, and Section 5.3, Rarity, for further discussion of the Edenius and Sjöberg [1997] study). Edenius and Sjöberg (1997) investigated territory size and habitat occupancy patterns in a natural "archipelago" — a landscape mosaic composed of old-growth forest and mire. They explored the effects of patch size, isolation, and matrix on the species richness of mature and old-growth forest associates. Edenius and Sjöberg (1997) find that occupancy has no relationship to the amount of forest cover in the landscape. They attribute this finding to the scale of the investigation (1 km^2), and conclude that avian species are responding to fine-grain pattern at this scale, rather than to coarse-grain pattern, implying that there might be an influence of habitat amount at a larger scale. Thus, they detected no fragmentation threshold, although forest habitat never decreased below 19% of the landscape. Threshold effects due to landscape spatial configuration were confined to response at the patch scale in this study; the authors found that there was a threshold fragment size (<5 ha), below which a species area curve indicated that patches were significantly depauperate, while there were higher than expected species numbers in patches of 10-20 ha (Edenius and Sjöberg 1997).

Edenius and Sjöberg (1997) suggest that boreal forests require greater amounts of habitat to maintain species than is required for similar species pools in temperate habitats. Edenius and Sjöberg (1997) compare their species area curve to that found in another study in northern Finland (Helle 1984, cited by Edenius and Sjöberg (1997)). Edenius and Sjöberg (1997) suggest that these curves are shallow relative to temperate forest curves. They propose this as evidence that higher proportional area thresholds than those found in temperate forests (30% *sensu* Andrén 1994), might be required for occupancy in boreal forests. They suggest that species density in boreal forests is lower than in temperate forests and therefore greater areas are required in the boreal compared to temperate forests, for similar numbers of species (Edenius and Sjöberg 1997). Presumably, Mönkkönen and Ruenanen's (1999) citation of this study as evidence for >30% thresholds refers to Edenius and Sjöberg's (1997) speculation about shallower species-area curves in the boreal.

Bender *et al.*'s (1998) meta-analysis of patch size effect studies also refutes Andrén's (1994) conclusions. They examined 25 patch size effect studies, involving 134 species of birds, mammals, and insects, primarily in forest settings, and also in wetland, marshland, and grassland habitats. The primary objective of the meta-analysis was to discern patterns in patch size effects; a test for the fragmentation threshold was one of several tests performed to determine the conditions under which patch size effects influence population density. Bender *et al.* (1998) find no fragmentation threshold; contrasting Andrén's (1994) result. Bender *et al.* (1998) suggest that their failure to detect a fragmentation effect might be due to one of two factors. First, the two studies used different methods. Andrén used a discrete "vote count" method to assess if the random sample hypothesis predicted population size, and Bender *et al.* used a continuous response variable. Second, Andrén looked at both patch size and isolation, and the meta-analysis looked only at patch size, so Andrén's result may be due to isolation effects (Bender *et al.* 1998; see also Section 5.1 Dispersal).

Few studies examine the threshold response of

Empirical evidence of thresholds in fragmentation is often measured directly as habitat loss or as a variable related to habitat loss.

species to configuration variables at the landscape-level in forest landscapes. Five landscape-level studies report a qualitative shift in the relative influence of habitat loss and spatial effects (Rolstad and Wegge 1987; Virkkala 1991; Hargis *et al.* 1999; Rodríguez and Andrén 1999; Virgos 2001). Virgos (2001) investigated Badger (*Meles meles*) abundance in remnant forests in two Iberian plateaux. Virgos (2001) used the number of Badger setts as a surrogate for Badger abundance. Forest-scrubland cover was examined in three classes (<20%, 20%-30% and >30% cover), and local habitat quality parameters related to tree cover, shrub cover, rock cover, and grass cover within forests were also measured. All selected fragments were large enough to support breeding den construction and feeding needs (see references in Virgos 2001). Virgos (2001) recorded fragmentation parameters including patch size, and several isolation parameters (distance to other suitable habitat or corridor woodland and distance to other "source" [>10,000 ha] forests). Virgos (2001) finds that patch isolation best explains abundance below a threshold of <20% habitat cover. Above 20% cover, habitat quality parameters better predict abundance than does isolation. However, Virgos (2001), does not control for the relationship between habitat amount and patch isolation (*sensu* Fahrig 2003), rendering ambiguous the interpretation that isolation effects due to fragmentation cause the threshold.

Hargis *et al.* (1999) examined the influence of spatial habitat loss effects on American Marten (*Martes americana)* in the Uinta Mountains of Utah. They discerned stand- and landscape-level thresholds for habitat use by evaluating differences in marten capture rates. This study was set in a landscape with low levels of fragmentation — non-forest cover ranged between 2% and 42%. Results show that there is a significant ($p< 0.05$) threshold in patch occupancy whereby martens avoid habitats with <100 m between openings surrounding a patch (those landscapes containing patches with virtually no patch interior). This is true even though small mammal (prey) species are significantly more abundant in openings. There is also a threshold in landscape occupancy (no martens) when natural and logged openings cover >25% of the landscape. A second study of martens provided corroboration to this result. Thompson and Harestad (1994) used a model calibrated with empirical data to show that martens are sensitive to habitat fragmentation at intermediate scales, showing that threshold occupancy declines when small openings cover greater than 20-30% of the landscape. However, both of these studies (Thompson and Harestad 1994; Hargis *et al.* 1999) equate fragmentation with habitat loss; hence, there are no controls on the influence of habitat loss alone as a cause of the threshold response.

Rolstad and Wegge (1987) examined the relative effects of habitat loss and spatial factors on Capercaillie (*Tetrao urogallus*) in the Norwegian boreal. They studied thresholds at the landscape level as well as at the patch level, in the relationship between patch parameters and lek (mating habitat) use by the old-forest (forest >60-70 years) associate. Rolstad and Wegge (1987) examined the size and distribution of Capercaillie leks in relation to the amount and configuration of old-forest patches. Because Capercaillie cocks spend their time outside of lekking grounds in surrounding old-forest during mating season, these habitat patches exhibit strong habitat "island" characteristics (see references in Rolstad and Wegge 1987). Their study area consisted of an old-forest "archipelago" in southeast Norway. From their data, Rolstad and Wegge (1987) developed predictive models to describe how habitat heterogeneity and fragmentation affects size and distribution of leks and lek use. Rolstad and Wegge (1987) find a threshold in habitat amount (approximately 50% habitat) below which fragmentation has negative effects on cock density, and larger patches are required for persistence (e.g., 50-ha patches were required when forest fragments were isolated by more than 100-200 m). Similarly, there is a threshold patch size, which varied with habitat loss, below which lek density, cocks per lek, and total cock density decreased rapidly (Rolstad and Wegge 1987). Rolstad and Wegge (1987) use the Capercaillie's change in response to the landscape, from a fine-grained pattern to a coarse-grained pattern, as their indication that Capercaillie are experiencing a threshold in fragmentation at the landscape level and patch level. However, their measure of grain size relates to the amount of habitat in the landscape; the graininess of mosaics was measured as the amount of edge per hectare of old forest (Rolstad and Wegge 1987). Their indicator of fragmentation at the landscape level is thus a function of area of old-forest habitat (Rolstad and Wegge 1987, 1989), depending on patch shape (Laurance and Yensen 1991), and, at the patch level (patch size), is directly related to the amount of habitat (*sensu* Bender *et al.* 1998; Fahrig 2003).

Andrén (1997) suggests that fragmentation threshold effects contribute to landscape level declines of a group of resident northern boreal birds (Virkkala 1991). Virkkala (1991) studied Siberian Tit (*Parus cinctus*), Three-toed Woodpecker (*Picoides tridactylus*), Siberian Jay (*Perisoreus infaustus*), Pine Grosbeak (*Pinicola enuclator*), and Capercaillie in harvested and unharvested landscapes. For these old-growth associates, species abundance is lower than expected from the habitat loss that occurred between the 1940s and 1980s. However, in a nearby nature reserve (>1000 km2) comprised of original forest habitat, there was no significant difference in population density during this time. Young (<20 years) forest in the landscape increased nine fold during this period, to 28% in 1980, while old (>120 years) forest decreased by almost half, to 38% (Virkkala 1991). Although the concomitant decrease in old-forest area confounds the results, Andrén (1997) infers from these data that landscape occupation of >40% by young forest and clearcuts in this landscape crosses the fragmentation threshold (this figure was reported in Väisänen *et al.* 1986, cited by Andrén 1997). Again, there is no differentiation between habitat loss effects and fragmentation effects in this interpretation. In the absence of an examination of the effects of habitat loss, the evidence for fragmentation on the observed decline in species abundance is inconclusive (Fahrig 2003).

In the final study that I examined about thresholds in fragmentation at the landscape level in forested habitats, Rodríguez and Andrén (1999) sought a model that could be adapted to management questions. Rodríguez and Andrén (1999) examined the ability of six logistic regression models describing Eurasian Red Squirrel distributions in six study areas across Europe, to describe distributions at local and all other study sites. All study sites were in fragmented landscapes; analysis examined the effects of habitat loss, patch isolation, patch area, and fragmentation thresholds. Although the success of individual models varied between sites, the models had similar success in predicting the probability in finding squirrels above minimum patch size and isolation thresholds. They demonstrated a threshold in patch size (10 ha) and isolation (600 m), which they suggest corresponds to minimum requirements for habitat in the areas with the lowest-quality habitat. These values correspond to the predicted minimum viable habitat area (between 6 and 8 ha) and the maximum daily distance covered by females and (to a lesser extent) males across a functionally continuous landscape (see references in Rodríguez and Andrén 1999). Rodríguez and Andrén (1999) found no significant effect ($p>0.05$) of proportion of habitat in the landscape (i.e., no effect of habitat amount at the landscape level) for predicting the probability of occupancy when squirrel density was high; they did not report results from this test when density was low. However, overall, study area does have a significant effect on the probability of occurrence, accounting for an additional 21% variation in the model beyond that accounted for by connectivity measures. Additionally, Rodríguez and Andrén (1999) used the random sample hypothesis to test for the fragmentation threshold (*sensu* Andrén 1994). The authors suggest that in landscapes with less than 26% habitat, a threshold in fragmentation occurs (Rodríguez and Andrén 1999). This study demonstrates that thresholds in the probability of occurrence for red squirrels appear at multiple scales, and demonstrates a novel method for developing a general model. Additionally, this study demonstrates the inherent influence of the amount of habitat in the surrounding landscape on thresholds in fragmentation.

Model inadequacy and sampling issues constrain empirical demonstrations of theoretical thresholds in fragmentation.

Models derived from percolation theory lead to the idea that fragmentation influences the extinction threshold. To examine the relevance of this proposition to forested landscapes, I framed my review of this portion of the literature on thresholds with two questions. First, as habitat loss increases, do real landscapes exhibit thresholds for indices of landscape structure, or a qualitative shift from habitat loss to spatial effects as the mechanisms influencing species response? Second, are threshold changes in effects on population size in response to changes in landscape structure accompanied by threshold changes to biological parameters? Only a few empirical studies approach fragmentation thresholds from this perspective. Overall, the evidence for thresholds in fragmentation is equivocal, due to important differences between modeled and empirical landscapes, and sampling issues (reviewed below). I find that the data are too few to answer the first question. Subsequently, the thresholds in species responses observed in many studies of fragmentation cannot be directly linked to thresholds in fragmentation per se; the effects of habitat loss confound most results.

Answering the first question, existing data show that there are many more studies reporting a qualitative shift from habitat loss to spatial effects as the mechanism causing species change (Rolstad and Wegge 1987; Virkkala 1991; Hargis *et al*. 1999; Rodríguez and Andrén 1999; Virgos 2001), than there are studies demonstrating spatial percolation thresholds in forests (Gardner *et al*. 1987). The empirical percolation studies show that landscape metrics in forests either do not exhibit thresholds with respect to spatial fragmentation parameters (Franklin and Forman 1987; Spies *et al*. 1994), or that landscape metric thresholds are predicted to occur at lower levels of remaining habitat in forests than the habitat amount predicted by percolation theory (Gardner *et al*. 1987), or that thresholds in forested landscapes occur due to the influence of agricultural land (Leimgruber *et al*. 2002). Data from several "micro-landscapes" or EMSs indicate that fragmentation thresholds either do not occur within the studied levels of habitat loss (Parker and Mac Nally 2002) (although power may have been too low to detect an effect; see below); or they occur at higher levels of habitat loss than predicted by percolation models (Wiens *et al*. 1997; McIntyre and Wiens 1999). The exception is the case of poor dispersers (With and Crist 1995), and rare species (Summerville and Crist 2001), for which thresholds appear at habitat loss levels at or above percolation thresholds (i.e., earlier along the habitat loss gradient than predicted by percolation models).

Percolation models do not accurately portray the components of habitat connectivity that may be important to species (Metzger and Décamps 1997). This may be due to the fact that, unlike percolation models, in forested habitats the matrix habitat is not hostile to many species (Spies *et al*. 1994; Edenius and Elmberg 1996). Species can also use habitat elements in the matrix as stepping stones (intermediate stops) to better habitat. Additionally, although not incorporated into many modeling studies, change occurs over time in real landscapes that experience habitat loss (Spies *et al*. 1994). In this way, succession ameliorates habitat loss that results from forest harvesting. Thresholds in landscape indices predicted by percolation theory also depend on the scale of examination (Gardner *et al*. 1987), and vary with changes to the modeled rules of movement behaviour (Stauffer 1985; Plotnick *et al*. 1993).The simplistic percolation models used to date may ignore some of the factors that have an effect on thresholds in fragmentation in real forest systems. Simplistic percolation models may thus be an inadequate analogy for forested landscapes.

Although thresholds occur in many of the empirical studies that examine spatial factors, this research provides only equivocal evidence for thresholds in fragmentation (*sensu* Fahrig 2003). Results are equivocal primarily because there is confusion defining "fragmentation" in the literature, with the result that there are often inadequate controls for the effects of habitat loss (Fahrig 2003). Reviewing 100 recent studies, Fahrig (2003) argues that the effects of fragmentation are confounded by the effects of habitat loss in many studies. She suggests that the term "fragmentation" should be confined to describe the literal "breaking up of habitat," and that many of the variables used in the literature to describe fragmentation effects, such as patch isolation and patch size, are actually secondary indicators of habitat loss. Reviewed by Bender *et al*. (2003), metrics used to evaluate patch isolation, such as "nearest-neighbour distance," are a measure of the amount of habitat, or lack of habitat, in the landscape surrounding the patch. Similarly, patch size is an ambiguous measure of fragmentation because both habitat loss and the breaking up (fragmentation) of habitat patch size cause reductions in patch size (Fahrig 2003). Furthermore, patch size relates to habitat amount at the landscape scale; large patches are often located in regions with greater amounts of habitat (Bender *et al*. 2003; Fahrig 2003). Observations of the effects of patch size in the absence of a landscape-scale assessment of the amount of habitat are thus an ambiguous metric for fragmentation.

Therefore, there is a lack of experimental or statistical control for the effects of habitat loss in several studies examining the spatial influence on thresholds in fragmentation (Virkkala 1991; Hargis *et al.* 1999; Bascompte and Rodríguez 2001; Summerville and Crist 2001; Virgos 2001). Alternatively, thresholds in fragmentation are a direct consequence of the amount of habitat in the surrounding landscape (e.g., Rodríguez and Andrén 1999). The lack of experimental or statistical control for the effects of habitat loss inhibits drawing causal links between spatial fragmentation thresholds and species decline (Fahrig 2003). However, constraining the definition of fragmentation to the pure effects of increasing the number of patches creates a different context for the question of fragmentation thresholds. The empirical data for this context are currently insufficient (Fahrig 2003).

Findings from empirical studies that examine spatial factors causing thresholds in fragmentation are also equivocal because of issues of statistical power. Statistical power is the probability of correctly rejecting a null hypothesis that is false (Sokal and Rohlf 1981), or, more simply, the probability that an experiment will detect a significant effect between treatments, if such an effect exists. Statistical power implies a relationship between the minimum numbers of replicates, the variation in the data, the effect size considered significant, and the desired *p*-value. If power is low, and no effect is detected (i.e., results are not significantly different), the failure to detect an effect may be due to insufficient replication, rather than to the absence of an effect.

Issues of power highlight a difference between experiments in modeled and empirical landscapes. This difference may result in different effects predicted by models than are observed in real systems. Replication in models is simple to achieve. In fact, hundreds or thousands of model iterations are the basis of many modeling results (e.g., Gardner *et al.* 1987). Models may thus have a high likelihood of detecting an effect, even if the effect size is insignificant in biological terms. Conversely, replication in empirical landscapes, particularly at the landscape level, is difficult to achieve (Fahrig 2003). For example, Summerville and Christ (2001) report no effect of thresholds in fragmentation for generalist butterfly species, and Parker and Mac Nally (2002) similarly report no effect for all butterfly species studied. However, both studies suggest that their replication (i.e., power to detect an effect) is inadequate. Although problems with replication at the landscape level may be difficult to overcome for studies of fragmentation thresholds (Summerville and Crist 2001), the discrepancy in power between theoretical and empirical studies suggests that effects that may be easily detected in modeling studies may be difficult to detect in empirical studies. Accordingly, empirical studies may report different or no effects of thresholds in fragmentation from those reported by theoretical studies.

Summary

Existing data are few, and insufficient to support the general idea of fragmentation thresholds at a particular, critical probability of habitat loss in forested landscapes. I attribute the lack of data in forested landscapes to inconsistent use of the term "fragmentation," simplistic modeling analogues, insufficient empirical and statistical controls for the effects of habitat loss, and inadequate statistical power. Because the term "fragmentation" is poorly defined (Fahrig 2003), studies of thresholds in fragmentation commonly use habitat loss as a measure of fragmentation, confounding results. On the theoretical side, the simplifying assumptions of percolation theory and related models constrain their credibility as analogues for habitat loss. Models also contain high replicates. Conversely, repetition of studies at the landscape level is problematic in real landscapes (Fahrig 2003). Issues of statistical power suggest that there is a greater ability for models than for empirical studies to detect a significant effect. Taken together, model inadequacy and sampling issues constrain the ability to observe congruency between results from real and modeled landscapes.

However, percolation theory and related modeling is useful for understanding processes and patterns. For example, spatial modeling shows that in landscapes with dispersed habitat, occupancy in remaining habitat declines with habitat loss, necessitating a greater habitat amount for species persistence in such landscapes. Accordingly, habitat aggregation results in a lower habitat amount threshold. Models also demonstrate that the effects of thresholds in spatial configuration are more widespread when the amount of habitat remaining in the landscape is low. In particular, poor dispersers and habitat specialists are sensitive to the spatial configuration of landscapes, even when there are high levels of suitable habitat available in the landscape.

Although the empirical studies of thresholds in fragmentation in forests do not partition the relative effects of habitat loss and fragmentation, reported thresholds appear to be a function of individual species traits. Particularly affected are rare species (Summerville and Crist 2001), habitat specialists (Rolstad and Wegge 1987; Virkkala 1991; Hargis *et al.* 1999), and species with low dispersal rates (Virgos 2001). However, Bascompte and Rodríguez (2001) report a threshold response in the overall measure of species richness. While poor dispersers and rare species appear to be particularly sensitive to thresholds, species respond to landscape composition at a scale consistent with their perception of the landscape (Wiens 1989; Kotliar and Wiens 1990). Additionally, the evidence is more widespread for thresholds in population size or species richness in forest/agricultural habitats (Appendix Table 1; Andrén 1994, 1999). However, thresholds reported for forest/agricultural habitats may be more strongly related to the effects of habitat loss than to fragmentation *per se*; most fragmentation measures are proxies for habitat loss (Bender *et al.* 1998; Fahrig 2003). Overall, due primarily to problems with sampling, the empirical data are currently insufficient for evaluating the general idea of critical thresholds in fragmentation in forests. However, the predicted occurrence of thresholds in fragmentation at a critical probability of habitat loss is inherently a question of the amount of habitat at the landscape scale.

4.3 Physical and Biological Effects of Habitat Loss

The spatial aspects of patch-based population dynamics (metapopulations), dispersal, and connectivity are the real-world corollary to the theory of percolation theory. Yet in a literature review to reconcile the theory of the ecological effects of fragmentation with the existing empirical evidence, Harrison and Bruna (1999) contend that the theory is inconsistent with the data. They suggest that the data are highly equivocal about spatial effects; they find that physical and biological edge effects can explain most of the reduced diversity and ecological function reported in fragmented forest habitats (Harrison and Bruna 1999). The emphasis on physical changes to forest edge and interior caused by habitat loss is echoed by other reviews of habitat loss effects (Saunders *et al.* 1991; Kremsater and Bunnell 1999; Debinski and Holt 2000). I briefly describe physical and biological edge effects, and then present data from modeling and empirical studies that examine thresholds and edges.

Physical changes to microclimate penetrating the edge of a forest stand remaining after timber harvesting include increased wind, higher daytime and lower nighttime temperatures, and changes in water flux (Saunders 1991). The latter effect is associated with reduced evapotranspiration and increased surface-water and groundwater flows. Biological edge effects include community "spillover" from surrounding habitats due to edge effects, including increased predation, competitive release at the edge, an increase in early successional species, and the influence of transient species (Holt *et al.* 1997).

Physical and biological edge effects defined.

With and King (2001) looked at the sensitivity of species to the amount of edge in the landscape (see Section 5.2, Reproductive Traits, for more discussion about this study). With and King (2001) modeled various amounts of area and edge with respect to reproductive parameters for area and edge sensitive and insensitive species in a spatially explicit environment, examining how the fragmentation threshold differed, based on these species traits. Their modeling suggests that sensitivity to edges can be a more important determinant of thresholds in habitat than can sensitivity to area. In "clumped" or aggregated habitat, species with low edge sensitivity can persist with as little as 1% of habitat. These same species go extinct when habitat falls below 20% or 30% in randomly fragmented landscapes, depending on area sensitivity. Species with high edge sensitivity require higher amounts (minimum of 50%) of clumped habitat for persistence. The latter threshold increases to 90% when species are both edge- and area-

Edge sensitivity can be more important to thresholds in habitat than can sensitivity to area. Edge-sensitive species require more, aggregated habitat than edge-insensitive species.

sensitive. In highly fragmented landscapes, all modeled species are doomed to extinction regardless of edge and area sensitivity.

Edge density shows threshold changes around critical shapes and sizes of patches.

In a second threshold edge study, Laurance and Yensen (1991) developed a "Core-Area Model," to discern edge effects on remnant patches, based on patch area, and distances and biotic and abiotic parameters along a gradient from the forest edge to the forest interior (i.e., stopping where edge effects were ameliorated). With this model, Laurance and Yensen (1991) estimated the appropriate reserve shape and size required to ensure a desired area of forest interior. The relationships between the area of the forest interior and the amount of edge are non-linear, and vary by patch shape. The Core-Area Model demonstrates that, for an edge-sensitive species, there is a critical range of fragment sizes in which the impacts of edge effects increase almost exponentially. This critical range of fragment sizes is relative to forest type, and depends primarily on the distance edge effects penetrate into remnant patches (Laurance and Yensen 1991).

Cutting rate and cutting pattern influence the amount of edge in the landscape.

A set of studies examines model predictions (Franklin and Forman 1987) and empirical findings (Spies *et al.* 1994) of edge thresholds in forests (see Section 4.2, Spatial Effects of Habitat Loss, for more discussion of these studies). Franklin and Forman (1987) created a percolation model to simulate cut and leave patterns in Pacific Northwest forests. They find that edge density peaks in the model at 50% habitat removal, and no interior forest (based on edge effects permeating two tree lengths [160 m] into patches) remains at 50% removal. In a separate study, Naiman *et al.* (1989, cited by Metzger and Décamps 1997) propose a conceptual model, whereby rapid decreases to biodiversity occur due to an increase in interior species extinctions, when the frequency of ecotones in the landscape is greater than 50%. Taken together, these model predictions suggest a critical loss of ecosystem function due to edge effects. Spies *et al.*'s (1994) empirical study examined the predictions of Franklin and Forman's (1987) percolation model. Findings in the empirical landscape (Spies *et al.* 1994) differ from those predicted by the model (Franklin and Forman 1987) in several respects. The empirical analysis shows that edge density peaks at 40% removal, somewhat lower than, but close to, the 50% prediction of the model. However, there is approximately 30% interior forest remaining at 50% habitat removal in the empirical landscape, versus no interior forest remaining in the simulated landscape.

The differences between Franklin and Forman's (1987) predictions and Spies *et al.*'s (1994) results arose for several reasons. Spies *et al.* (1994) point out that forest regrowth is not incorporated into the simulation model (also acknowledged as a shortcoming of the model by Franklin and Forman), whereas regrowth occurs in the empirical landscape. Forest regrowth mitigates edge effects, thereby reducing edge width and increasing forest interior over time. Forest regrowth also limits the maximum amount of cutover forest on the landscape, given harvest rates based on a rotation length of 80 years. A higher cutting rate in some landscapes resulted in higher amounts of edge and lower amounts of interior habitat than occur in landscapes with lower cutting rates. The effects of higher cutting rates demonstrate that cutting rate can have a greater influence than cutting pattern on the amount of edge and interior habitat (Spies *et al.* 1994).

Summary

Several authors attribute many of the changes caused by habitat loss to changes in forest edge and interior species, rather than to the spatial configuration of landscapes *per se*. Modeling suggests thresholds in species tolerance to habitat loss, depending on edge sensitivity. Models also predict loss of ecosystem function due to the increase in the number of patches, or due to the shape of patches, at high levels of habitat loss for dispersed cutting patterns. Although empirical data are few, important dynamics in real forested landscapes create more complexity than is accounted for by models to date. In particular, temporal change, which is not included in simple models, has a significant influence on edge and interior metrics. Empirical results show that, over time, succession can ameliorate some of the negative influence of edges resulting from dispersed cutting. Empirical data also show that if the rate of landscape change is too rapid, model predictions of loss of ecosystem function are more likely to occur in real landscapes.

4.4 Matrix Effects

Matrix quality has been shown to influence species response to habitat loss (Wiens *et al.* 1993; Fahrig and Merriam 1994; Gustafson and Gardner 1996; Moilanen and Hanski 1998; Norton *et al.* 2000; Fahrig 2001; Vandermeer and Carvajal 2001). Conversely, metapopulation and population structure studies have tended to focus on homogeneous habitat patches embedded in a "featureless and ecologically neutral matrix" (Wiens *et al.* 1993). The matrix exerts complex mitigating and/or exacerbating effects on species, depending on matrix quality, the individual species' level of habitat specificity, and natural landscape heterogeneity (Margules *et al.* 1982; Doak and Mills 1994; Schieck *et al.* 1995; Gustafson and Gardner 1996; Andrén *et al.* 1997; Norton *et al.* 2000). Where habitat loss and forest fragmentation are genuine (i.e., the forest is replaced by a different habitat type, or habitat loss is permanent), the "island" (MacArthur and Wilson 1967) analogy for forest patches may be appropriate for species that can neither disperse through nor utilize the matrix. For other species, matrix quality may also influence the rate of emigration and immigration between patches (Fahrig and Merriam 1994; Lamberson *et al.* 1994; Fahrig 2001). Still other species, particularly in naturally patchy environments, may experience no notable influence of the natural matrix (Edenius and Sjöberg 1997; Henle *et al.* 2004). Some species in habitat patches may be positively influenced by the matrix (Lomolino and Perault 2001), utilize the matrix to compensate for the loss of resources in removed habitat patches (Norton *et al.* 2000), or have higher presence in the matrix than in forested patches (Jules *et al.* 1999; Lomolino and Perault 2000).

Island biogeography and metapopulation theory predict that population persistence is determined by the balance between immigration (colonization) and extinction rates. A high-quality matrix is therefore likely to increase immigration (and emigration) rate, and a low-quality matrix will likely decrease immigration rate (Vandermeer and Carvajal 2001). In fact, the small body of threshold-related matrix studies generally shows that matrix dynamics are complex and difficult to quantify, while generally adding only moderate improvement to model predictions.

Incorporating the influence of the matrix is difficult, due the complexity of modeling movement, and does not always significantly improve model predictions.

Where comparisons exist, the relative influence of matrix quality on habitat thresholds is shown to be secondary to other landscape factors and species traits (Moilanen and Hanski 1998; Fahrig 2001; Goodwin and Fahrig 2002). Gustafson and Gardner (1996) come to this same conclusion in a matrix study that did not explicitly examine thresholds. In their individual-based dispersal model, patch size and configuration account for 89% of the variability in dispersal success, while matrix heterogeneity accounts for only 4% (Gustafson and Gardner 1996). However, the same model run on GIS-based maps of deciduous forest/agricultural landscapes shows a variable influence of matrix heterogeneity on dispersal, with matrix quality significantly improving or impeding dispersal for certain patches. This study highlights the fact that the relative influence of matrix heterogeneity on metapopulation dispersal depends on landscape context (Gustafson and Gardner 1996).

Moilanen and Hanski (1998) included a selection of attributes reflecting matrix quality into an existing spatially realistic metapopulation model of the Glanville Fritillary (butterfly). The model describes a fragmented habitat of patches of meadow interspersed with cultivated and grazed fields, swamps, clearcut forest, and standing forest. Similar to Gustafson and Gardner's (1996) result, accounting for matrix quality adds little explanatory power to the metapopulation model. Moilanen and Hanski (1998) suggest that modeling extra environmental data may result in marginal improvements to the model because the mapping of habitat in the original model took into account biological information, therefore accounting for some environmental variability. These two studies (Gustafson and Gardner 1996; Moilanen and Hanski 1998) conclude that accounting for matrix quality is complicated, due to the difficulty of modeling movement between patches. Gustafson and Gardner (1996) suggest that asymmetry occurs in immigration and emigration rates between patches due to irregularities in patch shape, size, and configuration. The heterogeneity of the matrix also influences asymmetry in movement rates. Movement in one direction may thus be more favourable than movement in the other (Gustafson and Gardner 1996). They further suggest that this may be the "rule rather than the exception for realistic landscapes" (Gustafson and Gardner 1996, p.105).

In a spatially explicit simulation model, Goodwin and Fahrig (2002) examined the effect of landscape structure on landscape connectivity, and tested their results in an empirical micro-landscape. Goodwin and Fahrig (2002) calibrated the model with movement behaviour of the specialized Goldenrod Beetle (*Trirhabda borealis*) in patches to examine the influence of the matrix on the beetles' movements in goldenrod patches. Patches in the micro-landscape were goldenrod habitat, cut vegetation matrix, or cut vegetation matrix covered with camouflage netting to impede movement. The focus of the study was to examine the influence of different patch types on different measures of patch connectivity. Although increasing interpatch distance significantly decreases landscape connectivity, the influence of matrix elements on landscape connectivity is small in comparison to the influence of habitat elements (Goodwin and Fahrig 2002). Goldenrod Beetles in the micro-landscape corroborate the simulation results.

If high-quality matrices reduce mortality in the matrix, improvements to matrix quality may result in a lower threshold in habitat amount

Fahrig (2001) used a spatially explicit population model to show that the effect of emigration rate on the habitat threshold partially depends on matrix quality. She investigated the relative effects of four factors (reproductive rate, emigration rate, matrix quality, and habitat pattern) on the extinction threshold. Reproductive rate exerts the strongest potential influence on the extinction threshold, followed by a strong influence of emigration rate, a moderate influence of matrix quality, and a small influence of habitat pattern (Fahrig 2001). Note that although Fahrig (2001) examines the relative importance of each of these factors, there is a close relationship between emigration rate and matrix quality: since higher emigration rates increase the time individuals spend in the matrix, for poor-quality matrices the habitat threshold occurs at a lower level of habitat loss, due to increased matrix mortality. High-quality matrices result in the opposite effect; that is, habitat thresholds at a higher level of habitat loss, due to increased colonization rates.

Lamberson (1994) modeled this interaction between emigration rates and dispersal mortality in a model of Northern Spotted Owl (*Strix occidentalis caurina*) occupancy in an abstract, cutover, forested landscape with different levels of habitat amount and aggregation. In this model, the matrix is hostile, and juvenile owls spend more time searching the landscape for suitable and unoccupied habitat when aggregation of habitat patches is low. When dispersal mortality is high, as would be the case in poor-quality matrix (Fahrig and Merriam 1994; Fahrig 2001) or when there is low affinity to certain habitats (With *et al*. 1997), landscape occupancy is reduced (Lamberson *et al*. 1994).

Vandermeer and Carvajal (2001) used a set of theoretical models to demonstrate a considerably greater effect of matrix quality on metapopulation dynamics than suggested by the above empirically calibrated modeling studies (i.e., Gustafson and Gardner 1996; Moilanen *et al*. 1998; Goodwin and Fahrig 2002). Vandermeer and Carvajal (2001) suggest that, under most conditions, increasing matrix quality relates to increased movement between patches, buffering a metapopulation against extinction (Vandermeer and Carvajal 2001). Consistent with Gustafson and Gardner's (1996) conclusion, Vandermeer and Carvajal suggest that the influence of matrix quality depends on patch isolation; that is, landscape context. A further result of Vandermeer and Carvajal's (2001) modeling is that increasing matrix quality from low to high quality can generate chaotic population dynamics, and, in effect, alter population structure from sub-population to metapopulation conditions. Under a narrow range of conditions (e.g., spatially correlated extinction), a high-quality matrix could therefore actually increase extinction risk. Unlike the Gustafson and Gardner (1996), Moilanen and Hanski (1998), and Goodwin and Fahrig (2002) studies, Vandermeer and Carvajal (2001) did not empirically test their model results.

The observed mitigating effects of the matrix may have several interpretations. The matrix may connect remnant patches (Taylor *et al*. 1993), or, alternatively, buffer remnant patches (Norton *et al*. 2000). For example, the matrix around a fragment may offer only suboptimal resources, but it may still function as additional foraging habitat, thereby enhancing the population living in the remnant patches, giving rise to inverse relations between fragment area and population density (Debinski and Holt 2000; Norton *et al.* 2000; Zschokke *et al.* 2000, cited by Tscharntke *et al.* 2002). For some species, matrix quality influences the amount of time (or distance) an individual will spend within the matrix, thereby influencing the colonization probabilities of different habitat fragments (Stamps *et al.* 1987; Andrén 1997). For example, in a study of Hazel Grouse (*Bonasa bonasia*) in the Swedish sub-boreal, Åberg *et al.* (1995) compared species occurrence in a forested landscape in-terspersed with a hostile (farmland) matrix with species occurrence in an intensively managed forest landscape. In this study, the hostile matrix (agricultural land) reduces by a factor of 20 the threshold in gap distance over which the Hazel Grouse travels, compared to the managed forest landscape. The influence of the matrix on migration probably ultimately depends on mortality while in the matrix; hence, higher-quality matrices generally improve movement rates by decreasing the probability of mortality (Fahrig 2001; Vandermeer and Carvajal 2001).

Summary

Little research on the influence of the matrix on habitat thresholds is available. The few studies that are available cover a variety of forested and agricultural landscapes; inferring general conclusions is problematic. Accurately incorporating matrix effects into modeling studies that examine thresholds has also proved to be complex, due to the difficulty of modeling movement. Given that mortality rates during movement between patches appear to be a key test of matrix quality, the difficulty in modeling movement imposes considerable constraints on studying the influence of the matrix in theoretical and empirically calibrated models. Studies incorporating the influence of matrix elements have demonstrated a range of effects, from model predictions of relatively modest influences on persistence thresholds for generic and real species in forested / agricultural and micro-landscapes, to considerable effects in theoretical models. It remains unknown if a greater influence on the habitat threshold would accompany improved modeling of matrix quality. Perhaps because the matrix potentially exerts negative *and* positive influence on individuals, the literature demonstrates that matrix quality exerts a variable degree of influence on metapopulation persistence. The variation in results indicates that it is not possible to deduce general, quantitative predictions about the effect of matrix quality on population dynamics. On the other hand, the variation in results highlights the idea that the effect of matrix quality is landscape-specific. This implies, for example, that an increase in metapopulation persistence is most likely to accompany improvements to matrix quality in landscapes with high patch isolation, or landscapes in which matrix quality is initially low.

4.5 Landscape Context

Several threshold studies report that the effect of habitat loss on organisms depends on landscape context (Åberg *et al.* 1995; Gustafson and Gardner 1996; Edenius and Sjöberg 1997; Groom 1998; Moilanen *et al.* 1998; Mönkkönen and Reunanen 1999; Vandermeer and Carvajal 2001; Lennartsson 2002; Pakkala *et al.* 2002; Fahrig 2003; Kreuzer and Huntly 2003). Landscape context can refer to several different factors of landscape composition; I divide these factors into three classes of landscape influence.

First, landscape context can refer to the degree of isolation of a patch in the landscape (e.g., Lennartsson 2002; Fahrig 2003). Used in this way, landscape context refers to the amount of habitat in the landscape surrounding the area of study. Patch size effects and isolation effects can vary with the amount of cover in surrounding landscape, with less severe effects of patch size observed in landscapes with greater cover of habitat (but also see Bender *et al.* 1998; Groom 1998; Lennartsson 2002; Fahrig 2003).

Second, landscape context can refer to the landscape type or quality that occurs in the matrix (Andrén 1994; Åberg *et al.* 1995; Mönkkönen and Reunanen 1999; Angelstam *et al.* 2002, cited by Angelstam *et al.* 2003; Pakkala *et al.* 2002). If the intervening landscape type between forest patches is hostile to forest species (e.g., agricultural land), different effects of habitat loss and fragmentation may be observed than if the matrix is comprised of less hostile type (e.g., early seral forest) (Åberg *et al.* 1995). Mönkkönen and Reunanen (1999) re-analyzed Andrén's (1994) frequently cited paper that reports empirical thresholds in fragmentation. Mönkkönen and Reunanen's (1999) re-analysis finds that landscape context significantly affects the probability of detecting an effect of fragmentation. Analysis of only the studies in forested landscapes (Mönkkönen and Reunanen 1999) finds no evidence for fragmentation thresholds in the forest studies of Andrén (1994). A second re-analysis (Andrén 1999) of the three non-forest landscape types shows that the effect of fragmentation thresholds becomes stronger when the forest landscape studies are removed. This debate over the generality of Andrén's (1994) results, and the importance of landscape type in this debate, suggests that results from simplified models (e.g., percolation models), and agricultural landscapes (e.g., Andrén 1994) cannot be extrapolated to forested landscapes.

A gradient of the quality of habitat may also occur in forested landscapes, reflecting the importance of landscape context to the presence of some species (Pakkala *et al.* 2002). Pakkala *et al.* (2002) studied patterns of habitat occupancy of the Three-toed Woodpecker in the Finnish boreal forest. They generated metrics of habitat quality — or the "metapopulation capacity" (Hanski and Ovaskainen 2000) of the landscape — the capacity of a fragmented landscape to support a viable metapopulation. The metapopulation capacity was based on stand characteristics (age, tree species composition), and spatial characteristics. They found that measures of the metapopulation capacity of the landscape were significantly ($p<0.05$) positively related to the fraction of the landscape that was occupied, and demonstrated a threshold for the occurrence of the woodpecker at the landscape level (Pakkala *et al.* 2002).

Angelstam *et al.* (2002, cited by Angelstam *et al.* 2003) similarly found changes in occupancy along a gradient of landscape quality in hemi-boreal forest in Poland. Habitat generalists (Black Woodpecker [*Dryocopus martius*] and Great Spotted Woodpecker [*Dendrocopos major*]) were found in all landscape types, whereas habitat specialists (Lesser Spotted Woodpecker [*D. minor*], White-backed Woodpecker, Middle Spotted Woodpecker [*D. medius*], Grey-headed Woodpecker [*Picus canus*] and Three-toed Woodpecker) were only observed in landscapes without intensive forest management, or where natural forest succession occurred following land abandonment. In particular, the White-backed Woodpecker exhibited a non-linear relationship between presence and the amount of dead wood, requiring between 10 and 20 m^3 ha^{-1} of dead wood over a 100 ha area (Angelstam *et al.* 2002, cited by Angelstam *et al.* 2003).

In the third interpretation of landscape context discussed here, the term can have historical or evolutionary implications (Holling 1992; Edenius and Elmberg 1996; Peterson 2002). Used in this way, landscape context refers to the natural heterogeneity of a landscape and the local disturbance regime. Landscape heterogeneity evolves over multiple scales of time and space. Landscape pattern emerges from processes that occur on geological time scales, such as glacier movement or soil forming processes, and on shorter time scales calibrated by local, natural disturbance regimes; for example, fire disturbance and pest outbreaks (Holling 1992). In some landscapes, a positive feedback between pattern and disturbance process results in strong landscape patterns that endure over time (Peterson 2002). Organisms evolve within or adapt to the constraints of landscape pattern (Holling 1992). From this perspective, members of a single species may adapt to the local landscape pattern, and exhibit different population dynamics in different landscapes (e.g., Moilanen and Hanski 1998; Kreuzer and Huntly 2003). The relationship between landscape patterns resulting from processes that occur on different temporal scales, and species ability to adapt to and persist through habitat disturbance, highlights the idea that species stand the best chance of survival in human disturbed landscapes that closely resemble naturally disturbed landscapes (Christensen *et al.* 1996; Landres *et al.* 1999; Thompson and Harestad 2003).

Summary

Landscape context often explains observations of threshold behaviour. Discussions of landscape context in the literature reflect three different usages of the term. First, landscape context can refer to the degree of isolation of a patch in the landscape. Second, landscape context can refer to the landscape type that occurs in the matrix. Third, landscape context can refer to the natural landscape pattern. Each of these usages implies that thresholds differ in different landscapes. Furthermore, the idea of landscape context emphasizes the importance of local variables in interpreting species response to habitat loss.

5 SPECIES CHARACTERISTICS INFLUENCING THRESHOLD RESPONSES

Although landscape characteristics significantly determine the effects of habitat loss, critical thresholds emerge from species *interactions* with landscape structure, as opposed to resulting solely from the structure of the landscape itself (With and Crist 1995). Critical thresholds may be influenced by species interactions such as plant-pollinator relationships, or particular life history traits such as dispersal or reproduction. The ultimate cause of extinction for all organisms is a higher mortality rate than reproductive rate (Fahrig 2002), but proximal causes of extinction are complex and varied. Since there are many species and landscape-specific parameters that influence critical thresholds (With and Crist 1995; Bascompte and Solé 1996; Metzger and Décamps 1997; Ney-Niefle and Mangel 2000; Swihart *et al.* 2001), generalizing across species and landscapes is nearly impossible (Andrén 1996; Henein *et al.* 1998; Fahrig 2001; With and King 2001).

Species response to habitat loss and fragmentation, and the location of individual thresholds (if they exist), will depend on the biological and demographic requirements of individual species or organisms — unique combinations of life history and dispersal parameters (Lande 1987; Metzger and Décamps 1997; Debinski and Holt 2000; With and King 2001). Biological and demographic characteristics include species properties such as dispersal range (Section 5.1), reproductive traits (Section 5.2), degree of habitat specialization (Section 5.3), geographic range (Section 5.4), meta-population or population-level spatial dispersion (Section 5.5), and inter-specific traits (Section 5.6) (Lande 1987; With and Crist 1995; Bryant 1996; Keitt *et al.* 1997; Debinski and Holt 2000; Terry *et al.* 2000). In turn, how much each of these characteristics is affected by habitat loss is highly species-dependent (Debinski and Holt 2000; With and King 2001). Revealing the continued influence of the concept of island biogeography, research on the extinction threshold has focused primarily on the characteristics of species that determine extinction and colonization rates of populations (e.g., Lamberson *et al.* 1992; Bascompte and Solé 1996; Bellamy *et al.* 1996; Keymer *et al.* 2000; Fryxell 2001; Swihart *et al.* 2001). In the following sections, I review the literature on the species traits considered to influence habitat thresholds.

5.1 Dispersal

Both TIB and metapopulation models identify patch size and patch isolation as the key features associated with extinction, because of their influence on extinction and colonization rates (MacArthur and Wilson 1967; Levins 1969). Since colonization is inherently a landscape-scale process, most landscape-scale studies of population change focus on factors relevant to colonization such as dispersal and other movement behaviour (e.g., Lamberson *et al.* 1992; With *et al.* 1997; McIntyre and Wiens 1999; With *et al.* 1999; With and King 1999a). A species' dispersal capability determines, in part, its perception of landscape connectivity (With and Crist 1995; Keitt *et al.* 1997; King and With 2002). Because habitat loss alters landscape connectivity, interest in fragmentation thresholds is inherently concerned with species' ability to disperse in fragmented habitats. As a result, studies examining habitat thresholds emphasize the effect of landscape change and dispersal behaviour on movement factors and colonization rates (Lande 1987; Keitt *et al.* 1997; With and King 1999a; Fahrig 2002; King and With 2002). Dispersal is thus one of the most frequently studied species-specific characteristics thought to determine a species' response to habitat loss and fragmentation (Mader 1984; With and Crist 1995; Bryant 1996; Gustafson and Gardner 1996; Keitt *et al.* 1997; Wolff *et al.* 1997; Sutherland *et al.* 2000; Terry *et al.* 2000; Ovaskainen *et al.* 2002). In this section, I review the evidence for habitat fragmentation thresholds as they pertain to dispersal.

A seminal demonstration of a threshold in habitat amount related to dispersal capability.

The relationship between dispersal and thresholds in habitat amount is illustrated by Lande (1987), who shows that a habitat threshold occurs at a certain amount of habitat in the landscape, and that the threshold (when extinction rates exceed colonization rates) is crossed when the amount of suitable but unoccupied habitat in the landscape is insufficient compared to dispersal (see Section 4.1, Effects of Habitat Loss, for further discussion of Lande's work). The Lande (1987) model was groundbreaking because it not only provided theoretical evidence for the presence of a threshold but it also showed that the location of the threshold is influenced by life history and dispersal parameters. Lande also highlighted the importance of demographic factors, relative to genetic factors, in determining MVP sizes (Lande 1988b). Lande applied these concepts in a model of the Northern Spotted Owl in the Pacific Northwest states to demonstrate the existence of a habitat amount threshold (Lande 1988a). The Lande model is limited because it is aspatial, in that suitable territories are distributed randomly across the landscape, and dispersal occurs randomly. The Lande model has been developed in both the generic sense (i.e., modeling a range of parameters for dispersal and reproductive traits) (e.g., With and King 1999b), and in the specific sense, by improving the modeling for the Northern Spotted Owl (e.g., Lamberson *et al.* 1992; Carroll and Lamberson 1993; Lamberson *et al.* 1994). Modeling studies since Lande's work have consequently demonstrated a key factor in dispersal success: the spatial arrangement of habitat.

Spatial modeling demonstrates that the arrangement of habitat, and the influence on dispersal of patch size and patch isolation, affects species primarily at high levels of habitat loss.

Many modeling studies have used the spatial dimension to show that at moderate to high levels of habitat loss, the increasing spatial effects of habitat loss — patch isolation and reduced patch size — influence the extinction threshold (e.g., Fahrig 1997; Hill and Caswell 1999; With and King 1999b; Fahrig 2001, 2002; Flather and Bevers 2002). Incorporating the spatial arrangement of habitat generally demonstrates that the habitat supply threshold is lower in aggregated than in fragmented habitats (Lamberson *et al.* 1992; Lamberson *et al.* 1994; Dytham 1995a; Moilanen and Hanski 1995; With and King 1999b; Fahrig 2002). In further modeling conducted on the Northern Spotted Owl, subsequent authors improved model realism related to dispersal success by considering the spatial arrangement of habitat. The spatial component increased the overall habitat area needs at the habitat threshold when habitat was fragmented, whereas aggregating habitat resulted in an overall lower habitat area requirement than predicted by Lande (e.g., Lamberson *et al.* 1992; Lamberson *et al.* 1994). Compared directly to the predictions of Lande's (1987) model, an examination of a range of dispersal and reproductive rates for generic species showed that spatially aggregating habitat resulted in a lower (or non-existent) habitat supply threshold across virtually all parameter values (With and King 1999b). Dispersal rate is also affected by the number of times migrants can search for suitable habitat. Accordingly, several models show that increasing the number of times migrants can search for suitable patches increases the proportion of suitable patches occupied and lowers the extinction threshold. (e.g., Lande 1987; Lamberson *et al.* 1994; With and King 1999b; Hill and Caswell 2001). The modeling studies that add a spatial component demonstrate that the arrangement of habitat affects species success primarily at high levels of habitat loss.

Dispersal is scale-specific; habitat configuration and thresholds in habitat amount are relevant only at scales consistent with species' perception of the landscape.

Theory and simulation modeling show that important changes in population dynamics can be expected when dispersal and spatial factors are considered, but these changes are particular to specific scales and dispersal rates (Kareiva 1990). Movement factors such as dispersal occur at a scale consistent with species size, trophic status, and morphology (Harestad and Bunnell 1979; Sutherland *et al.* 2000). Because dispersal is scale-specific, the perception of fragmentation — or (synonymously) of landscape connectivity — is pervasively a question of scale (Doak *et al.* 1992; Lamberson *et al.* 1992; With and King 1999b). This was nicely demonstrated by With and King (1999b), who compared the effects on the habitat supply threshold of random dispersal versus dispersal scaled to the neighbourhood of natal territory. By re-defining dispersal as fine scale phenomena, With and King (1999b) showed that the threshold in habitat amount is lower in clumped habitats. In another model examining spatial factors on population distribution, With *et al.* (1997) showed that a change in the scale of observation results in different components of habitat influencing threshold behaviour. They also showed that the amount of habitat has the greatest effect on dispersion at fine scales in aggregated habitats, but that habitat affinity has the greatest effect at coarse scales.

The relationship between habitat elements, dispersal capability and scale was investigated in a real landscape in the central United States (Keitt *et al.* 1997). This spatially explicit Geographic Information System (GIS) study of habitat shows that the location of a threshold in landscape connectivity[7] depends on the scale at which a species perceives the landscape as connected (Keitt *et al.* 1997). A range (0-100 km) of "threshold" dispersal distances represented a range of scales at which to compute connectivity measures. Keitt *et al.* (1997) identified a distance (between 40 and 45 km) at which they observed an abrupt change in connectivity — a percolation threshold. Organisms operating at dispersal distances less than 45 km observed their environment to be almost half as connected as did organisms with greater dispersal (Figure 11). Keitt *et al.* (1997) examined the distribution of suitable habitat for Mexican Spotted Owls (*Strix occidentalis lucida*). Although the results of this study are species- and landscape-specific, they could be easily modified to create a model for studying other species in other landscapes.

In Keitt *et al.*'s (1997) GIS study, dispersal capability influences the relative importance of habitat components at different scales. Keitt *et al.* (1997) suggest that the existence of large patches remains important for all of the species they modeled, regardless of dispersal capability. Results from Keitt *et al.* (1997) suggest that for species with low dispersal distances (<40 km), the landscape configuration (i.e., relative position and orientation of patches) was of relatively little importance. At this scale, patch size was of greatest importance to connectivity, with the largest patches being most important. Keitt *et al.*'s (1997) result differs from the fine-scale result in a study of Toucans (*Ramphastos sulfuratus*), where configuration is more important than area (Graham 2001, see below). Keitt *et al.* (1997) find that for species characterized by a dispersal distance near the threshold (at about 40-45 km), large patches are still of high importance to landscape connectivity; however, landscape configuration is also important. Accordingly, smaller patches that may act as corridors and stepping stones make an important contribution to connectivity (stepping stones are patches that connect larger areas of habitat). Keitt *et al.* (1997) find that for species with high dispersal distances (above the threshold), the configuration of particular patches was not important, although, at this scale, large habitat patches had the greatest contribution to connectivity.

Reconciling Keitt *et al.*'s (1997) findings with the predictions of percolation theory is not straightforward. According to percolation theory, habitats are thought to experience a drastic loss of connectivity at and below the percolation threshold. Keitt *et al.* (1997) find that habitat areas of a size for organisms with dispersal distances <45 km are only half as connected as larger habitats. However, examining the relative contribution of patch size and configuration at this scale, Keitt *et al.* find that landscape configuration is of relatively little importance below the percolation threshold. On the other hand, a second key conclusion from Keitt *et al.*'s (1997) examination of the scale-dependent role of habitat features is that the influence of different components of fragmentation (patch isolation and patch size reduction) may operate at different scales.

In percolation theory, abrupt discontinuity of landscape configuration is implicit at moderate to high levels of habitat loss (because the largest patch no longer percolates across the landscape). In Keitt *et al.*'s study, patch isolation is of secondary importance to connectivity at finer scales. Keitt *et al.* find that below the percolation threshold, patch area is the most important component of connectivity. The emphasis on patch area corroborates evidence from simulations that show that, at low habitat amounts, habitat aggregation lowers the habitat supply threshold. By demonstrating that landscape configuration is of little importance below the fragmentation threshold, Keitt *et al.*'s results appear to contradict the predictions of percolation theory. In fact Keitt *et al.*'s findings focus on a sub-component of fragmentation and habitat loss — patch area. Research in an experimental model system may offer insight into

---

[7] Landscape connectivity is measured as the average distance an individual, if placed randomly in the landscape, is capable of dispersing before reaching a barrier.

the findings of Keitt *et al.*'s system (Wiens *et al.* 1997). Studying beetle movements in a grassland/sand matrix, Wiens *et al.* (1997) concluded that spatial arrangement appeared to be important only after basic habitat area needs were met.

Quantifying the importance of connectivity to dispersal is difficult, because connectivity is a poorly defined concept.

The apparent contradiction between the theory and modeling results demonstrated by Keitt *et al.* (1997) also highlights a weakness in many dispersal studies: connectivity is a poorly defined concept (Tischendorf and Fahrig 2000; Goodwin and Fahrig 2002). Landscape connectivity is the study of both structural and functional elements in a landscape. Landscape connectivity links landscape structure to movement details at the species level (Taylor *et al.* 1993), and is by definition a species-specific phenomenon (Wiens 1989; Wiens and Milne 1989). However, in a literature review on the usage and measurement of landscape connectivity, Tischendorf and Fahrig (2000) find the literature frequently divided among the study of either one or the other of the structural or functional aspects of connectivity. The lack of consistency in the study of connectivity has led to the emergence of incoherent patterns from the literature (Tischendorf and Fahrig 2000). A study comparing results from different, commonly-used connectivity metrics further demonstrates how estimates of landscape connectivity vary, depending on the metric used (Goodwin and Fahrig 2002). Tischendorf and Fahrig (2000) call for a narrower use of the term "connectivity" than that currently found in the literature, suggesting that the term should be restricted to describe the "…degree to which the landscape facilitates or impedes movement among resource patches…" They also suggest standardization of empirical and modeling methods to facilitate comparisons of results (Tischendorf and Fahrig 2000).

Dispersing species may respond to habitat quality, not just quantity; therefore, superior dispersal ability may not overcome habitat degradation.

The positive relationship between successful dispersal and habitat availability is well demonstrated for numerous groups of taxa at many different scales (Gaston and Lawton 1990). Debate exists about the processes or mechanisms through which this pattern arises (see Venier and Fahrig 1996 for a review of competing theories). In their study of dispersal and habitat components, Venier and Fahrig (1996) elegantly demonstrate the relationship between dispersal and habitat availability, showing that dispersal ability *per se* is insufficient to explain the positive relationship between species abundance and species distribution (Venier and Fahrig 1996) (see Section 5.2, Reproductive Traits for more about this study). Venier and Fahrig (1996) build on Hanski *et al.*'s (Gyllenberg and Hanski 1992; Hanski *et al.* 1993) metapopulation hypothesis: that differences in species movement patterns explained the positive relationship between species abundance and distribution. Venier and Fahrig (1996) propose a mechanism to explain Hanski *et al.*'s observed differences in species movement patterns: breeding habitat availability. Venier and Fahrig model the effect of variation in habitat availability on abundance and distribution, and demonstrate a positive relationship between the availability of breeding habitat and the number of successful dispersers. The relationships between breeding habitat and abundance, and breeding habitat and distribution, both demonstrated threshold behaviour at lower levels of breeding habitat (Figure 12). Venier and Fahrig's result is significant, because it demonstrates that abundance and distribution cannot be predicted unequivocally by dispersal ability alone

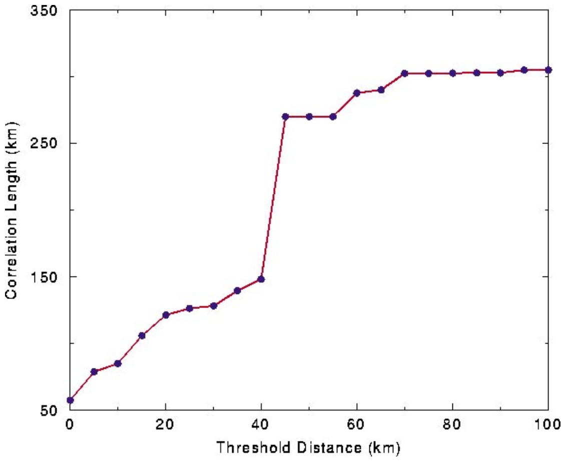


Figure 11. Correlation length of the habitat distribution vs. threshold distance. (Figure 4 in Keitt et al. 1997.)

Reprinted with permission

— habitat quality plays a role. Furthermore, within-species variation in response to habitat alteration is expected in different landscapes — superior dispersal ability will not necessarily overcome habitat degradation (Venier and Fahrig 1996).

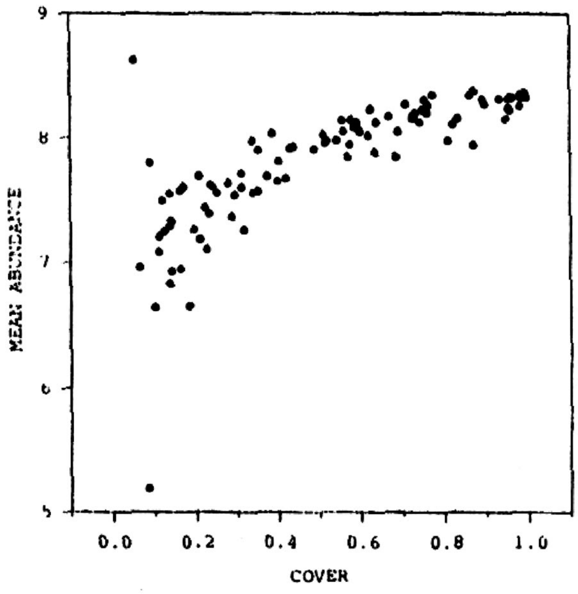
Thresholds in habitat amount and requirements for habitat aggregation depend on species dispersal capability; poor dispersers suffer from the spatial effects of habitat loss at lower levels of habitat loss than do generalist dispersers; however, most species require aggregated habitat when the availability of habitat is low.

Species with large area requirements and low dispersal rates are particularly sensitive to thresholds in habitat loss; thus, these species will exhibit threshold responses to habitat amount at lower levels of habitat loss (McClellan *et al.* 1986; Hanski *et al.* 1995; With and Crist 1995; Andrén 1996). Accordingly, one simulation study shows that, for populations with local dispersal, population density is entirely dependent on the spatial arrangement of habitat, with no effect of habitat amount (Hiebeler 2000). Similarly, King and With (2002) designed a study to discern the conditions (i.e., amount of habitat loss, degree of habitat aggregation, and dispersal behaviour) under which landscape structure affects dispersal success. Overall, dispersal success is highest on contiguous landscapes. In particular, King and With (2002) show that when the amount of habitat is low (<30-40%), habitat aggregation is important for all dispersal types. Above 40% habitat, spatial pattern generally matters less, although habitat aggregation is always important for weak dispersers, unless habitat availability is very high (≥80%). With and Crist (1995) also modeled the effect of dispersal capability, finding that limited dispersal ability results in a requirement for aggregated habitat at a lower level of habitat removal, compared to the connectivity requirements of generalist dispersers. With and Crist's (1995) modeling results are corroborated by an empirical test of movement behaviour by grasshoppers (Acrididae spp.) in shortgrass prairie (see Section 5.3, Rarity, for further discussion about this study).

Ovaskainen *et al.* (2002) also demonstrate that increasing habitat aggregation positively influences metapopulation capacity, and that this increase is more evident for species with short-range dispersal than long-range dispersal. Furthermore, Ovaskainen *et al.* (2002) show that metapopulation size benefits most when the range of habitat aggregation is at least a few times greater than the dispersal range of the species. Another key conclusion is, therefore, that dispersal success may be positively correlated with habitat arrangement at scales beyond a species' home range.

The positive response of species to aggregation of habitat is greatest when the aggregation occurs at a scale a few times greater than the species dispersal range.

While most studies investigated thresholds in patch structure metrics relative to dispersal, several studies explicitly investigated thresholds in the structure of "gaps" or openings within the range of habitat (Dale *et al.* 1994; With and King 1999a; Graham 2001). Inter-patch distance is the measure of a gap. The gap structure of a landscape refers to the distribution of



Reprinted with permission

Figure 12. Mean abundance per occupied breeding cell plotted against COVER (proportion of the total landscape area in breeding habitat) for 100 simulation runs. Data are from the 500th time step for each run. Spearman rank correlation: p = 0.81, p = 0.0001, n = 97. (Figure 3 in Venier and Fahrig 1996.)

Species may exhibit threshold responses to the spatial components of habitat loss because of the movement barriers posed by the structure and size of openings, or "gaps" among habitat patches, rather than in response to patch configuration.

gap sizes, and depends on the amount and pattern of habitat loss (With and King 1999a). With and King (1999a) hypothesized that if dispersal is important to species persistence, and connectivity is scaled with respect to movement behaviour, dispersal success could be predicted with landscape metrics that examine patch and gap structure. In their study modeling dispersal success in fragmented and aggregated habitats, dispersal success exhibits a threshold at low habitat abundance for area-limited dispersers. No thresholds occur in aggregated landscapes using patch-based metrics, although percolation thresholds reflected percolation predictions in fragmented landscapes. On the other hand, With and King's analysis of landscape-level gap structure revealed strong thresholds in the variability of gap sizes at low levels of habitat abundance, corresponding to the region where dispersal success exhibited threshold behaviour. With and King (1999a) concluded that for predicting the consequences of fragmentation, gap structure is a more important determinant than patch structure.

Thresholds in gap size relate to the size of a non-habitat opening that an organism perceives as a barrier to movement. Empirical studies of thresholds in gap size and their influence on behavioural decisions affecting movement are almost exclusively confined to birds (Bowman and Fahrig 2002; Harris and Reed 2002). However, gap thresholds are reported in several empirical studies (Dale *et al.* 1994; Desrochers and Hannon 1997; Jansson and Angelstam 1999; Bélisle and Desrochers 2002; Graham 2001; I present the forgoing studies here, for a review of the literature on gap thresholds related to birds, and findings from a further six studies, see Harris and Reed 2002). In a study set in a fragmented tropical forest landscape, Graham (2001) finds a threshold in cost-distance beyond which Keel-billed Toucans' movements were rare. The cost-distance value was derived from Euclidian distances and a measure of habitat quality. Below the threshold cost-distance, a preference is shown for remnants in close proximity to other remnants and fruit availability, but not for area. Similarly, fine-scale fragmentation is shown to create gap thresholds for species with large area requirements but low gap-crossing ability, under a range of land change scenarios in tropical forest (Dale *et al.* 1994).

Desrochers and Hannon (1997) studied the response of forest songbirds across gaps and through forest to recorded mobbing calls of Chickadees (*Parus atricapillus*)[8] in mixedwood boreal forest and agricultural landscapes near Quebec City. They find non-linear probabilities of response by birds to crossing gaps. Most birds preferred to travel along forested routes, even when shortcuts through openings would reduce travel time by two thirds. Birds responded significantly ($p<0.05$) less to mobbing calls when they were required to cross open vs. forested areas. Birds' reluctance to cross gaps also increased significantly as gap size increased (Desrochers and Hannon 1997).

Bélisle and Desrochers (2002) conducted a study similar to that of Desrochers and Hannon (1997) on resident and migratory bird species in a mixedwood boreal forest / agricultural matrix in Quebec. Bélisle and Desrochers (2002) were interested in whether differences would occur in gap-crossing behaviour between species, between residents and migrants, and between seasons (winter and late summer). Bélisle and Desrochers (2002) found a threshold distance of 25 m from forest edge describing movement choices. Birds prefer to take longer routes under forest cover, even in the presence of short-cuts across gaps. Short-cuts through openings (<25 m) are used in a manner consistent with a trade-off between length of detour relative to length of the short-cut, and suggests a gap crossing threshold of 50 m between forest patches. Species cross in the open at increasing distances from forest edges as the forest detour increases relative to the short-cut in the open. Bélisle and Desrochers (2002) found that their results were generally consistent among species (with the exception of Hairy Woodpeckers [*Picoides villosus*], which travel further in openings), between residents and migrants and between seasons.

---

[8] In British Columbia, this species is known as the Black-capped Chickadee (*Poecile atricapilla*).

In a study of gap-crossing ability of Eastern Chipmunks (*Tamias striatus*) set in upland hardwood forest / farmland in Ontario, Bowman and Fahrig (2002) find no gap or connectivity thresholds, due to the gap being comprised of suitable habitat. Bowman and Fahrig (2002) conclude that this does not dispute findings from an earlier modeling study that demonstrates connectivity thresholds for chipmunks (Henein *et al.* 1998). Bowman and Fahrig (2002) instead suggest that the matrix in their study (pasture grass) is not hostile; hence their studied landscape is still connected.

The role that patch isolation plays in the relationship between habitat loss and fragmentation was nicely demonstrated for Long-tailed Tit populations (*Aegithalos caudatus*) (Jansson and Angelstam 1999). The study examined two landscape variables, distance to next habitat patch, and percent suitable habitat within 1 km^2. The occurrence of Long-tailed Tits was positively related to the amount of habitat within 1 km^2 and negatively related to the distance between habitat patches. When combined, the two variables explained >78% of the variation in local patch occupancy. Distinct thresholds occurred in these landscape variables for the probability of local Long-tailed Tit presence. In the model calibrated with empirical data, the presence probability increased from 0.1 to 0.8 when inter-patch distance decreased from 500 to 100 m with 5% total habitat coverage. With a total proportion of 15% suitable habitat, the same probability jump occurred when inter-patch distance changed from 900 to 500 m. This study demonstrates that, at higher levels of habitat availability, species can persist with greater spacing of habitat patches. Greater habitat availability results in a greater tolerance to habitat isolation.

Summary

Although the research on dispersal thresholds is largely theoretical, some distinct patterns have emerged. One of the strongest is that poor dispersers appear to be affected more detrimentally by fragmentation thresholds than are good dispersers. Accordingly, habitat aggregation appears to mitigate some of the effects of habitat loss, particularly when habitat loss is high, and particularly for poor dispersers. Research demonstrates that differences in the size and isolation of forest patches can account for much of the variability in dispersal success, with closer and larger patches having a significantly greater exchange of dispersing organisms (reviewed by Adler and Nuernberger 1994; see also Gustafson and Gardner 1996). The details of the relative importance of patch size and isolation are inconclusive from the threshold literature. However, a meta-analysis of patch size effects (not specific to the threshold literature) finds that patch size has a greater effect on interior and edge species density (negative and positive effects, respectively) than the effect on density for habitat generalists (Bender *et al.* 1998). Although generally confined to birds, there is substantial empirical evidence about movement barriers that result from behavioural responses to gaps in habitat or patch isolation.

Sudden changes in landscape connectivity and observed variation in the importance of different habitat components, both as a function of scale, are phenomena that are fundamental to determining connectivity thresholds. Species perception of connectivity, defined as dispersal capability, is thus an important consideration for the scale of investigation when examining the effects of habitat loss and fragmentation. However, a systematic approach to studying connectivity is lacking, confusing the interpretation of results from multiple studies (Tischendorf and Fahrig 2000). Dispersal studies further demonstrate that abundance and distribution cannot be unequivocally predicted by dispersal ability alone — habitat quality plays a role. Moreover, within-species variation in response to habitat alteration is expected in different landscapes — superior dispersal ability will not necessarily overcome habitat degradation (Venier and Fahrig 1996). A key conclusion regarding dispersal capabilities and habitat fragmentation is that because the critical connectivity threshold varies by species relative to their perception of the landscape, a single connectivity threshold for an entire community is very unlikely (With and Crist 1995; Debinski and Holt 2000). Likewise, maintaining connectivity for a focal species (*sensu* Lambeck 1997) will not necessarily ensure habitat connectivity for all other species.

5.2 Reproductive Traits

Despite the importance of the variables (e.g., dispersal) tested by spatially explicit population models, reproductive traits tend to be the most important factor influencing habitat thresholds (e.g., Akçakaya and Raphael 1998; With and King 1999a; Donovan and Lamberson 2001; Fahrig 2001; With and King 2001). The ultimate cause of extinction is due to a higher mortality than reproductive rate (Fahrig 2002). Additionally, few studies have clearly demonstrated that reduced dispersal or movement is a primary cause of extinction (Harrison and Bruna 1999). In the following section, I detail studies that link habitat thresholds with reproductive traits, and present examples of persistent, but unviable populations. Empirical studies follow the presentation of modeling research.

Compared to the influence of other factors, reproduction has the greatest relative effect on the threshold in habitat.

A series of spatially explicit simulation models has demonstrated the effect of reproductive parameters on the habitat threshold (Pulliam *et al.* 1992; Fahrig 1998, 2001; With and King 1999a, 1999b, 2001). Two of these are unique in examining fecundity and survival as separate parameters (Pulliam *et al.* 1992; With and King 2001). Pulliam *et al.* (1992) created a spatially explicit model incorporating landscape change as a function of timber harvest and avian demographics, to discern the relative impacts of dispersal, reproductive success, and survivorship on population size and extinction probability. They parameterized the model with Bachman's Sparrow (*Aimophila aestivalis*) life history characteristics. Sensitivity analysis shows that variation in demographic variables affects population size more than variation in dispersal ability. In particular, increasing reproductive success from 0.5 to 1.5 female offspring resulted in a 100% increase in population size, and decreasing juvenile and adult survivorship by 25% resulted in increases in extinction probability of 100% and 400%, respectively (Pulliam *et al.* 1992).

Some of the most useful studies for understanding the influence of ecological thresholds are those that explicitly test competing hypotheses (Pulliam *et al.* 1992; Venier and Fahrig 1996; Fahrig 1998; Fagan *et al.* 2001). For example, the competing hypotheses for the cause of habitat thresholds include fragmentation (Andrén 1994), or species life history traits such as reproduction (Fahrig 1998, 2001). Fahrig (2001) created a spatially explicit simulation model to discern the magnitude of the relative effects of four factors on the habitat threshold: reproductive rate, rate of emigration of the organism from habitat, habitat pattern (fragmentation), and matrix quality. In her study, reproductive rate had the largest potential effect on the habitat threshold, and fragmentation had the least effect (Fahrig 2001).

In another spatially explicit simulation model, reproductive success is more important than dispersal in ameliorating extinction risk for populations in fragmented and aggregated landscapes (With and King 1999b). While fragmented landscapes require higher habitat levels for population persistence, dispersal success is generally high on contiguous landscapes, and thus does not have as great an effect on population persistence as does reproductive output. This is consistent with findings from a source-sink study of highly vagile migratory songbirds, for which reproductive failure is a more serious consequence of habitat fragmentation than is dispersal disruption (Donovan *et al.* 1995). Furthermore, in the modeling study, no threshold effects are found for species with high (>1.10) reproductive output (With and King 1999b).

For mammals, age at first reproduction is one of the primary traits that influences extinction probability.

In the absence of detailed data for population viability analysis, other comparative studies show that reproductive traits can help discern species groups that are particularly extinction-prone (Fahrig 1998; Fagan *et al.* 2001). Fagan *et al.* (2001) classified species into three groups: persistent — those that experience such low variability relative to their growth rates that extinction is highly unlikely regardless of carrying capacity; refuge-dependent — species that experience such high variability relative to growth rate that extinction seems likely regardless of carrying capacity; and carrying capacity-dependent — species with low growth rates and low variability for which habitat size does make a difference. In the latter case, larger populations are better able to withstand higher levels of variability (Fagan *et al.* 1999, cited by Fagan *et al.* 2001). In the case of refuge-dependent species, long-term persistence likely hinges on refugia that support "rescue" populations (*sensu* Brown and Kodric-Brown 1977). Fagan *et al.*

(2001) modeled data on 758 species from the Global Population Dynamics Database, and found, depending on model assumptions, that between 40% and 90% of species require refugia to persist over a 100-year time span, based on extinction probabilities measured when a "variation" threshold, quantified via sampling error (σ), was crossed. For mammals, knowledge of body size, age at first reproduction, and average number of offspring enables prediction of the correct extinction categories for 83% of species.

Aggregating landscape structure improves reproductive output.

With and King (2001) used a spatially structured demographic model to examine the habitat threshold. Their approach was unique because it explicitly incorporated the effect of patch structure on reproductive success, as well as examining fecundity and survival as separate parameters. They used reproductive output (Ro) to elucidate source (Ro>1) and sink (Ro<1) habitats, and to indicate species edge sensitivity. Reproductive output was highest on aggregated landscapes (i.e., landscapes with low fragmentation), and lowest on landscapes with high fragmentation. Additionally, the effect of edge sensitivity on reproductive output had the greatest influence on whether species persisted in a given landscape, affecting primarily the level at which thresholds in population persistence occurred in random landscapes. With and King (2001) found that thresholds of habitat loss for population persistence, defined by the net lifetime reproductive output, ranged widely (between 5 and 90%), depending on species edge sensitivity, with low edge-sensitive species not persisting when the landscape had <40% habitat, regardless of habitat configuration (With and King 2001). Their findings caused the authors to caution against the application of "cookbook prescriptions" (e.g., the 20% rule) with respect to management targets (With and King 2001).

The strict influence of fragmentation appears to influence extinction tendency only under a narrow range of conditions.

Fahrig (1998) also links particular reproductive characteristics to extinction tendency. She uses a spatially explicit simulation model to examine the effects of breaking apart (fragmenting) breeding habitat. No loss of habitat occurs in this model. The combined effects of the following narrow range of conditions create population vulnerability: (1) inter-generational dispersal is about 1-3 times the expected nearest distance between breeding sites; (2) the breeding habitat of the organism is low (covers less than 20% of the landscape); (3) the habitat is not ephemeral; (4) the organism has high breeding site fidelity; and (5) a hostile matrix results in higher mortality than that in breeding habitat areas (Fahrig 1998). Strictly examining the effect of fragmentation in this study helps to focus on the conditions that require spatially explicit models, suggesting that simpler, spatially implicit models have wide application (Fahrig 1998).

Species may respond to the availability of breeding habitat as well as to the abundance of habitat.

Venier and Fahrig (1996) examined three long-standing hypotheses about the positive relationship between species abundance and distribution. The three hypotheses examined were: (1) the sampling hypothesis (Wright 1991); (2) the patterns of resource use (Brown 1984); and (3) the differences among species in movements within metapopulations (Gyllenberg and Hanski 1992). Venier and Fahrig (1996) built on Gyllenberg and Hanski's (1992) prediction, showing that the positive relationship between species abundance and distribution is due to differences among (and within) species movements with respect to breeding habitat availability. In the simulations, thresholds in species distribution and abundance occur when suitable cover (i.e., breeding habitat) in the landscape is just over 20% and 40%, respectively.

Area sensitivity causes birds to seek out the best patches, and may be a strategy to overcome the negative effects of fragmentation.

Donovan and Lamberson (2001) also examined the effects of fragmentation on reproductive success. Their study incorporated fecundity patterns and area sensitivity of a hypothetical forest-nesting passerine in a model of fragmentation effects on population growth. Varying the distribution of patch sizes while holding the habitat amount constant created a range of model landscapes, from highly fragmented to continuous. Donovan and Lamberson (2001) find that as landscapes become more continuous (greater number of larger patch sizes), a threshold response of fecundity to patch size causes a threshold increase in population growth. As landscapes become more continuous, area sensitive species respond (seek out and breed in) larger patch sizes, and thus experience greater population growth in fragmented landscapes than do area-insensitive species. Area-insensitive species also nest in larger patches as landscape continuity increases, simply because larger patches become more predominant in the landscape; however, because they differentiate less between nesting sites, they experience lower growth at moderate fragmentation than do area-sensitive passerines. Donovan and Lamberson (2001) perceive species area sensitivity as a strategy to overcome the negative effects of habitat fragmentation on breeding success in birds.

Fecundity was similarly the focus of an empirical study that examined the threshold size required for a patch to function as a source habitat (Burke and Nol 2000). A source habitat is defined as one in which recruitment of young is sufficient to compensate for adult and juvenile mortality (Pulliam 1988) (also see Section 3.5, Metapopulation Theory for a review of source-sink habitats). The focus of their study was forest-breeding songbirds in fragmented upland deciduous forests in south-central Ontario. To maintain sufficient core habitat, the most sensitive species, Ovenbird (*Seiurus aurocapillus*), requires a 500-ha fragment in order for the patch to function as a source habitat in this landscape. In this study, patches below 500 ha act as sink habitats, in that productivity is insufficient to maintain the population. Donovan and Lamberson (2001) and Burke and Nol (2000) demonstrate that reproductive parameters are key to predicting habitat capability, as species may be present in sub-optimal habitat, but incapable of persisting in these habitats without periodic rescue from source habitats.

Reproductive parameters may exhibit threshold declines at lower levels of habitat loss than do presence parameters.

Few empirical studies explicitly link reproduction to thresholds (Lamont *et al.* 1993; Eriksson 1996a, 1996b, 1997; Eriksson and Kiviniemi 1999). Swift and Hannon (2002) find thresholds related to reproductive parameters in a fragmentation threshold study in the Canadian boreal forest (see Section 4.2, Spatial Effects of Habitat Loss, for a detailed description of this study). They detect a rapid decrease in pairing success data for White-breasted Nuthatch between 40% and 60% remaining forest cover. A second species, Downy Woodpecker, displays a threshold decrease in mated pair occurrence between 20-30% forest cover. Presence thresholds occur at higher levels of habitat loss. Swift and Hannon's (2002) results indicate that reproductive parameters may be early, and more appropriate, warning signals of threshold response to habitat loss.

Abundance measures may also obscure true threats to persistence in the case where long-lived individuals persist on the landscape, but are no longer capable of reproduction.

Abundance measures may obscure thresholds, and hence true threats to persistence, where long-lived individuals persist but are no longer capable of reproduction. Several authors have found that even after reproduction and recruitment are hindered due to habitat loss and fragmentation, several Scandinavian plants persist by way of long-lived life cycle stages, such as dormant seeds and clonal propagules (Lamont *et al.* 1993; Eriksson 1996a, 1996b, 1997; Eriksson and Kiviniemi 1999). Several other authors have noted the potential failure to discern population trends, as a result of the limitation of abundance measures (Schieck *et al.* 1995; Schmiegelow *et al.* 1997).

Reproductive measures are the most relevant to evaluating and determining the probability of species persistence.

Most studies examine population abundance rather than life history parameters. However, population viability is not synonymous with population abundance (van Horne 1983); the importance of reproductive characteristics may be understated. Not only potentially misleading, abundance studies may also miss early warning signals that thresholds are imminent, which reproductive studies may elucidate (e.g., Burke and Nol 2000; Donovan and Lamberson 2001; Swift and Hannon 2002). The fact that reproductive measures have the greatest influence on extinction, taken together with the fact that species presence or abundance is a poor indicator of species viability, indicates that reproductive measures are the most relevant to evaluating and determining the probability of species persistence.

Summary

Reproductive traits tend to be the most important factor influencing habitat thresholds. Modeling demonstrates that, compared to dispersal rates and survival rates, reproductive rates are the most important determinants of population size and persistence probability (Fahrig 2001). Additionally, modeling has highlighted the conditions under which an increase in patch numbers (fragmentation) is most likely to affect breeding success (Fahrig 1998). Investigations of thresholds related to reproduction indicate that habitat amount thresholds are greater than indicated by presence parameters (Swift and Hannon 2002). Reproductive success in a given habitat or patch is the best indicator of habitat suitability, distinguishing source (viable) habitats from sink (unviable) habitats (Donovan and Lamberson 2001; With and King 2001). Reproductive measures thus have the greatest influence on extinction, are early indicators of habitat thresholds, and are also the most relevant to evaluating habitat suitability. Taken together, these results indicate that reproductive measures are the best means to determine species persistence probability in a landscape.

5.3 Rarity

Because forest harvesting is specific to certain habitats (e.g., mature and old-growth forests), habitat specialists may be differentially affected by harvest regimes (Schmiegelow and Mönkkönen 2002). Additionally, habitat loss differentially affects rare species, due simply to chance alone (Conner and McCoy 1979). Clearly, there are exacerbated risks of extirpation and / or extinction for rare species that are mature and old-growth habitat specialists. This group of species falls into one of "seven types of rarity," a classification scheme that enables a qualification of relative rarity based on geographic range, habitat specificity, and local population size (Rabinowitz 1986). Rarity, including the subset of descriptors defined by Rabinowitz (1986), affects both the location of species-specific thresholds and the nature of species response to habitat loss and fragmentation (With and Crist 1995; Keitt *et al.* 1997; Summerville and Crist 2001). Following is a review of the modeling and empirical research that examines the relationship between thresholds and rarity.

Rare species appear to exhibit a threshold response to habitat loss at an earlier stage of habitat loss than common species.

Two empirical studies examined species loss along habitat-loss gradients, finding that rare species are vulnerable to habitat thresholds at relatively high amounts of habitat (Gibbs 1998; Summerville and Crist 2001). Summerville and Crist (2001) predicted that rare species are more likely to experience threshold area effects, in that they may be absent from habitats with sufficient area to support more common species. In their study of butterflies and skippers in fragmented grassland habitat, fragmentation disproportionately affected rare species. In this landscape, the presence of habitat generalists decreases proportionally to habitat amount, and only rare species show thresholds. No rare species occurred in patches with <40% habitat remaining, and over half of the rare species pool of Lepidoptera were never observed in plots with <60% habitat remaining (Summerville and Crist 2001). Gibbs (1998) investigated a gradient of habitat loss and fragmentation to determine if different amphibian species "dropped out" at different levels of habitat destruction (see Sections 4.1, Effects of Habitat Loss; 5.1, Dispersal; and 5.2, Reproductive Traits for further discussion of this study). Gibbs (1998) found correlation between several species' biological traits, among them habitat specificity, which predisposed woodland amphibians to local extinction resulting from fragmentation.

In a study of birds in the boreal forest, Schmiegelow and Mönkkönen (2002) were interested in discerning thresholds (the inflection point) in species richness accumulation curves, with the notion that these data could inform conservation guidelines with respect to area requirements. The study also examined the features of bird species that would make them sensitive to the loss of old forests. The authors established benchmark communities based on long-term reference data, to establish the expected number of mature and old-forest specialists in samples of varying sizes. Bird species richness and mean annual abundance are higher in the

Canadian than in the Finnish reference area, and the proportion of old-forest specialists differs markedly between the systems. Abundance of old-forest specialists is higher in Canada than in Finland, but the density of these species relative to the larger community is similar (Finland 31%, Canada 30%). A sharp inflection point in the species richness curve and the 90th percentile both occurred at lower sample sizes in Canada relative to Finland. The authors conclude that a certain class of rare species — resident old-growth associates — exhibit the greatest sensitivity to habitat loss due to their lower abundance (Schmiegelow and Mönkkönen 2002). Lower abundance indicates that a greater amount of habitat is required to maintain a viable population than that required if abundance is higher (Edenius and Sjöberg 1997); and, furthermore, indicates vulnerability to habitat loss due simply to chance alone (Conner and McCoy 1979).

For rare species, the abundance of habitat is more important than the configuration of habitat.

With and Crist (1995) developed landscape models to identify critical thresholds of habitat loss. They showed that the critical threshold of habitat loss depends on the dispersal range for generalists but not for specialists. Habitat generalists with good dispersal characteristics experience a critical threshold of habitat loss when preferred habitat occupies less than 35% of the landscape; generalists with limited dispersal reach a critical threshold when preferred habitat occupies less than 20% of the remaining landscape. The critical threshold for habitat specialists occurs at a lower level of habitat loss, when preferred habitat occupies less than 40% of the landscape. The critical threshold for habitat specialists is not as dependent on dispersal range because specialists respond primarily to the abundance of preferred habitat. With and Crist (1995) confirmed the predictions of their model with an empirical test examining the distribution of two grasshopper species (*Psoloessa delicatula* and *Xanthippus corallipes*), which encountered different amounts of their preferred habitat.

Using a set of analytical and simulation models, Swihart *et al.* (2001) examined the effect of habitat destruction on predator-prey systems. Their focus was to discern the effect of allowing predators to consume alternative prey (resource supplementation). In their model, a comparison between generalist predators (using resource supplementation) and specialist predators shows that the benefits of resource supplementation to generalist predators increase non-linearly as habitat destruction occurs. Furthermore, the effect of habitat destruction is most pronounced for specialist predators, in that extinction occurs at a lower level of habitat loss (Swihart *et al.* 2001).

Specialist predators experience extinction at lower levels of habitat loss, while generalist predators show a non-linear increase in the benefit of resource supplementation as habitat loss progresses.

Generalizations are equivocal about the vulnerability to extinction based on different types of rarity and specialization.

Modeling and literature reviews[9] that focus on identifying general trends in species vulnerability to extinction show that different systems show different results about the vulnerability of different types of rare species to extinction (McCarthy *et al.* 1997; Tilman *et al.* 1997; Aizen *et al.* 2002). In a modeling study, Tilman *et al.* (1997) examined competitive systems and the prediction of Tilman *et al.* (1994) and Nee and May (1992) that superior competitors are the species most vulnerable to extinction due to habitat loss. Tilman *et al.* (1997) found that the prediction of the vulnerability of superior competitors was robust to a range of modeled parameters, but that, nonetheless, when compared to abundant species, rare species experience thresholds at lower levels of habitat loss (see Section 5.6.1, Competition, for more discussion about this study). Accordingly, McCarthy *et al.* (1997), in a limited literature review examining the findings of Tilman *et al.*'s (1997) work, found that rare species are disproportionately more common on extinction lists and show the greatest vulnerability to extinction in field studies. Aizen *et al.* (2002) focused their review on the

---

[9] These literature reviews are not specific to the threshold literature.

vulnerability of plants and pollinators to extinction caused by habitat loss. Plant-pollinator systems that depend on this mutualism represent the type of rarity described by specificity (Rabinowitz 1986). However, Aizen *et al.* (2002) found no predisposition to fragmentation vulnerability based on existing data on compatibility system and pollination specialization. Self-compatible and self-incompatible plants show similar, negative, significant ($p<0.05$) effects of fragmentation, as do plants requiring specialist and generalist pollinators. Aizen *et al.* (2002) suggested that, because complex interactions occur among species traits, examining only a small subset of traits is unlikely to yield generalizations.

Summary

Rarity affects both the location of species-specific thresholds and the nature of species response to habitat loss and fragmentation (With and Crist 1995; Keitt *et al.* 1997; Summerville and Crist 2001). Modeling shows that habitat specialists experience habitat thresholds at lower levels of habitat loss than those experienced by habitat generalists (With and Crist 1995). Similarly, modeling shows that specialist predators experience habitat thresholds at a lower level of habitat loss than that experienced by generalist predators (Swihart *et al.* 2001). Empirical data show that rare species disappear at lower levels of habitat loss than do generalist species (Gibbs 1998), and that rare species show threshold responses, even when generalist species do not (Summerville and Crist 2001). However, generalizations are equivocal about the vulnerability to extinction based on different types of rarity. In competitive systems, rare species are more susceptible than are common species to habitat loss at lower levels of loss (Tilman *et al.* 1997). On the other hand, the existing literature does not demonstrate a significant relationship between specificity in plant-pollinator systems and vulnerability to extinction in general (Aizen *et al.* 2002). In some cases, specialization likely interacts with other traits to make species more sensitive to habitat loss (Aizen *et al.* 2002). However, rare species are generally prominent in a limited review of field studies reporting vulnerability or extirpation caused by habitat loss (McCarthy *et al.* 1997).

5.4 Geographic Range

The metapopulation model, describing species existence in a patchy habitat network, implies that species distributions do not occur evenly across species ranges. The distribution of resources is not even across landscapes (Holling 1992); hence, response to habitat alteration can differ across the geographic range. Average population density tends to decrease toward range margins, while population variability tends to increase toward range margins (citations in Moilanen *et al.* 1998). Experiments rarely examine a species across its full geographic range; and the omission of some portions of a range can lead to false conclusions about the role a particular species plays in the ecosystem and about its response to habitat loss, including the potential existence of a threshold in habitat requirements (Wellnitz and Poff 2001). In this section, I present studies that consider species persistence in the context of geographic range.

Simple measures of habitat area may be insufficient to predict the effects of habitat loss, because habitat loss has different effects on populations, depending on where the habitat loss occurs.

Studies of species tendency toward extinction often do not consider geographic range. Several studies have used species-area relationships to predict species extinction based solely on the amount of habitat reduction (e.g., Pimm and Askins 1995; Pimm *et al.* 1995; Brooks *et al.* 1997; Pimm 1998 cited by Ney-Niefle and Mangel 2000). However, assumptions in these studies were such that the magnitude of species loss depended only on the quantity of the habitat removed, not on the location of the habitat lost. (Range requirements of species were considered uniform, and species abundance determined which particular species was threatened with extinction.) Contrary to the studies that predict species extinction based solely on the amount of habitat reduction (e.g., Pimm and Askins 1995; Pimm *et al.* 1995; Brooks *et al.* 1997; Pimm 1998), Ney-Niefle and Mangel (2000) assumed that geographic distribution influenced the magnitude of species loss. Ney-Niefle and Mangel (2000) illustrated the importance of geographical distribution by comparing two species that occupy the same proportion of area within a habitat. One species may be confined to a particular region, whereas the other species may be equally distributed — a distribution that will affect response to habitat loss. Ney-Niefle and Mangel (2000) showed that spatial effects such as habitat loss and fragmentation alter species-area relationships and consequently the number of species predicted to be lost due to habitat loss. When the geographic range of a species is included in the species-area relationship, Ney-Niefle and Mangel (2000) showed that the location of habitat loss becomes important, increasing species loss. According to this study, strict interpretation of the species-area relationship is not likely to provide an accurate estimate of the area required to sustain species after habitat loss (Ney-Niefle and Mangel 2000).

Non-uniform behaviour of a species across its distribution suggests that we should treat the species as a separate ecological entity at various points along its range.

Goward (1995) emphasized the importance of considering geographic range with his study of *Nephroma occultum*, a lichen dependent on old-growth forest. He observed that the lichen species did not exhibit uniform behaviour throughout its geographic range. He argued that, because of this lack of uniform behaviour, we should treat the species as a separate ecological entity at various points along its range. According to Goward (1995), considering differing ecological behaviour along a geographic range is of importance because old-growth-dependent lichens in British Columbia are more at risk of local or regional extirpation than any other single group of organisms, since they are highly vulnerable to habitat disruption associated with current forestry practices.

Species may be particularly predisposed to respond negatively to habitat alteration in their range boundaries.

A recent study of the American Pika (*Ochotona princes*) spanning 20 years provides the best mammalian example of classic metapopulation dynamics, and provides insight into metapopulation dynamics in marginal populations (Moilanen *et al.* 1998). Moilanen *et al.* (1998) modeled the importance to the pika's persistence, of single patches in the small network. They found that the stochasticity of extinctions and colonizations amplifies the tendency toward extirpation (Moilanen *et al.* 1998). Their findings also demonstrated that extinction/colonization dynamics could modify the geographical range limit of species. This nicely complements studies of population variability that reveal that density decreases toward range margins, and that variability typically increases toward the range margin (citations in Moilanen *et al.* 1998). Hence, marginal populations, by nature subject to increasing amplitude of fluctuation, may experience boundary shifts in the absence of systematic environmental changes (Moilanen *et al.* 1998). Species may thus be particularly predisposed to respond negatively to habitat alteration in their range boundaries.

Summary

Population density is not constant across the geographic range of a species. Average population density tends to decrease toward range margins. Extinction / colonization dynamics can modify the geographical range limit of species. Species may thus be particularly vulnerable to habitat alteration in their range boundaries. Variation in species density across a geographic range and vulnerability at range margins suggest that we should treat a single species as a separate ecological entity at various points along its range. Geographic range is an issue of particular consideration for those species and ecosystems that occur in British Columbia at their distributional limits.

5.5 Metapopulation Structure

Species have minimum requirements for habitat. Hanski *et al.* (1996) use the terms "minimum amount of suitable habitat" (MASH) and "minimum viable metapopulation" (MVM) to describe these threshold conditions. Levins (1969, 1970) implied that MASH was equal to the number of unoccupied but suitable patches present prior to habitat destruction, based on the assumption that, at equilibrium occupancy, a constant number of empty patches will exist in the landscape. By extension, if this number of patches is present in the landscape following habitat destruction, a sufficient condition for metapopulation survival would be met — the so-called "Levins Rule" (Hanski *et al.* 1996). This was a compelling hypothesis because very little information would be required to calculate the threshold amount of habitat necessary for persistence of a species in a fragmented landscape.

In the 35 years since Levins' groundbreaking work, metapopulation structure has been increasingly used to describe species dynamics in patchy environments. The development of metapopulation theory has been stimulated by the goal to improve the predictive ability of metapopulation models. As a result, the Levins model has been modified to incorporate the landscape and species dynamics thought to influence MASH. The most significant advancements to the metapopulation model for predicting MASH incorporate:

- the physical aspect of the patch network (Hanski 1994b, 1999a);
- complex dynamics arising from migration patterns (Hanski *et al.* 1996; Pagel and Payne 1996; Harding and McNamara 2002; Hill *et al.* 2002);
- environmental and demographic stochasticity (Harrison and Quinn 1989; Hanski *et al.* 1996);
- environmental correlation (Frank and Wissel 1998); and
- non-equilibrium dynamics (Lamberson *et al.* 1992; Hanski *et al.* 1996).

These concepts are (re-)defined and the literature is presented below (see also Section 3.0 Review of Related Ecological Theory for concept definitions). Section 3.5 covers the development and current state of metapopulation theory. Current metapopulation modeling research has several branches, including a spatially realistic metapopulation theory (Hanski 2001; Hanski and Ovaskainen 2003), and an approach that links models describing eradication thresholds in epidemiology to wildlife metapopulation studies (Anderson and May 1991; Lawton *et al.* 1994; Nee 1994; Harding and McNamara 2002).

Habitat configuration is shown to influence the threshold amount of habitat required for metapopulation persistence (Adler and Nuernberger 1994; Hill and Caswell 1999; With and King 1999b; Ovaskainen *et al.* 2002). Because the original metapopulation model is aspatial (assumes no effect of space), it does not account for the influence that landscape spatial structure has on metapopulation viability. Independent work by several authors finds a difference between the predictions of spatially implicit metapopulation models (Nee and May 1992) and their spatially explicit counterparts (Dytham 1995a; Moilanen and Hanski 1995; Bascompte and Solé 1996). The spatially explicit models show that the predictions of spatially implicit models (e.g., constant patch occupancy throughout habitat destruction) are not observed, but that the increasing effects of habitat loss (patch isolation) result in a reduction in patch occupancy as habitat loss increases. As patches become more isolated in the landscape, colonization is increasingly unlikely. As a result, the amount of habitat required to maintain populations above the extinction threshold increases with dispersed habitat removal (Dytham 1995b). To increase precision in the estimate of the habitat threshold, metapopulation models have thus evolved to incorporate landscape spatial structure (Hanski 1994, Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001).

Because the increasing effects of habitat loss (patch isolation) result in a reduction in patch occupancy as habitat loss increases, metapopulation models have evolved to incorporate landscape spatial structure

Complex dynamics arising from migration behaviour limit the ability of models to predict threshold conditions (Gustafson and Gardner 1996; Hanski 1999a). For example, model predictions show that if decreased colonization rate is insufficient to compensate for increased extinction rate, regional extirpations (alternate stable equilibria) may result (Hanski 1985) (see also Section 3.3 Systems with Multiple Stabile States for a review of equilibrium concepts). The predictions of Hanski's (1985) model are empirically demonstrated by the extirpation-prone dynamics of forest ground beetles in woodlands fragmented by agriculture in the Netherlands (citations

The minimum conditions for metapopulation persistence are underestimated by the number of empty but suitable patches, depending on the strength of the rescue effect.

in Hanski 1985). Furthermore, a particular case of fluctuating stable states may arise if some sites support large populations, whereas other sites alternate between long-term commonness and rarity due to environmental stochasticity (Hanski 1985). In the latter case, immigration from the large populations periodically "rescues" the smaller populations before they become extinct (Brown and Kodric-Brown 1977).

Hanski *et al.* (1996) find that previous studies (Levins 1969, 1970) likely underestimated MASH because migration dynamics such as the rescue effect were not considered. The rescue effect is operating if migrants are more likely to colonize a patch with a few individuals than they are to colonize an empty patch (Brown and Kodric-Brown 1977). Hanski *et al.* (1996) use existing data for Glanville Fritillary (*Melitaea cinxia*) metapopulations (Hanski 1994b) to explore how MASH and MVM may be estimated. Studies on the butterfly species provide the first empirical evidence of a population persisting as a true metapopulation, and further demonstrate that increasing habitat fragmentation causes declining habitat occupancy and increasing survival threat. Hanski *et al.* (1996) suggest that the Levins model severely underestimated the threshold metapopulation condition because it did not consider the role of occupied patches in decreasing the probability of metapopulation extinction via re-colonization occurring simultaneous to extinction — the rescue effect. Hence, the minimum conditions for metapopulation persistence are underestimated by the number of empty but suitable patches, depending on the strength of the rescue effect.

Another recent study of the American Pika (*Ochotona princes*), spanning 20 years, provides the best mammalian example of classic metapopulation dynamics, and further demonstrates the importance of the rescue effect (Moilanen *et al.* 1998). Moilanen *et al.* (1998) modeled the importance of single patches in the small network to the pika's persistence. They found that the stochasticity of extinctions and colonizations amplified the tendency toward extinction due to rescue effects (Moilanen *et al.* 1998). If not "rescued," a patch could decline rapidly from an apparently stable, occupied state to extinction. Two important conclusions arise from Moilanen *et al.*'s (1998) consideration of rescue effects. If the rescue effect is important in a metapopulation, the threshold metapopulation condition is not met by the fraction of empty patches at equilibrium. Furthermore, stochasticity in the occurrence of the rescue effect can lead to an alternative stable state (extinction) not otherwise accounted for by the extinction rate in Levins' (1969, 1970) metapopulation model.

Movement between patches is complex; the mean time to extinction varies, depending on the assumptions about movement dynamics.

Other studies also address the constraining assumptions about migration in the Levins and subsequent metapopulation models (Pagel and Payne 1996; Harding and McNamara 2002; Hill *et al.* 2002). Harding and McNamara (2002) suggest that the spatially structured metapopulation models are too complex, even while their applicability is limited because population level dynamics (specifically colonization and extinction) are poorly described. Harding and McNamara (2002) suggest that assumptions in the Levins model about migration do not account for a threshold immigration rate above which extinction rate is drastically lower (May 1977). The Levins model also does not account for an increased extinction rate when immigration increases, due to migrants carrying parasites or disease (the "anti-rescue" effect), or for gene flow reducing local adaptation (see references in Harding and McNamara 2002). By relaxing assumptions about migration, and the influence of migration on extinction rate in the Levins model, Harding and McNamara (2002) show that the mean time to extinction varies, depending on the assumptions about migration dynamics. The immigration threshold suggested by May (1977) is shown by Baguette *et al.* (1998) to influence patterns in population establishment. Asynchronous immigration and emigration rates are also modeled to show that estimates of the extinction threshold are significantly influenced if a system is considered "open" to immigration from outside, rather than if it is assumed to be closed (Pagel and Payne 1996).

---

[10] Note that Hill, M. F., A. Hastins, and L. W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. American Naturalist. 160(3):389-402 is paper about fish.

Hill *et al.* (2002) similarly relaxed constraints on the modeling of the rescue effect to determine how actual "straying" rates affect metapopulation persistence.[10] Hill *et al.* (2002) found that there is a threshold rate of dispersal that minimizes extinction probabilities, enabling populations to tolerate habitat change. These modeling approaches (Pagel and Payne 1996; Harding and McNamara 2002) demonstrate that it is increasingly possible to address different conditions of metapopulation structure, and, in doing so, they introduce new techniques to simplify metapopulation modeling, and to link wildlife metapopulation modeling to epidemiology (see below for more discussion on epidemiological models).

Demographic stochasticity implies that extinction can occur despite the availability of suitable habitat.

Stochasticity, with its influence on the tendency toward an alternative equilibrium (e.g., extinction) when the rescue effect is important, has two other important permutations in metapopulation modeling of the habitat threshold. The original Levins model was deterministic, and therefore did not incorporate extinctions that may occur, owing to chance variation in the number of extant populations; a type of demographic stochasticity, termed "colonization-extinction stochasticity" (Hanski 1991). In a spatially realistic metapopulation model for the Glanville Fritillary, Hanski *et al.* (1996) analyzed the results derived from an aspatial, stochastic Levins model (Nisbet and Gurney 1982, cited by Hanski *et al.* 1996). Hanski *et al.* (1996) concluded that incorporating colonization-extinction stochasticity into the metapopulation model highlights the idea that a small number of local populations are subject to increased risk of extirpation. Modeling by Moilanen and Hanski (1995) also showed that when there are few occupied patches in the landscape, there is a high likelihood of metapopulation extinction due to stochastic processes; extinction can occur while there is still suitable habitat available in the landscape.

Environmental stochasticity that is spatially correlated may have a negative influence on metapopulation persistence.

Regional-scale environmental stochasticity has further implications for metapopulation persistence of some organisms. While the original metapopulation model assumed that patches are close enough to exchange organisms, but separated enough to experience extinction independently, the more likely case is that environmental variation is correlated among adjacent habitats (Harrison and Quinn 1989). The persistence of a metapopulation is therefore related to the dispersal capacity of organisms relative to the scale of disturbance (Crowley 1977). Spatially correlated environmental stochasticity is termed "regional stochasticity" (Hanski 1991). Harrison and Quinn (1989) created a spatially homogeneous simulation model to discern the conditions under which regional stochasticity could be expected to influence metapopulation persistence. They showed that when the mean and variance of the probability of subpopulation extinction are both high (e.g., 0.25), and populations are large, regional stochasticity may have a negative influence on the persistence of a metapopulation. Examining empirical values of extinction rate parameters, Harrison and Quinn (1989) concluded that, if representative, the existing (1989) data indicated that regional stochasticity will not have a large effect on the metapopulation persistence times of large vertebrates, except in the case of small local population sizes or under conditions of rare, large-scale catastrophes (Harrison and Quinn 1989, and references therein). On the other hand, extinction rates tend to be high, and have high variation for organisms with short generation times. Terrestrial arthropods fall in this category; the model predicts that regional stochasticity could have a significant impact on groups of these organisms (Harrison and Quinn 1989, and references therein).

In a more recent modeling study, Frank and Wissel (1998) contend that Harrison and Quinn's (1989) result may overlook regional stochasticity that occurs on a smaller scale than that examined by spatially homogeneous models. To quantify "rules of thumb" for management intervention, Frank and Wissel (1998) created a spatially heterogeneous, stochastic metapopulation model. Their goal was to first discern (in a spatially homogeneous environment) which landscape and species properties influenced long-term metapopulation persistence, and then to integrate (account for spatial influence on) these factors in a spatially heterogeneous model, to reveal the set of conditions under which management intervention could be expected to positively influence metapopulation persistence. The spatially homogeneous model reveals that the distance over which environmental correlation occurs (correlation length) is one of three critical properties that influence long-term metapopulation persistence. The critical correlation length is thus taken as a relevant scale of the metapopulation dynamics. The spatially heterogeneous model reveals that only when dispersal range of the species is greater than the correlation length is manipulation of spatial configuration expected to positively influence long-term metapopulation persistence. These studies (Harrison and Quinn 1989; Frank and Wissel 1998) highlight the fact that spatially correlated environmental change can be significant enough to influence estimates of the extinction threshold.

Incorporating the time lags between the disturbance of an ecosystem and the response of the species to the disturbance often shows that species can become extinct long after disturbance occurs.

Upon rejecting the simple hypothesis of the Levins Rule in order to incorporate the rescue effect and environmental stochasticity, Hanski *et al.* (1996) proposed that the number of extant populations, defined by the product of p* (fraction of occupied patches at steady state) and h (number of suitable habitat patches), is the most useful and practical measure to assess the viability of a metapopulation. Nevertheless, Hanksi *et al.* (1996) concluded that this type of assessment assumes that the metapopulation is at a stochastic steady state. Disturbed metapopulations are likely in a non-equilibrium state. In areas with rapid habitat fragmentation, it is likely that metapopulations have not had time to reach a new equilibrium (which may be extinction), resulting in an unsustainably high number of occupied habitat patches in the landscape (Lamberson *et al.* 1992; Hanski *et al.* 1996). Several authors have independently concluded that this condition may lead to a state of "extinction debt" (Hanski 1994c; Tilman *et al.* 1994) (see also Section 3.8 Extinction Debt). Extinction debt refers to situations of habitat loss in which the threshold condition for survival is no longer met, but in which the species have not yet gone extinct due to the time delay in their response to environmental change.

Models calibrated with empirical data have incorporated non-equilibrium dynamics (ongoing landscape change) into studies on the extinction threshold, highlighting some of the dynamics of extinction debt (Lamberson *et al.* 1992; Hanski *et al.* 1996; Eriksson and Kiviniemi 1999). For the Northern Spotted Owl, extinction would take place long (>100 years) after landscape change would have occurred and ceased (Lamberson *et al.* 1992). In this model, occupancy parameters during harvest were unusually high, due to "crowding" of mature owls into remaining habitat during timber harvest; predictions based on these numbers would lead to erroneous conclusions about long-term persistence probability in this landscape. Similarly, metapopulation modeling for the Glanville Fritillary shows a time lag of tens to hundreds of years, between habitat change and extinction (Hanski *et al.* 1996). Hanski *et al.* suggest that the decline to extinction may be slow because the largest populations (possessing the smallest extinction risk) are the last to go extinct. Given the positive relationship between patch size (carrying capacity) and population (Hanski and Ovaskainen 2003, and references therein), this is therefore consistent with Hanski *et al.*'s (1996) interpretation. Another modeling study finds that when the largest patches are removed, metapopulations usually go extinct (Moilanen and Hanski 1995).

Other empirical work has applied the MASH concept by incorporating non-equilibrium dynamics (extinction debt) into a "quasi-equilibrium" habitat threshold estimate (Eriksson and Kiviniemi 1999). These authors propose that plant species are at "quasi-equilibrium" because long-lived life cycle stages mean that occupancy is more likely to remain constant during habitat loss, contrary to model results (see above) that demonstrate that occupancy decreases as habitat becomes increasingly isolated. This apparent resistance to extinction is another example of extinction debt; quasi-equilibrium assumes a delay in extinctions when the fraction of suitable habitat decreases. Eriksson and Kiviniemi (1999) estimated habitat thresholds for metapopulations of plants, using analysis of site occupancy and recruitment of 18 semi-natural grassland species in Scandinavia. For comparison, the habitat threshold was also calculated using equilibrium assumptions. The analysis reveals that for three species in particular (*Agrimonia eupatoria, Antennaria dioica,* and

Gentianella campestris) the landscape contains suitable habitat far below the plants' habitat threshold. Eriksson and Kiviniemi (1999) report that all three of these species are known from other sources to be declining or endangered, corroborating the habitat threshold findings. The quasi-equilibrium habitat threshold is greater than that calculated using equilibrium assumptions, for 16 of 18 plants, corroborating other work that suggests that equilibrium assumptions may underestimate the critical habitat threshold for organisms in changing environments (Eriksson and Kiviniemi 1999).

Species in ephemeral environments may be more sensitive to changes in habitat persistence than they are to the amount or spatial configuration of habitat.

Improving metapopulation model realism with respect to habitat elements has focused primarily on the spatial heterogeneity of habitat (landscape structure), and has ignored temporal heterogeneity or "habitat life span" (Keymer *et al.* 2000). The few metapopulation studies examining the importance of habitat persistence demonstrate that rate of habitat change is important to metapopulation persistence (Hanski 1999a; Keymer *et al.* 2000), and that temporal scale may be relatively more important to metapopulation persistence than spatial scale (Fahrig 1992). Although it is generally agreed that extinction in patches is a critical determinant of metapopulation dynamics, and in fact, given long enough, all populations on all patches will eventually become extinct, the mechanisms of extinction are poorly understood (Mangel and Tier 1994; Hanski 1999a; Harding and McNamara 2002). Some authors suggest that local extinctions may partially or entirely result from habitat change (Hanski 1999a, and references therein). Several studies present models for incorporating future landscape change into the metapopulation model, to evaluate the effect of habitat patch destruction on threshold conditions for metapopulation persistence (Hanski 1999a; Keymer *et al.* 2000). Results of this modeling suggest that species in ephemeral environments are more sensitive to changes in habitat persistence than to the spatial configuration or amount of habitat (Fahrig 1992; Keymer *et al.* 2000). Additionally, related to life history traits such as propagule production rate, there is a critical threshold of habitat change that must not be exceeded if the metapopulation is to persist (Keymer *et al.* 2000). For some species, threshold conditions for persistence are therefore dictated by interdependent rates of habitat change and life history traits (Keymer *et al.* 2000).

A range of tools exists to estimate the threshold for metapopulation persistence.

Lande's (1987, 1988a) derivation of the extinction threshold from Levins' (1969) metapopulation model shows that the threshold amount of habitat required for persistence is equal to the fraction of suitable but unoccupied patches at equilibrium. A similar conclusion is reached for disease control in epidemiology (citations in Lawton *et al.* 1994; Nee 1994; Doncaster *et al.* 1996). Of interest here is the "eradication threshold" — the maximum fraction of a population that can avoid immunization while still eradicating the disease. In epidemiology, the eradication threshold is shown to be equal to the uninfected fraction of suitable hosts. Therefore, the number of individuals that a vaccination program can afford to miss is equal to the unused amount of the disease's limiting resource (citations in Doncaster *et al.* 1996). The eradication threshold is thus equivalent in scope to the habitat threshold, in that a disease can be eradicated (extinction occurs), even when diseased hosts (patches) remain (Nee and May 1992). Specifics of biology (e.g., dispersal rates, dispersal mortality) are apparently irrelevant (cancel each other out), and are ignored in the simplified epidemiological model (citations in Lawton *et al.* 1994; Nee 1994). A qualitative evaluation of results from the simplified model is then made.

The habitat threshold is underestimated by the epidemiological model if habitat destruction causes isolation of remaining patches (the fraction of suitable patches does not remain constant during habitat removal), or if patches are heterogeneously distributed (i.e., if there are spatial effects on colonization rates). The epidemiological model was used to estimate the habitat threshold for hedgehogs (*Erinaceus europaeus*) (Doncaster *et al.* 1996) and plants (Eriksson and Kiviniemi 1999). The simplifying assumption of equilibrium is addressed by a quasi-equilibrium estimate in the plant study (see above; Eriksson and Kiviniemi 1999). In the hedgehog study, isolation of patches due to habitat removal, the rescue effect, and spatial heterogeneity of patches is also simulated using a spatially realistic model (Hanski 1994b) to demonstrate the effect of these factors on the habitat threshold as estimated by the epidemiological model (Doncaster *et al.* 1996). The studies of Doncaster *et al.* (1996) and Eriksson and Kiviniemi (1999) demonstrate that the epidemiological model is a useful tool, although limited in its applicability.

At the other end of the spectrum of tools used to evaluate the threshold condition for metapopulation persistence is Hanski and Ovaskainen's (2000) spatially realistic model, which is calibrated for individual species in individual landscapes. This model approximates the "metapopulation capacity" of individual landscapes by incorporating aspects of landscape structure — habitat amount and spatial structure — from the species perspective (set by dispersal distance), and by incorporating colonization and extinction rates of the focal species (Adler and Nuernberger 1994; Hanski and Ovaskainen 2000). To enable metapopulation persistence in a landscape, the metapopulation capacity (landscape structure) must exceed a threshold value, which is determined by the properties of the focal species (Hanski and Ovaskainen 2000, 2003; Hanski 2001). The metapopulation capacity can be used to rank landscapes for their relative ability to support a given species (even in the absence of data on colonization and extinction rates), or to asses the contribution of individual patches to landscape metapopulation capacity (Hanski 2001; Hanski and Ovaskainen 2003).

Representing an approach of intermediate applicability between the very general and the very specific approaches above is one in which landscape characteristics are combined with "ecological profiles" to develop ecologically scaled landscape indices. (Vos *et al.* 2001). Ecological profiles represent clusters of species that differ in their sensitivity to fragmentation, based on dispersal capability and habitat area requirements. Empirical data and model simulations are then used to determine the variables that best predict metapopulation viability.

Summary

The threshold amount of habitat loss tolerated by a metapopulation varies as a result of patch arrangement, life history characteristics of individual populations, and stochastic influences on extinction and colonization rates. In turn, these factors are influenced by landscape context — species evolve and adapt to the conditions in their local environments, and the same species may use different strategies for persistence in different landscapes. Because human activity in forested landscapes alters the structure of the environment differently than natural disturbance (Hanski 1985; DeLong and Tanner 1996; Edenius and Elmberg 1996), patch size and location dynamics resulting from fragmentation may increase extinction rates (Hanski 1985). A range of tools exists to estimate the threshold for metapopulation persistence, which incorporates the physical aspects of the patch network, the complex dynamics arising from migration patterns, the environmental and demographic stochasticity, the environmental correlation, and nonequilibrium dynamics. These tools range from simple models requiring minimal information (which provide coarse estimates of habitat thresholds), to more complex tools incorporating detail about species and their environments, enabling a more realistic evaluation of landscape metapopulation capacity. The complex model (Hanski and Ovaskainen 2000) is applicable even in the absence of details on colonization and extinction rates, because model calibration can occur with knowledge of only one species parameter — dispersal distance.

5.6 Inter-specific Dynamics

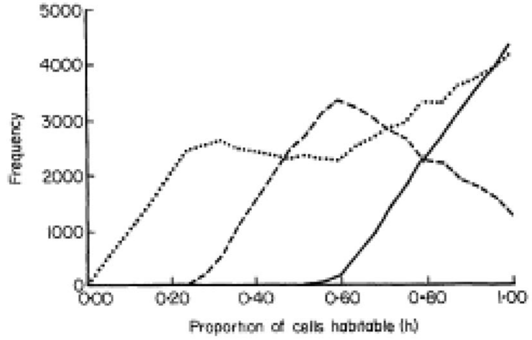
In addition to species-specific responses, the nature of inter-specific interactions such as competition also affects the location of thresholds (Levins 1969; Nee and May 1992; Tilman 1994; Kareiva and Wennergren 1995; Moilanen and Hanski 1995; Debinski and Holt 2000). Inter-specific relationships are of interest to the degree that these relationships influence the habitat threshold. I review here three types of inter-specific interactions: those that occur in competitive systems (Section 5.6.1), plant-pollinator interactions (Section 5.6.2), and keystone species (Section 5.6.3). The influences of predator-prey interactions on habitat thresholds are also of interest, but threshold data were few on this topic, and are not presented here (but see Bascompte and Solé 1998, and see Section 5.2, Reproductive Traits, for Swihart 2001).

5.6.1 Competition

Inter-specific tradeoffs maintain diversity, resulting in an array of species competing for limiting resources (Tilman 1994). These species' competitive abilities predispose them to respond differently to habitat loss. As a result, habitat thresholds differ among species, depending on their competitive ability. Theory predicts that a superior competitor should out-compete all other species for a single limiting resource (see references in Tilman 1994). Experimental data on the native bunchgrass, little bluestem (*Schizachyrium scoparium*), confirm this prediction (Tilman and Wedin 1991; Wedin and Tilman 1993). Given that little bluestem, and most species, occur in diverse communities, species that compete for the same limiting resource in a local area must therefore use different strategies to gain a competitive advantage. Many studies confirm that co-existence is based on inter-specific trade-offs between dispersal ability and competitive ability (see references in Neuhauser 1998 and Tilman 1997). Thus co-existence occurs as long as the inferior competitor (but superior disperser — the so-called fugitive or ruderal species) either disperses more effectively or has a lower patch extinction rate than that of the superior competitor (Moilanen and Hanski 1995). Under this model of community dynamics, species must be dissimilar enough for coexistence to occur (Tilman 1994; Neuhauser 1998). Possible outcomes of habitat destruction on the habitat threshold of species with different competitive abilities are demonstrated by a series of modeling studies on sessile species, presented below (Nee and May 1992; Tilman *et al.* 1994; Dytham 1995a; Moilanen and Hanski 1995; Tilman *et al.* 1997; Klausmeier 1998; Neuhauser 1998). I found no empirical literature that explicitly evaluates the effects of habitat loss on the threshold conditions for species based on competitive ability.

Nee and May (1992) extend Levins' (1969) model of a single species to evaluate the effect of habitat loss on the regional abundance of two competitive species (one competitively inferior, but a superior disperser; the second competitively superior, but an inferior disperser). Nee and May's (1992) spatially implicit model uses simple assumptions about the two species: the inferior competitor cannot invade a patch occupied by the superior competitor, and the superior competitor displaces the inferior competitor during invasion of a patch occupied by the inferior competitor. During the early stages of habitat loss, the superior competitor's abundance is reduced, but, surprisingly, the inferior competitor's abundance increases (Figure 13). This is because habitat destruction effectively lowers the colonization rates of both species, which has the greatest impact on the species with the lower colonization rate (Tilman *et al.* 1994). The inferior competitor benefits more than it loses from habitat destruction because of reduced competition (Moilanen and Hanski 1995). Specifically, the inferior competitor benefits from the early stages of habitat loss because habitat destruction results in reduced density of the superior competitor, while fewer individuals of the superior species attempt births into sites that are already occupied by the inferior competitor (Neuhauser 1998).

Spatially implicit modeling shows that the trade-off between competitive ability and dispersal causes different species to experience the effects of habitat loss differently along a habitat loss gradient.



Reprinted with permission

Figure 13. Number of cells, in a 100 x 100 grid, occupied by the superior competitor, the inferior competitor, colonization rate, or empty, but still available for colonization when habitat patches are permanently destroyed

When the fraction of the number of patches suitable for occupancy falls below a critical value, the superior competitor can no longer persist (Nee and May 1992). Only the inferior competitor persists beyond this point, and the number of patches it occupies declines as habitat decreases further. As habitat destruction continues, the inferior competitor also disappears.

The spatial models agree with the main findings of the aspatial models, in that superior competitors go extinct first, and the inferior competitor initially benefits from habitat destruction.

Two studies extend the spatially implicit model of competitive species (Nee and May 1992), to the spatially explicit case using a cellular automaton model (Dytham 1995a) and to the spatially realistic case (actual patches are modeled by Moilanen and Hanski 1995), the latter using the incidence function model (Hanski 1994b). Incorporating the spatial dimension, Dytham (1995a) and Moilanen and Hanski (1995) use the same simple assumptions about competitive tradeoffs as are modeled in the spatially implicit case by Nee and May (1992). The main difference between the spatially implicit model and those that explicitly incorporate the spatial arrangement of habitat is that dispersal is modeled as a local phenomenon in the latter case. As a result, the inferior competitor (superior disperser) in particular experiences the effect of ongoing habitat loss through the increasing isolation of remaining habitat patches. The spatial models agree with the main findings of the aspatial models, in that superior competitors go extinct first, and the inferior competitor initially benefits from habitat destruction. Although not specific to the case of competition, when only the inferior competitor remains, the spatial models diverge from the aspatial models regarding the effect of habitat destruction on the increasing isolation of patches. Representing a critical breakthrough in modeling the habitat threshold, the spatial models show that increasing isolation increases the proportion of empty patches (Figure 13), whereas the spatially implicit model showed that the proportion of empty patches remained constant as habitat destruction continued and the inferior competitor declined. The effect of patch isolation is to increase the habitat threshold in fragmented habitat; that is, more habitat is required for species persistence than is required if patch isolation is not considered, or if habitat is aggregated (Moilanen and Hanski 1995). (See Section 4.2, Spatial Effects of Habitat Loss, and Section 5.5, Metapopulation Structure, for further discussion on the implications of spatial effects.) In the current context of competition, the main findings of the spatial models (Dytham 1995a; Moilanen and Hanski 1995) with simple assumptions about competitive traits support the results of the aspatial model (Nee and May 1992).

In multi-species models the rank order of competitiveness also predicts the order of extinction, with the best competitor going extinct first, and the poorest competitor going extinct last.

Building on the findings of Nee and May's (1992) spatially implicit model, Tilman *et al.* (1994) extend Levins' (1969) model to the case of *n*-species (multiple competitors). Tilman *et al.*'s (1994) analytical model of *n*-species is also extended to the spatially explicit case in a stochastic cellular automaton model (Tilman *et al.* 1997). In the aspatial model (Tilman *et al.* 1994), species are hierarchically ordered based on their competitive ability, following the simplified assumption (Nee and May 1992) that superior competitors are inferior dispersers. An additional assumption is that abundance is linked to competitive ability, thus the most abundant species are the best competitors and poorest dispersers. The findings of the aspatial *n*-species (Tilman *et al.* 1994) model are consistent with those of the two species models (Nee and May 1992; Dytham 1995a; Moilanen and Hanski 1995). The rank order of competitiveness predicts the order of extinction, with the best competitor going extinct first, and the poorest competitor going extinct last. Additionally, the multi-species model demonstrates that, at higher levels of habitat loss, additional habitat loss results in an increasing number of species extinctions (Figure 6) (Tilman *et al.* 1994). The results of the aspatial n-species model (Tilman *et al.* 1994) are robust over a range of assumptions in the spatial model (Tilman *et al.* 1997). In Tilman *et al.*'s (1997) spatial multi-species model, the best competitors go extinct first whether abundant or rare, given short or long range dispersal, and in clumped, uniform, or randomly fragmented habitat. In the spatial multi-species model, the effect of rarity and, separately, of habitat fragmentation, is to cause extinction at a lower thresholds of habitat loss (Tilman *et al.* 1997).

Under different assumptions about the "rules" of species coexistence, inferior competitors may experience a higher habitat threshold than do superior competitors.

Not all studies are in full agreement with the finding that superior competitors experience extinction first (McCarthy *et al.* 1997; Klausmeier 1998; Neuhauser 1998; Klausmeier 2001). Under different assumptions about the "rules" of species coexistence, inferior competitors may experience a higher habitat threshold than do superior competitors (McCarthy *et al.* 1997; Klausmeier 1998; Neuhauser 1998; Klausmeier 2001). Alternatively, both competitors may go extinct simultaneously (Klausmeier 2001). The models that predict that superior competitors are the most vulnerable to habitat loss assume that community structure results from the competition-colonization trade-off (Nee and May 1992; Tilman *et al.* 1997). Additionally limitations on the similarity between competing organisms (so-called limiting similarity) are necessary, to enable an infinite number of organisms to have sufficient competitive advantage (Tilman *et al.* 1994). Relaxing the assumption of limiting similarity, spatially implicit and explicit models show that the ratios of colonization rates of adjacent species in the competitive hierarchy determines the order of extinction (Klausmeier 1998).

In a second modeling study refuting the argument that superior competitors are the most vulnerable to extinction, Klausmeier (2001) examined community models structured by weak competition or mutualism. Differing from communities structured by competition (Nee and May 1992; Tilman *et al.* 1994), in the Klausmeier (2001) model competition-colonization trade-offs are not required for co-existence. In populations structured by weak competition, poorest dispersers are the species most prone to extinction due to habitat loss (Klausmeier 2001). Because, in this model, poor dispersal ability is not offset by superior competitive ability, a poor disperser may also be a poor competitor. In fact, it is these species, generally defined by the lowest ratio of colonization rate to mortality rate, that experience their habitat threshold first (Klausmeier 2001). Similarly, the "best rule of thumb" suggested by Tilman *et al.* (1997) from their work, is that the species with the poorest dispersal relative to mortality are most susceptible to extinction, whether abundant or rare.

The details of spatial arrangement result in different effects on species with different competitive abilities, based on the relative dispersal ability of the species, compared to the distance between habitable and inhabitable sites.

Extinction probabilities and habitat thresholds of competitors also depend on the spatial details of habitat arrangement (Neuhauser 1998). In an analytical study, Neuhauser (1998) examined the effect of different spatial patterns of habitat destruction (random fragmentation, uniform fragmentation, and clumped fragmentation) on extinction probabilities of superior and inferior competitors. The details of spatial arrangement result in different effects on species with different competitive abilities, based on the relative dispersal ability of the species, compared to the distance between habitable and inhabitable sites. If the distance between habitable and inhabitable patches exceeds the dispersal capability of the superior competitor, but not the superior disperser, the superior competitor is more vulnerable to habitat loss, akin to the results discussed above. This vulnerability is due to the likelihood of the superior competitor dispersing into an inhabitable patch. On the other hand, if the habitat remains connected from the perspective of the limited dispersal range of the superior competitor (i.e., does not reduce the effective dispersal of the superior competitor) the inferior competitor is more vulnerable to habitat loss (Neuhauser 1998).

Another criticism of the model that predicts that superior competitors are the most vulnerable to habitat thresholds is based on the fact that empirical data demonstrate otherwise (McCarthy *et al.* 1997). McCarthy *et al.'s* (1997) limited review of the literature shows that rare species have disproportionately higher representation on extinction lists than do superior competitors. McCarthy *et al.* (1997) also report that rare species suffer greater extirpation in field studies.

However, McCarthy *et al.*'s (1997) results are not incompatible with Tilman *et al.*'s (1997) model predictions, which also demonstrate the greater vulnerability of rare species to extinction, compared to abundant species.

Whether superior or inferior or both, competitors experience higher habitat thresholds depends on the congruency between the modeled rules of species co-existence and the observed ecosystem.

Between the models that predict that superior competitors are most vulnerable to habitat loss and the models that predict otherwise, the critical points of departure are the assumptions about the rules of species coexistence. The general applicability of model findings therefore depends on the general applicability of the differing assumptions. Although critics dispute the general assumption of competitive-colonization trade-off and superior competitor vulnerability, few other hypotheses are advanced by these authors to describe community structure, except communities structured by weak competition (Klausmeier 2001) and mutualistic interactions (Nee *et al.* 1997; Klausmeier 2001). Similarly, although the spatial pattern of habitat loss is shown to influence the relative habitat threshold of superior and inferior competitors, superior dispersers are shown to be more vulnerable to extinction only in the unique case of a habitat loss pattern where habitat remains connected (Neuhauser 1998).

Summary

The effect of species competitive traits on the habitat threshold is found, by theoretical research, to depend on assumptions about the rules of species co-existence. Models that assume that community structure is based on competition colonization trade-offs show that habitat loss and fragmentation result in the extinction of the superior competitor first (Nee and May 1992; Dytham 1995a; Moilanen and Hanski 1995). Models that incorporate different details about species' relative dispersal capability and detail about landscape structure find that these specifics can influence extinction probabilities, and in certain cases, inferior competitors are most vulnerable (Neuhauser 1998; Klausmeier 2001). Therefore, whether superior or inferior or both competitors experience higher habitat thresholds depends on the congruency between the modeled rules of species co-existence and the observed ecosystem. Models agree that whether abundant or rare, and under different assumptions about the spatial pattern of habitat loss, competitors with poor dispersal suffer the highest extinction thresholds (Tilman *et al.* 1997; Neuhauser 1998; Klausmeier 2001). Furthermore, modeled rare species are more vulnerable to habitat thresholds than are abundant species (Tilman *et al.* 1997). Hence the observation by McCarthy *et al.* (1997) — that rare species are disproportionately more affected by extinction than are common species — is not incongruent with the hypotheses about community structure and species extinction probabilities.

5.6.2 Plant-pollinator systems

Plants possess characteristics distinct from those of animals. Reproductive strategies in plants are particularly unique; plants often rely on animals to disseminate pollen and seed, although the occurrence of this strategy decreases as one moves north from the equator (Bawa 1990). Because minimum densities of plants are required to attract pollinators, thresholds are of interest in the context of Allee effects (Bronstein *et al.* 1990; Lamont *et al.* 1993; Lennartsson 2002). Allee effects refer to mechanisms for which an increase in the number or density of an organism results in an increase in the fitness of individuals or populations (Allee 1938; Stephens *et al.* 1999) (also see Section 3.7, Effects on Small Populations, for a discussion about Allee effects). In plants, if the number or density of individuals is not sufficient to attract pollinators, fitness may be reduced because of reduced seed production or inbreeding depression caused by reduced pollen transfer (Lamont *et al.* 1993; Groom 1998; Lennartsson 2002). While plants are often patchily distributed at some spatial scale (see references in Schemske *et al.* 1994), habitat loss and fragmentation alters the patch shape and configuration that naturally occurs (Lamont *et al.* 1993; Lennartsson 2002). In particular, human-induced habitat change alters interactions between plants and pollinators (see references in Lennartsson 2002). If habitat loss and fragmentation result in populations below the threshold size or density to attract pollinators, fitness decreases and extinction risk increases (Lamont *et al.* 1993; Lennartsson 2002). In this section I review some of literature relevant to Allee thresholds in plant-pollinator systems.

Theory predicts that the existence of critical thresholds is a general feature of plant-pollinator systems.

General mathematical models describing Allee effects exist (Dennis 1989), and Ingvarsson and Lundgerg (1995) and Lundberg and Ingvarsson (1998) present analytical solutions and simulation modeling that particularly demonstrate critical thresholds in plant-pollinator systems. Ingvarsson and Lundgerg (1995) demonstrate that a threshold number of pollinators is necessary for long-term plant population persistence. The threshold number of pollinators depends on demographic parameters for both species, and the efficiency of the pollinators' search rate. In a second theoretical plant-pollinator study Lundberg and Ingvarsson (1998) examine the influence of the plant population on pollinators. This analysis demonstrates multiple equilibria in plant-pollinator systems: an unstable domain above which a stable equilibrium corresponding to system persistence is assured, and below which both species tend toward extinction (extinction is also a stable equilibrium) (also see Section 3.3, Systems with Multiple Stable States). Lundberg and Ingvarsson (1998) conclude from the combined results of these theoretical and simulation studies that the existence of critical thresholds is a general feature of plant-pollinator systems.

In empirical studies, plant-pollinator thresholds are associated with population size, and with landscape factors, such as patch size and isolation.

While empirical studies attribute reduced fitness in plant-pollinator systems to Allee effects (Widén 1993), few empirical studies explicitly determine threshold densities or numbers of plants. Similarly, although research links reduced fitness in plant-pollinator systems to reduced patch size (Jennersten 1988; Aizen and Feinsinger 1994a, 1994b; Jacquemyn *et al.* 2002) and patch isolation (Powell and Powell 1987; Jacquemyn *et al.* 2002), empirical studies explicitly linking landscape structure to plant-pollinator thresholds are uncommon. At least four empirical studies (or empirically calibrated simulation models) do find evidence to support the Allee effect and thresholds below which local extinction is inevitable. Thresholds are associated with population size (Bronstein *et al.* 1990), and with landscape factors, such as patch size (Lamont and Klinkhamer 1993; Lamont *et al.* 1993; Groom 1998; Lennartsson 2002) and isolation (Groom 1998).

In a simulation modeling study Bronstein *et al.* (1990) examined the minimum population size necessary to maintain pollinator populations. The African fig tree (*Ficus natalensis*) has temporally separate sexual phases, and wasp pollinators survive only a short time away from trees. Therefore, asynchronous flowering at the population level is required if trees are to outcross, and a minimum population of trees in close proximity is required to maintain wasps throughout the year (Bronstein *et al.* 1990). Bronstein *et al.* (1990) calibrated a stochastic simulation model with data from a population in Gabon to determine this Allee threshold. Simulations showed that 95 trees is the median critical population size to maintain pollinator populations for 4 years for *F. natalensis*. At this population size, no gap in flowering sequence occurs, hence wasps avoid extinction. The model was sensitive to the probability of overlap between male and female flowers on separate trees, resulting in a range of 64-294 trees required for pollinator maintenance. The authors pointed out that the study does not rule out other factors influencing the fig tree population size required for persistence above the Allee threshold, such as (poorly understood) pollinator flight distance (Bronstein *et al.* 1990).

Three studies examine the effect of patch size on plant-pollinator thresholds (Lamont *et al.* 1993; Groom 1998; Lennartsson 2002). Seed production was assessed in all known populations of the woody prostrate species *Banksia goodie* in Australia (Lamont and Klinkhamer 1993; Lamont *et al.* 1993). Reduction in fertile cones in small populations occurs, with no fertile cones found in five of nine of the smallest populations (patches<200 m^2). With a significantly (p=0.004) lower number of seeds per unit population size, small populations do not have the same conservation value as do larger populations (Lamont *et al.* 1993). Additionally, there is an area threshold below which extinction might be inevitable: no fertile cones occur in patches <200 m^2.

Among Banksias, seed set is rare or zero in the absence of pollinators (Ramsey and Vaughton 1991, cited by Lamont *et al.* 1993), and high levels of out crossing are the norm. Because loss of bird pollinators is well known (see references in Lamont and Klinkhamer 1993, Lamont *et al.* 1993), there might be a cascading effect on the reduction of pollination; therefore, pollen transfer may increasingly occur between siblings as population size is reduced, decreasing genetic variability (Lamont and Klinkhamer 1993; Lamont *et al.* 1993).

In a second patch-size study, Lennartsson (2002) examined the effects of patch size and landscape context on Swedish populations of field gentian (*Gentianella campestris*). Fragmentation effects were measured as the amount of grassland in patches of varying (2.5-15 ha) size, and landscape context referred to the amount of semi-natural grassland in the surrounding (1.5 km radius) area. Plants with a reduced ability to self-pollinate show reduced population viability due to inbreeding depression and reduced seed production. These factors are in turn due to pollinator deficit caused by local fragmentation, such that a seed set threshold occurs between 40% and 55% habitat loss. Patch size and landscape context exacerbate fragmentation effects. Extinction (fragmentation) thresholds vary with overall patch area, ranging from thresholds at 65% habitat loss in large (12-15 ha) grasslands, and 30% habitat loss in small grasslands. The effect of landscape context is to lower population viability in landscapes with low amounts (2%-5%) of semi-natural grasslands, compared to landscapes with higher amounts (12%-15%) of grasslands (Lennartsson 2002). Although Lennartsson (2002) attributed the extinction thresholds to fragmentation effects, the effects of habitat amount and fragmentation are confounded (*sensu* Fahrig 2003). The relative amount of grassland in a patch is a proxy for fragmentation; in fact, the thresholds could be a result of pure habitat amount effects.

Groom (1998) also examined the effects of patch isolation on the reproductive success of lovely clarkia (*Clarkia concinna concinna*) in California. Isolation explains, better than patch size or plant size, the level of seed set and the amount of pollen received. Isolation thresholds are evident, and interact with patch size in such a way that isolation effects increase as patch size decreases. For example, pollen receipt declines rapidly beyond an isolation distance of 26 m for tiny patches (containing <10 plants), and the seedset isolation threshold is 16 m for these patches. Small (containing 11-50 plants) patches experience an isolation threshold for pollen receipt at 104 m, whereas no isolation threshold was evident for large (containing >50 individuals) patches. Additionally, more patch extinctions due to reproductive failure occur in small patches than in large, providing weak empirical evidence for Allee thresholds leading to extinction (Groom 1998).

Criteria for ranking the vulnerability of plants to extinction exists.

The degree to which plants are vulnerable to Allee thresholds depends on pollinator specificity and on the degree of dependence on the plant-pollinator mutualism, and the degree of dependence on seeds for dispersal (Bond 1994). Plants most vulnerable to Allee thresholds are therefore those that are dioecious and self-incompatible, those that have a single pollinator, and those that propagate only by seeds (Kearns and Inouye 1997). Many plants may have evolved compensatory mechanisms, which reduce extinction risk (Bond 1994). For example, a plant may require a specific pollinator to produce seeds, but also reproduce clonally. In this case, reproduction can occur in the absence of the specific pollinator. One study suggests that, compared to animals, plants generally possess traits that allow them to persist in remnant populations (Eriksson 1996b). Such plants are more resistant to extirpation or extinction than are other organisms, and this "inertia" may scale up, creating community stability (Eriksson 1996b). Criteria for ranking the vulnerability of plants to extinction exists, incorporating pollinator specificity, dependence on the plant-pollinator mutualism, and dependence on seeds for dispersal (Bond 1994). This model incorporates compensatory mechanisms, enabling a realistic and subjective assessment of extinction risk in plants.

Summary

Allee effects in plant-pollinator systems are important because they lead to patch extinctions (Dennis 1989; Amaraskare 1998; Groom 1998), thereby increasing extinction probabilities for populations at low densities. Modeling demonstrates that Allee thresholds are a general property of plant-pollinator systems (Dennis 1989; Ingvarsson and Lundberg 1995; Lundberg and

Ingvarsson 1998). Empirical data provide compelling evidence for Allee thresholds (Bronstein *et al.* 1990; Lamont *et al.* 1993; Groom 1998). Empirical data show links between patch area and Allee thresholds for specific plants (Lamont *et al.* 1993; Groom 1998; Lennartsson 2002). For the studied species, isolation of patches exacerbates the detrimental effects of patch size (Groom 1998; Lennartsson 2002), demonstrating the importance of landscape context. The importance of Allee effects in native plants of British Columbia is poorly studied; hence, the magnitude of Allee effects is unknown. However, occurrence in small, isolated patches characterizes the natural distribution of many native plants in British Columbia; additionally, the conservation status of approximately 10% of the rare and endangered plants in British Columbia is the result of habitat loss and fragmentation (Douglas *et al.* 2002). Overall, the vulnerability of plants to Allee thresholds depends on the degree to which reproduction depends on pollinators and seed production (Bond 1994). Ranking criteria exist to aid assessment of plant vulnerability to extinction, incorporating the species traits that lead to Allee thresholds in plant-pollinator mutualisms (Bond 1994).

5.6.3 Keystone species

Broadly defined, keystone species are those that are exceptional within the community for maintaining organization and diversity (Paine 1966, 1969; Mills *et al.* 1993). Keystone species interact with other species in a community or ecosystem via linkages such as predation or pollination. The concept of keystone species arose from the study of predator-removal from a rocky intertidal system (Paine 1966, 1969). In this system, the mechanisms employed by the keystone predator were competition and preferential predation to control the density of a prey species (Paine 1969). The concept of keystone species has since been generalized to describe species involved in other ecosystem interactions, and keystone species are currently defined as those whose impact on the community or ecosystems is disproportionately large relative to their abundance (Mills *et al.* 1993; Power *et al.* 1996).

Establishing which species are keystones is problematic (Mills *et al.* 1993). Keystones vary relative to temporal and spatial scales — a species may act as a keystone in one particular spatial or temporal setting and not in another. This vagary is demonstrated by the first "keystone" described, the starfish *Pisaster ochraceus*, which acts like a keystone in wave-exposed rocky headlands, but shows weak or no evidence of being a keystone in adjacent sheltered habitats (Menge *et al.* 1994, cited by Power *et al.* 1996). Because keystones are context-dependent (Power *et al.* 1996), they are difficult to determine.

Despite its variable nature, the keystone concept exemplifies how small changes in the components of an ecosystem can generate shifts in the properties of the system. The keystone concept suggests that undesirable community- or ecosystem-level effects will accompany the removal of a keystone species. Therefore, where identified, keystones represent a tangible entity around which can occur ecosystem-level planning. This is demonstrated by a simulation model that examined the effects of dispersed habitat removal on the Army Ant (*Eciton burchelli*) in neotropical forest (Boswell *et al.* 1998). The Army Ant creates species diversity by modifying the habitat mosaic. Using a spatially explicit model, the authors showed that dispersed habitat loss and fragmentation cause a fragmentation threshold. Removing habitat in larger blocks increases the number of colonies at a given level of habitat loss. As a result of their model findings, the authors suggested a method of habitat removal better suited to maintaining a greater number of colonies than occurs with dispersed habitat loss (Boswell *et al.* 1998).

The keystone concept emphasizes the relative importance of some species in maintaining community or ecosystem properties. Keystones represent a unique type of species interaction. Keystones may interact with one or several species, or interact with habitat, but their presence is important to a wider range of species. Maintaining above-threshold conditions for keystones implies a community or ecosystem level management approach. Conversely, habitat loss exceeding the threshold conditions for keystones has community- or ecosystem-level consequences.

6 SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

6.1 Summary

Thresholds are pervasive in ecosystems, causing rapid change to species and populations.

Thresholds characterize many components of species response to habitat loss in ecosystems. In the ecological literature, the concept of thresholds in the amount of habitat arises in part from the idea that organisms have minimum requirements for habitat. Changes can occur in the amount of suitable habitat that drive population numbers down rapidly (Carlson 2000). Threshold change resulting from habitat loss creates small, unviable populations. Once they become small, threshold declines also characterize the deterioration of populations due to genetic or stochastic factors (Lande 1993; Reed and Frankham 2003).

Habitat loss is the primary cause of the threshold response of species to habitat change.

The focus for this review was the characteristics of habitats and species that cause rapid declines of populations. In particular, I wished to determine the degree to which the existing literature was sufficient to support using the concept of thresholds as a scientific basis for forest management.

The literature on thresholds in habitat suggests that the effects of habitat loss are the primary cause of species decline. Species differ in their requirements for minimum habitat; hence, species loss occurs along a gradient of habitat loss (Gibbs 1998). Empirical evidence shows that species can exhibit threshold responses to the amount of habitat at the landscape level (Hargis *et al.* 1999; Swift and Hannon 2002). Some species also exhibit threshold responses to habitat loss at the stand level (Penteriani and Faivre 2001).

Although data are scarce about the rate of species loss, modeling suggests that the gradient of species loss appears to be an accelerating curve (Tilman *et al.* 1994). Species loss per unit area lost increases along the habitat-loss gradient (Tilman *et al.* 1994). Retaining sufficient habitat and habitat structures at the stand and landscape level is the best strategy to mitigate declines in populations and species.

Reproductive traits tend to be the most important species traits influencing thresholds in habitat amount.

Compared to the influence of other factors, reproduction has the greatest relative effect on the threshold in habitat. The ultimate cause of extinction is due to a higher mortality than reproductive rate (Fahrig 2001). Modeling demonstrates that, compared to emigration and dispersal rates, reproductive rates are the most important determinants of population size and persistence probability (Pulliam *et al.* 1992; With and King 1999b; Fahrig 2001); this emphasizes the importance of habitat quality, as well as the importance of the amount of habitat.

Aggregating landscape structure improves reproductive output (With and King 2001), although modeling also shows that the strict influence of fragmentation on reproductive success appears to influence extinction tendency under only a narrow range of conditions (Fahrig 1998). Species distribution and abundance may respond to the availability of breeding habitat as well as to the amount of habitat more generally (Venier and Fahrig 1996). Additionally, area sensitivity causes birds to seek out the best patches for breeding, and may be a strategy that can to some extent overcome the negative effects of fragmentation (Donovan and Lamberson 2001).

Time lags between habitat alteration and species response constrain the ability to interpret the response of species to landscape change in the present.

Modeling has shown that threshold response can be delayed (Tilman *et al.* 1994). Complex responses to habitat alteration may result in a time delay between cause and effect — the “extinction debt” (Tilman *et al.* 1994). Other modeling suggests that an overabundance of rare species will occur in the time between habitat loss and extinction (Hanski and Ovaskainen 2002). There is also substantial empirical evidence of time lags in ecosystem response to habitat change (Petit and Burel 1998; Hanski 2000; Gu *et al.* 2002). Time-lag concepts are important to ecological thresholds because they mean that we cannot expect the results of habitat loss and fragmentation to be apparent until some undetermined and possibly long time afterwards. The notion of delayed response constrains our ability to interpret what we see in the present landscape.

Because there may be a delay in response to change in ecosystems, reproductive measures are the most relevant to evaluating and determining the probability of species persistence.

Reproductive parameters exhibit threshold declines at lower levels of habitat loss than do presence parameters (Swift and Hannon 2002). Abundance measures may also obscure true threats to persistence in the case where long-lived individuals persist on the landscape, but are no longer capable of reproduction (Carlson 2000). Because most studies examine population abundance rather than life history parameters, and because population viability is not synonymous with population abundance (van Horne 1983), the importance of reproductive characteristics may be understated. Reproductive success in a given habitat or patch is the best indicator of habitat suitability, distinguishing source (viable) habitats, from sink (unviable) habitats (Donovan and Lamberson 2001; With and King 2001). Because there may be a delay in response to change in ecosystems, reproductive traits are a better gauge than are presence parameters of the sufficiency of habitat amount and quality, and are appropriate as early warning signals of habitat thresholds.

Existing data are few, and insufficient to support the general idea of thresholds in fragmentation in forests at a particular, critical probability of habitat loss in forested landscapes.

The influence of secondary effects of habitat loss on habitat thresholds, such as spatial effects, remains unclear. Some authors suggest that thresholds in landscape connectivity, "fragmentation thresholds," accompany moderate to high levels of habitat loss in forests. However, empirical evidence of the spatial effects of habitat loss in real forested landscapes differs from the predictions of the theory. Existing data are few, and insufficient to support the general idea of thresholds in fragmentation in forests at a particular, critical probability of habitat loss in forested landscapes.

Model inadequacy, experimental design, experimental scale, and sampling constrain empirical demonstrations in forests of theoretical thresholds in fragmentation.

I attribute the lack of data on thresholds in fragmentation in forested landscapes primarily to inconsistent use of the term "fragmentation," and to the lack of experimental separation, which flows from the confounded use (Fahrig 2003). Most fragmentation measures are proxies for the loss of habitat; for example, decreases in patch size occur because of habitat loss (Bender *et al.* 1998). The effects of habitat loss thus confound the evidence for thresholds in fragmentation in most studies (Fahrig 2003). Additionally, the idea of thresholds in fragmentation at a critical level of habitat loss is essentially a question of the *amount* of habitat at the landscape level.

Empirical evidence to support thresholds in fragmentation is also inhibited by simplistic modeling analogues and inadequate statistical power in large-scale field experiments. The simplifying assumptions of theoretical models that demonstrate thresholds in fragmentation (e.g., not accounting for the influence of the matrix or forest regrowth) constrain the credibility of these models as analogues for habitat loss. Models also contain high replicates. A basic premise of modeling is repeated "runs" of the model to capture the variation in modeled attributes, as a proxy for repetition of sampling effort. Conversely, repetition of studies at the landscape level is problematic in real landscapes (Summerville and Crist 2001; Fahrig 2003). Issues of statistical power suggest that there is a greater ability for models than for empirical studies to detect a significant effect. Taken together, model inadequacy and sampling issues constrain the ability to observe congruency between results from real and modeled landscapes.

Good evidence exists for thresholds related to the spatial arrangement of habitat in landscapes comprised of forest in an agricultural matrix (Andrén 1994, 1999). This environment, where habitat loss is genuine, more closely resembles the theoretical modeling of the spatial effects of habitat loss. Additionally, considerably more studies of habitat thresholds occur in this landscape than

Landscape context matters. The more substantial empirical evidence relates high levels of habitat loss and spatial factors to threshold responses in population size and species richness in forest/agricultural landscapes.

in forested landscapes. Urban and agricultural developments are among the leading threats to species decline and loss provincially (B.C. Ministry of Water, Land and Air Protection 2002). Habitat restoration will be most effective if augmented with retention of remaining habitat elements and habitat area, particularly in locales with high numbers of threatened and endangered species.

Modeling has been useful for understanding processes and patterns. For example, the spatial arrangement of habitat is shown to influence the habitat amount at which habitat thresholds occur. Spatial modeling shows that in landscapes with dispersed habitat loss, patch isolation causes a greater habitat amount requirement for species persistence (Bascompte and Solé 1996). Accordingly, habitat aggregation lowers the habitat amount threshold (Hill and Caswell 1999). Spatial models also demonstrate that spatial threshold effects are widespread when the amount of habitat remaining in the landscape is low, partly due to the influence of patch size and patch isolation on dispersal (With and King 1999a, 1999b).

Habitat aggregation appears to mitigate some of the effects of habitat loss, particularly at high levels of habitat loss.

Poor dispersers appear to be affected more detrimentally than are good dispersers by thresholds in habitat amount, requiring greater aggregation at lower levels of habitat loss.

Modeling shows that thresholds in habitat amount and the requirements for habitat aggregation depend on species dispersal capability (King and With 2002). Poor dispersers suffer from the spatial effects of habitat loss at lower levels of habitat loss than do generalist dispersers (With and King 1999b). However, dispersal is scale-specific; habitat configuration and thresholds in habitat amount are relevant only at scales consistent with species' perception of the landscape (Wiens *et al.* 1997). The positive response of species to the aggregation of habitat may be greatest when the aggregation occurs at a scale a few times greater than the species' dispersal range (Ovaskainen, 2002 *et al.*).

Quantifying the importance of connectivity to dispersal is difficult, because connectivity is a poorly defined concept (Tischendorf and Fahrig 2000). Dispersing species may respond to habitat quality, not just quantity; therefore, superior dispersal ability may not overcome habitat degradation (Venier and Fahrig 1996). Species may also exhibit threshold responses to the spatial components habitat loss because of the movement barriers posed by the structure and size of openings, or "gaps," among habitat patches, rather than in response to patch configuration (With and King 1999a).

Species may respond more to the quality of habitat patches and to barriers such as openings, than they do to the configuration of patches.

Species vary in their tolerance of edge habitat. Changes in the type and amount of edge are thought to have a large influence on changes to biodiversity (Harrison and Bruna 1999; Kremsater and Bunnell 1999). Modeling suggests that, for some species, sensitivity to edges can be a more important determinant of thresholds in habitat than can sensitivity to area (With and King 2001). Edge density shows threshold changes around critical shapes and sizes of patches. Modeling demonstrates that, for an edge-sensitive species, there is a critical range of fragment sizes in which the impacts of edge effects increase almost exponentially (Laurance and Yensen 1991). Modeling also suggests different thresholds in species tolerance to habitat loss, depending on edge sensitivity (With and King 2001). Similar to its influence on poor dispersers, the aggregation of habitat lowers the amount of habitat loss at which edge-sensitive species experience threshold decline.

Through their influence on the amount of edge in a landscape, the rate, amount, and pattern of habitat loss may cause secondary thresholds in edges.

Habitats vary in the amount of edge they contain. Harvesting rate and pattern influence the amount of edge in the landscape, with rapid, dispersed harvesting resulting in greater amount of edge than slower, aggregated harvesting (Franklin and Forman 1987; Spies *et al.* 1994). In particular, temporal change, which is not included in simple models, can have more influence on the amount of edge than does spatial pattern (Spies *et al.* 1994). Over time, forest regrowth mitigates edge effects, thereby reducing edge width and increasing the forest interior.

Complex population dynamics influence thresholds in response to habitat change for meta-populations with patchy distribution.

Simple models for predicting the threshold persistence of metapopulations fail to capture many important dynamics that influence populations with patchy distribution. Stochasticity in demographic factors implies that extinction can occur while there is still suitable habitat available in the landscape (Moilanen and Hanski 1995). Stochasticity in environmental factors that is spatially correlated may influence populations simultaneously in many patches (Frank and Wissel 1998). Behavioural choices of dispersing individuals are also difficult to quantify; different dynamics arise under different assumptions about emigration, altering the predictions of threshold conditions (Moilanen *et al.* 1998).

The difficulty in modeling movement between patches imposes considerable constraints on studying the influence of the matrix in theoretical and empirically calibrated models.

Movement between patches is complex. In models, the mean time to extinction varies depending on the assumptions about movement dynamics. For some species, matrix quality may influence the rate of emigration and immigration between patches (Fahrig and Merriam 1994; Lamberson *et al.* 1994; Fahrig 2001). Asymmetry occurs in immigration and emigration rates between patches due to irregularities in patch shape, size, and configuration (Gustafson and Gardner 1996). Accurately incorporating matrix effects into modeling studies that examine thresholds has proved to be complex due to the difficulty of modeling movement. Given that mortality rates during movement between patches appear to be a key test of matrix quality (Fahrig 2001), the difficulty in modeling movement imposes considerable constraints on studying the influence of the matrix in theoretical and empirically calibrated models.

If high-quality matrices reduce mortality in the matrix, improvements to matrix quality may result in a lower threshold in habitat amount.

The value of improving the quality of the matrix is clear from many studies (e.g., Lamberson *et al.* 1994; With *et al.* 1999; Fahrig 2001). The matrix may influence thresholds in species response if it is conducive to movement (With *et al.* 1999), particularly if it contains intermediate habitat elements or "stepping stones" to other habitat (Keitt *et al.* 1997). The influence of the matrix on movement of individuals between patches ultimately depends on mortality while in the matrix (Lamberson *et al.* 1994; Fahrig 2001). Higher-quality matrices generally improve movement rates by decreasing the probability of mortality (Fahrig 2001; Vandermeer and Carvajal 2001). Several studies suggest that the relative influence of matrix quality on thresholds in habitat depends on patch isolation (i.e., landscape context), implying that the importance of the quality of the matrix is most pronounced in landscapes with high habitat loss (Gustafson and Gardner 1996; Vandermeer and Carvajal 2001).

Habitat loss has different effects on populations, depending on where the habitat loss occurs.

Population density is not constant across the geographic range of a species. Simple measures of habitat area may be insufficient to predict the effects of habitat loss, because habitat loss has different effects on populations, depending on where the habitat loss occurs (Ney-Niefle and Mangel 2000). Species may be particularly predisposed to respond negatively to habitat alteration in their range boundaries (Moilanen *et al.* 1998).

Rare species display threshold responses at lower levels of habitat loss than do common species.

Habitat loss differentially affects rare species, due simply to chance alone (Conner and McCoy 1979). Modeling (With and Crist 1995) and empirical (Gibbs 1998; Schmiegelow and Mönkkönen 2002) evidence also shows that uncommon species and habitat specialists appear to exhibit a threshold response to habitat loss at an earlier stage of habitat loss than do common species. Additionally, for rare species, the abundance of habitat appears to be more important than the configuration of habitat (With and Crist 1995).

Thresholds in habitat amount may influence species as a consequence of their interaction with other species.

Species interactions also influence threshold responses to habitat loss. Species involved in plant-pollinator interactions depend on the presence of a critical mass of the mutualist species for persistence. Thresholds for plant-pollinator systems are associated with landscape factors, such as patch size (Lamont *et al.* 1993; Groom 1998; Lennartsson 2002) and patch isolation (Groom 1998). Threshold effects in plant-pollinator systems are important because they lead to patch extinctions (Dennis 1989; Amaraskare 1998; Groom 1998), thereby increasing extinction probabilities for populations at low densities.

Whether superior or inferior or both competitors experience higher habitat thresholds depends on the congruency between the modeled rules of species co-existence and the observed ecosystem.

The effect of species' competitive traits on the habitat threshold depends on assumptions about the rules governing species co-existence. In models that assume that community structure is based on competition-colonization trade-offs, it is the species that disperse poorly, but that are superior competitors, that exhibit threshold responses at earlier stages of habitat loss (Tilman *et al.* 1997; Neuhauser 1998). Models that incorporate details about species relative dispersal capability, and about landscape structure, find that these specifics can influence extinction probabilities, and, in certain cases, inferior competitors are most vulnerable (Neuhauser 1998; Klausmeier 2001). Models that examine thresholds for two or more species in competitive systems agree that, whether abundant or rare, and under different assumptions about the spatial pattern of habitat loss, competitors with poor dispersal suffer the highest extinction thresholds (Tilman *et al.* 1997; Neuhauser 1998; Klausmeier 2001).

Threshold studies are not distributed well among species and ecosystems. For application to management, thresholds are relevant primarily within ecosystems with similar disturbance regimes and ecologies, suggesting the need for local work in order to characterize and manage B.C. ecosystems.

The thresholds literature does not equally represent all taxonomic groups. Most studies focus on the threshold response of birds or insects to changes in habitat. Additionally, there is over-representation of individual species in the literature (e.g., Glanville Fritillary and Northern Spotted Owl). Limited taxonomic representation may constrain a general application of the findings from the thresholds literature. Angelstam *et al.* (2001) suggest defining thresholds in habitat through the use of different guilds of species at different spatial scales. The guilds of species should be associated with specific habitat and functional elements in forests. Working on an initiative to characterize thresholds for boreal forests, Angelstam *et al.*'s work (see abstracts in Angelstam and Breuss 2001a)[11] suggests that, for application to management, thresholds are relevant primarily within ecosystems with similar disturbance regimes and ecologies, suggesting the need for local work in order to characterize and support management of B.C. ecosystems.

6.2 Conclusions

Habitat loss is the primary cause of the threshold response of species to habitat change. Species-level details about movement, behaviour, and life history traits demonstrate that threshold responses vary by species. However, threshold changes appear to occur at low levels of habitat loss for rare species, poor dispersers, and habitat specialists. Thresholds are increasingly

---

[11] Papers from this collection of abstracts are just beginning to appear as journal papers (e.g., Angelstam et al. 2003); interested readers can expect more of this work to be available in the near future.

important to other species in forested habitats as habitat loss progresses. Reproductive traits appear to be the life history traits most sensitive to habitat change, and are appropriate as an early indicator of threshold response.

The influence of the spatial features of habitat loss on thresholds in habitat loss is unclear in forested systems. It appears that matrix habitat that is of high quality can mitigate some of the negative, spatial factors associated with thresholds in habitat loss. The spatial features of habitat loss appear to primarily affect poor dispersers and rare species at low levels of habitat loss, and are more widespread at moderate to high levels of habitat loss. Thresholds influenced by the spatial features of habitat loss are predominantly relevant in moderately or heavily disturbed urban and agricultural landscapes, where the loss of habitat is genuine.

The literature on thresholds in habitat amount is currently inadequate to provide a general, quantitative, scientific basis for forest management in B.C. Non-linearity in response and *de facto* thresholds in many variables are pervasive in the literature. However, there is little in the literature to indicate universal thresholds in habitat; there is no general consistency as to when thresholds occur numerically across species and ecosystems. Formal evidence for "threshold responses to linear habitat loss" thus remains limited. Rather, the literature shows that systems under management are capable of producing unexpectedly non-linear responses to management actions in surprising circumstances (Holling and Meffe 1996). The range of threshold behaviour demonstrated by the literature can inform a working hypothesis for managing ecosystems and conducting research, however, thresholds are relevant primarily within ecosystems with similar disturbance regimes and ecologies, suggesting the need for local work in order to characterize and incorporate thresholds into management of B.C. ecosystems.

6.3 Recommendations to Improve Science Concerning Thresholds

The literature review highlights the following points:

1. Retention of sufficient habitat and habitat elements is the primary means of maintaining species above habitat thresholds. In heavily developed urban and agricultural locales, conservation depends on habitat restoration and habitat retention. Habitat configuration cannot usually mitigate the effects of habitat loss.
2. The range of response reported in the thresholds literature frames a general range of risk associated with progressive habitat change. In the short term, the range of risk demonstrated by the literature can inform a working hypothesis for managing ecosystems and conducting research.
3. In the long term, research would determine habitat thresholds in regional systems. Tools and methods are available to evaluate species threshold requirements, and to evaluate landscapes to determine whether they meet species threshold requirements (see Appendix Table 2).
4. Research would increase understanding about habitat suitability, patch dynamics, species tolerance for matrix habitat, and the efficacy of maintaining habitat elements. Improving modeling to account for these factors will increase the congruency between modeled and real landscapes.
5. Research would increase knowledge about the threshold responses of taxa other than birds and insects.
6. Research and monitoring of species focussed on reproductive traits would provide information about early threshold responses. Simple species occupancy or abundance accounts are insufficient measures of long-term population and habitat viability.
7. Monitoring programs that include the concept of time lags in species response to habitat change would provide insight into the likely, long-term effects of habitat change.
8. Provincially consistent interpretation and application of the term "fragmentation" would be most useful to support management. Studies examining fragmentation effects would be most useful if they used experimental or statistical methods to control for the effects of habitat loss.

REFERENCES CITED*

Åberg, J., G. Jansson, J.E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of Hazel Grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia 103(3):265-269.

Adler, F.R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biol. 45(1):41-75.

Aizen, M.A., L. Ashworth, and L. Galetto. 2002. Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? J. Vegetation Sci. 13(6): 885-892.

Aizen, M.A., and P. Feinsinger. 1994a. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. Ecology 75(2): 330-351.

—. 1994b. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano." Ecol. Appl. 4(2):378-392.

Akcakaya, H.R., and M.G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conserv. 7(7):875-894.

Allee, W.C. 1938. The social life of animals. W.W. Norton & Co., New York, NY. (Article not seen, citation from Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3(4): 481-538.)

Allen, C.R., E.A. Forys, and C.S. Holling. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems 2:114-121.

Amaraskare, P. 1998. Allee effects in metapopulation dynamics. Am. Nat. 152(2):298-302.

Anderson, R.M., and R.M. May. 1991. Infectious diseases of humans. Oxford Univ. Press, Oxford, England.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71(3):355-366.

—. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos 76(2):235-242.

—. 1997. Habitat fragmentation and changes in biodiversity. Ecol. Bull. 46:171-181.

—. 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. Oikos 84(2): 306-308.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos 80(1):193-196.

Andrewartha, H.G., and L.C. Birch. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago, IL. (Book not seen, citation from Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics — brief-history and conceptual domain. Biol. J. Linn. Soc. 42(1-2): 3-16.)

Angelstam, P. 2001. Habitat thresholds and landscape patch dynamics explain the distribution and abundance of Tetraonid birds in boreal forest. Page 23 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., and S. Bleckert. 2001. The biodiversity threshold index — towards a quantitative integrated assessment of forest biodiversity. Page 38 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., and G. Jansson. 2001. Effects of habitat thresholds and the dynamics of old deciduous forest patches on the occurrence of resident bird species in boreal forest. Page 21 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

****Please Note: some URLs link only to the home page of an organization - the path shown may be the result of a search feature within the site, which must be followed each time the site is visited.***

Angelstam, P., S. Boutin, L. Fahrig, G. Mikusiñski, and I. Storch. 2001a. Response variables for analyses of habitat thresholds at the landscape scale. Page 12 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., A. Bjärvall, R. Franzén, and G. Mikusiñski. 2001b. Relationships between the amount of old boreal forest in a landscape and the presence of vertebrate predators and herbivores during winter. Page 32 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., M. Breuss, and T. Edman. 2001c. Measuring forest biodiversity at the landscape scale using land use management data and expert knowledge about large birds and mammals. Page 37 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., and M. Breuss, eds. 2001a. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., and M. Breuss. 2001b. A system for measurement of components of boreal and mountain forest biodiversity at the stand scale. Page 36 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Angelstam, P., M. Breuss, G. Mikusiñski, M. Stenström, K. Stighäll, and D. Thorell. 2002. Effects of forest structure on the presence of woodpeckers with different specialisation in a landscape history gradient in NE Poland. Pages 25-38 in Chamberlain, D. and A Wilson, eds. Proceedings of the 2002 annual IALE(UK). University of East Anglia, East Anglia, UK. (Article not seen, citation from Angelstam, P.K., R. Bütler, M. Lazdinis, G. Mikusiñski, and J.M. Roberge. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation-dead wood as an example. Annales Zoologici Fennici 40(6): 473-482.)

Angelstam, P.K., R. Bütler, M. Lazdinis, G. Mikusiñski, and J.M. Roberge. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation—dead wood as an example. Annales Zoologici Fennici 40(6):473-482.

Augustine, D.J., L.E. Frelich, and P.A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecol. Appl. 8(4):1260-1269.

Baguette, M., C. Vansteenwegen, I. Convi, and G. Neve. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. Acta Oecologica-Int. J .Ecol.19(1): 17-24.

Bascompte, J., and M.A. Rodríguez. 2001. Habitat patchiness and plant species richness. Ecol. Letters 4:417-420.

Bascompte, J., and R.V. Solé. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. J. Anim. Ecol. 65(4):465-473.

Bawa, K.S. 1990. Plant-pollinator interactions in tropical rain forests. Ann. Rev. Ecol. Syst. 21:399-422.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conserv. Biol. 7(1): 94-108.

Bélisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecol. 17(3):219-231.

Bellamy, P.E., S.A. Hinsley, and I. Newton. 1996. Local extinctions and recolonisations of passerine bird populations in small woods. Oecologia 108(1): 64-71.

Bender, D.J., T.A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79(2):517-533.

Bender, D.J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecol. 18(1):17-39.

Berec, L., D.S. Boukal, and M. Berec. 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. Am. Nat. 157(2):217-230.

Bertness, M.D., G.C. Trussell, P.J. Ewanchuk, and B.R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology 83(12):3434-3448.

Bierregaard, R.O.J., and T.E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazonica 19(1):215-242.

Bond, W.J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Trans. Royal Soc. London Series B-Biol. Sci. 344:83-90.

Boswell, G.P., N.F. Britton, and N.R. Franks. 1998. Habitat fragmentation, percolation theory and the conservation of a keystone species. Proc. Royal Soc. London Series B-Biol. Sci. 265(1409): 1921-1925.

Bowman, J., and L. Fahrig. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. Can. J. Zoo.-Revue Canadienne De Zoologie 80(9):1556-1561.

Box, G.E.P. 1979. Robustness is the strategy of scientific model building. Pages 201-236 *in* G.N. Wilkinson, ed. Robustness in statistics. Acad. Press, New York, NY.

Boyce, M.S. 1987. A review of the U.S. Forest Services' viability analysis for the Spotted Owl: final report to the National Council of the Paper Industry for Air and Stream Improvement. Unpublished. (Article not seen, citation from Lamberson, R.H., B.R. Noon, C. Voss, and K.S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conserv. Biol. 8(1): 185-195.)

—. 1992. Population viability analysis. Ann. Rev. Ecol. Syst. 23:481-506.

British Columbia Ministry of Water, Land and Air Protection. 2002. Environmental trends in British Columbia 2002. State of Environ. Reporting. Victoria, BC.

Bronstein, J.L., P.-H. Gouyon, C. Gliddon, F. Kjellberg, and G. Michaloud. 1990. The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. Ecology 71(6):2145-2156.

Brooks, T.M., S.L. Pimm, and N.J. Collar. 1997. Deforestation predicts the number of threatened birds in insular southeast Asia. Conserv. Biol. 11: 382-394. (Article not seen, citation from Ney-Niefle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. Conserv. Biol. 14(3):893-898.)

Brooks, T.M., S.L. Pimm, and J.O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13(5): 1140-1150.

Brown, J. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. Am. Nat. 105:467-478.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:225-279.

Brown, J.H., and A.B. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58(2):445-449.

Brown, L. 1985. State of the world 1985: A Worldwide Institute report on progress toward a sustainable society. WW. Norton & Co., New York, NY.

Bryant, A.A. 1996. Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats. Can. J. Zoo. 74:678-687.

Burke, D.M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecol. Appl. 10(6): 1749-1761.

Burkey, T.V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. Oikos 55: 75-81.

Bütler, R., P. Angelstam, P. Ekelund and R. Schlaepfer. 2003b. Dead wood threshold values for the three-toed woodpecker in boreal and sub-Alpine forest. Pages 121-147 *in* Bütler, R. (Ph.D. thesis) Swiss Federal Institute of Technology, Lausanne, Switzerland. Dead wood in managed forests: how much and how much is enough? Development of a snag-quantification by remote sensing & GIS and snag targets based on three-toed woodpeckers' habitat requirements. (Article not seen, citation from Angelstam, P.K., R. Bütler, M. Lazdinis, G. Mikusiñski, and J.M. Roberge. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation—dead wood as an example. Annales Zoologici Fennici 40(6): 473-482.)

Bütler, R., P. Angelstam and R. Schlaepfer. 2003a. Quantitative snag targets for the three-toed woodpecker, *Picoides tridactylus*. Ecological Bulletins 51: [In press]. (Article not seen, citation from Angelstam, P.K., R. Bütler, M. Lazdinis, G. Mikusiñski, and J.M. Roberge. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation — dead wood as an example. Annales Zoologici Fennici 40(6):473-482.)

Buza, L., A. Young, and P. Thrall. 2000. Genetic erosion, inbreeding and reduced fitness in fragmented populations of the endangered tetraploid pea *Swainsona recta*. Biol. Conserv. 93(2):177-186.

Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (*Dendrocopos leucotos*). For. Ecol. Manage. 131(1-3):215-221.

Carlson, A., and I. Stenberg. 1995. White-backed Woodpecker (*Dendrocopos leucotos*)— population and habitat viability analysis (in Swedish). Department of Wildlife Ecology, SLU. Report No. 27. (Report not seen, citation from Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (*Dendrocopos leucotos*). For. Ecol. Manage. 131(1-3):215-221.)

Carroll, J.E., and R.H. Lamberson. 1993. The owls' odyssey — a continuous model for the dispersal of territorial species. Siam J. Appl. Math. 53(1): 205-218.

Chapin, F.S., E.S. Zavleta, V.T. Eviner, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature 405:234-242.

Christensen, N.L., A.M. Bartuska, J.H. Brown, S. Carpenter, C. Dantonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecol. Appl. 6(3):665-691.

Connell, J.H., and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121(6):790-824.

Conner, E.F., and E.D. McCoy. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113:791-833.

Crist, T.O., D.S. Guertin, J.A. Wiens, and B.T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. Functional Ecol. 6:536-544.

Crowley, P.H. 1977. Spatially distributed stochasticity and the constancy of ecosystems. Bull. Math. Biol. 39:157-166.

Curnutt, J.L., S.L. Pimm, and B.A. Maurer. 1996. Population variability of sparrows in space and time. Oikos 76(1):131-144.

Dale, V.H., S.M. Pearson, H.L. Offerman, and R.V. Oneill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. Conserv. Biol. 8(4):1027-1036.

Darveau, M., P. Beauchesne, L. Belanger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. J. Wildl. Manage. 59(1):67-78.

Debinski, D.M., and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14:342-355.

DeLong, S.C. and D. Tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodiv. Conserv. 5:1191-1205.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Nat. Resour. Modeling 3(4):481-538.

Desrochers, A., and S.J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conserv. Biol. 11(5):1204-1210.

Diamond, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol. Conserv. 7:129-146.

Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biol. 41(3):315-336.

Doak, D.F., and L.S. Mills. 1994. A useful role for theory in conservation. Ecology 75(3):615-626.

Doncaster, R.J.R., T. Micol, and J.S. Plesner. 1996. Determining minimum habitat requirements in theory and practice. Oikos 75:335-339.

Donovan, T.M., and R.H. Lamberson. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. Ecology 82(4):1170-1179.

Donovan, T.M., F.R. Thompson, J. Faaborg, and J.R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conserv. Biol. 9(6):1380-1395.

Douglas, G.W., D.V. Meidinger, and J.L. Penny. 2002. Rare native vascular plants of British Columbia. Conservation Data Centre, B.C. Minist. Water, Land and Air Protection, Victoria, BC.

Drapeau, P., A. Leduc, J.F. Giroux, J.P.L. Savard, Y. Bergeron, and W.L. Vickery. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. 70(3):423-444.

Drolet, B., A. Desrochers, and M.-J. Fortin. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. Condor 101(3):699-704.

Dytham, C. 1995a. Competitive coexistence and empty patches in spatially explicit metapopulation models. J. Anim. Ecol. 64:145-146.

—. 1995b. The effect of habitat destruction pattern on species persistence: a cellular model. Oikos 74(2): 340-344.

Edenius, L., 2001. Critical habitat thresholds for the Siberian Jay in boreal forest. Page 24 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Edenius, L., and J. Elmberg. 1996. Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. Landscape Ecol. 11(6):325-338.

Edenius, L., and K. Sjöberg. 1997. Distribution of birds in natural landscape mosaics of old- growth forests in northern Sweden: relations to habitat area and landscape context. Ecography 20(5):425-431.

Egerton, F.N. 1973. Changing concepts of the balance of nature. Q. Rev. of Biol. 48(2):322-350.

Eiswerth, M.E., and J.C. Haney. 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. Ecolog. Econ. 38(2):259-274.

Eriksson, O. 1996a. Population ecology and conservation: some theoretical considerations with examples from the Nordic flora. Symbolae Bonanicae Upsaliensis 31:159-169.

—. 1996b. Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. Oikos 77(2):248-258.

—. 1997. Colonization dynamics and relative abundance of three plant species (*Antennaria dioica, Hieracium pilosella* and *Hypochoeris maculata*) in dry semi-natural grasslands. Ecography 20(6): 559-568.

Eriksson, O., and K. Kiviniemi. 1999. Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. Biol. Conserv. 87(3):319-325.

Fagan, W.F., E. Meir, J. Prendergast, A. Folarin, and P. Karieva. 2001. Characterizing population vulnerability for 758 species. Ecol. Letters 4(2): 132-138.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biol. 41(3):300-314.

—. 1997. Relative effects of habitat loss and fragmentation on population extinction. J. Wildl. Manage. 61(3):603-610.

—. 1998. When does fragmentation of breeding habitat affect population survival? Ecol. Model. 105(2-3):273-292.

—. 2001. How much habitat is enough? Biol. Conserv. 100(1):65-74.

—. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecol. Appl. 12(2):346-353.

—. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34(1):487-515.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conserv. Biol. 8(1): 50-59.

Fahrig, L., and J. Paloheimo. 1988. Determinants of local population size in patchy habitats. Theoretical Population Biol. 34(2):194-213.

Ferson, S., and M.A. Burgman. 1990. The dangers of being few: demographic risk analysis for rare species extinction. Ecosystem Management: Rare Species and Significant Habitats New York State Mus. Bull. 471:129-132.

Fiedler, P.L., and S.K. Jain. 1992. Conservation biology: the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York, NY.

Flather, C.H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. Am. Nat. 159(1):40-56.

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival — from model results to rules of thumb for landscape management. Landscape Ecol. 13(6):363-379.

Frankel, O.H., and M.E. Soulé. 1981. Conservation and evolution. Cambridge Univ. Press, Cambridge, England.

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecol. 1:5-18.

Frelich, L.E., and P. Reich. 1998. Disturbance severity and threshold responses in the boreal forest. Conserv. Ecol. 2(2).

Fryxell, J.M. 2001. Habitat suitability and source — sink dynamics of beavers. J. Anim. Ecol. 70(2):310-316.

Gardner, R.H., B.T. Milne, M.G. Turner, and R.V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecol. 1(1):19-28.

Gardner, R.H., and R.V. O'Neill. 1991. Pattern, process and predictability: the use of neutral models for landscape analysis. Pages 289-307 *in* M.G. Turner. and R.H. Gardner eds. Quantitative methods in landscape ecology. Springer-Verlag, New York, NY.

Gaston, K.J., and J.H. Lawton. 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. Oikos 58(3): 329-335.

Gibbs, J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecol. 13(4):263-268.

Gilpin, M.E., and J.M. Diamond. 1982. Factors contributing to non-randomness in species co-occurrence on islands. Oecologia 52:75-84.

Gonzalez, A. 2000. Community relaxation in fragmented landscapes: the relation between species richness, area and age. Ecol. Letters 3(5):441-448.

Goodwin, B.J., and L. Fahrig. 2002. How does landscape structure influence landscape connectivity? Oikos 99(3):552-570.

Gove, P.B., ed. 1961. Webster's third new international dictionary. G. & C. Merriam Company, New York, NY.

Goward, T. 1995. Nephroma occultum and the maintenance of lichen diversity in British Columbia. Mitteilungen der Eidgenoessischen Forschungsanstalt fuer Wald Schnee und Landschaft 70(1):93-101.

Graham, C.H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conserv. Biol. 15(6):1789-1798.

Grant, W.E., E.K. Pedersen, and S.L. Marin. 1997. Ecology and natural resource management:

systems analysis and simulation. Wiley, New York, NY.

Grimm, V., and I. Storch. 2000. Minimum viable population size of capercaillie Tetrao urogallus: results from a stochastic model. Wildl. Biol. 6(4): 219-225.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 190:323-334.

Groom, M.J. 1998. Allee effects limit population viability of an annual plant. Am. Nat. 151(6): 487-496.

Gu, W.D., R. Heikkila, and I. Hanski. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecol. 17(8):699-710.

Gustafson, E.J., and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of path colonization. Ecology 77:94-107.

Gustafson, E.J., and G.R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecol. 7(2): 101-110.

Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics — a structured model. Theoretical Population Biol. 42(1):35-61.

Hagan, J.M., W.M. Vander Haegen, and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conserv. Biol. 10(1):188-202.

Hager, H.A. 1998. Area-sensitivity of reptiles and amphibians: Are there indicator species for habitat fragmentation? Ecoscience 5(2):139-147.

Haila, Y., and I.K. Hanski. 1984. Methodology for studying the effect of habitat fragmentation on land birds. Annales Zoologici Fennici 21:393-397.

Haila, Y., I.K. Hanski, and S. Raivio. 1983. Turnover of breeding birds in small forest fragments: the sampling colonization hypothesis corroborated. Ecology 74(3):714-715.

Halliday, T. 1978. Vanishing birds: their natural history and conservation. Hold, Rinehart and Winston, New York, NY. (Book not seen, citation from Wilcove, D.S. 1987. From fragmentation to extinction. Nat. Areas J. 7:23-29.)

Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. Ecology 66(2):335-343.

—. 1991. Single-species metapopulation dynamics — concepts, models and observations. Biol. J. Linn. Soc.42(1-2):17-38.

—. 1994a. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecol. and Evol. 9:131-135.

—. 1994b. A practical model of metapopulation dynamics. J. Anim. Ecol. 63:151-162.

—. 1994c. Spatial scale, patchiness and population-dynamics on land. Philosophical Trans. R. Soc. London Ser. B-Biol. Sci. 343(1303):19-25.

—. 1999a. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscape. Oikos 87: 209-219.

—. 1999b. Metapopulation ecology. Oxford Univ. Press, Oxford, England.

—. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37(4):271-280.

—. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88(9):372-381.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics — brief-history and conceptual domain. Biol. J. Linn. Soc. 42(1-2):3-16.

Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pages 106-116 *in* J.D. Schluter, ed. Species diversity in ecological communities: historical and geographical perspectives. Univ. Chicago Press, Chicago, IL.

Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. Am. Nat. 147(4):527-541.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755-758.

—. 2002. Extinction debt at extinction threshold. Conserv. Biol. 16(3):666-673.

—. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biol. 64(1): 119-127.

Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72: 21-28.

Harding, K.C., and J.M. McNamara. 2002. A unifying framework for metapopulation dynamics. Am. Nat. 160(2):173-185.

Harestad, A.S., and F.L. Bunnell. 1979. Home range and body weight — a re-evaluation. Ecology 60(2): 389-402.

Hargis, C.D., J.A. Bissonette, and D.L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. J. Appl. Ecol. 36(1): 157-172.

Harris, R.J. and J.M. Reed. 2002. Behavioral barriers to non-migratory movements of birds. Annales Zoologici Fennici 39:275-290.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biol. J. Linn. Soc. 42:73-88.

—. 1994. Metapopulations and conservation. Pages 111-128 *in* N.R. Webb, ed. Large-scale ecology and conservation biology. Blackwell Sci., Oxford, England.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22(3):225-232.

Harrison, S., and J.F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56(3):293-298.

Harrison, S., and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 *in* M.E. Gilpin, ed. Metapopulation biology: ecology, genetics and evolution. Acad. Press, San Diego, CA.

Havlicek, T.D., and S.R. Carpenter. 2001. Pelagic species size distributions in lakes: Are they discontinuous? Limnology and Oceanography 46(5):1021-1033.

Helle, P. 1984. Effects of area on breeding communities in northeastern Finland. Ann. Zool. Fennici 21: 421-425. (Article not seen, citation from Edenius, L., and K. Sjöberg. 1997. Distribution of birds in natural landscape mosaics of old- growth forests in northern Sweden: relations to habitat area and landscape context. Ecography 20(5):425-431.)

Henein, K., J. Wegner, and G. Merriam. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos 81(1):168-186.

Henle, K., K.F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conserv. 13(1): 207-251.

Heywood, V.H., and I. Baste. 1995. Introduction. Pages 1-19 *in* V.H. Heywood, ed. Global Biodiversity Assessment. Cambridge Univ. Press, Cambridge, England.

Hiebeler, D. 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. Ecology 81:1629-1641.

Hildner, K.K., M.E. Soule, M.S. Min, and D.R. Foran. 2003. The relationship between genetic variability and growth rate among populations of the pocket gopher, *Thomomys bottae*. Conserv. Genet. 4(2): 233-240.

Hill, M., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. Ecol. Letters 2(2):121-127.

Hill, M.F., and H. Caswell. 2001. The effects of habitat destruction in finite landscapes: a chain-binomial metapopulation model. Oikos 93(2):321-331.

Hill, M.F., A. Hastings, and L.W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. Am. Nat. 160(3):389-402.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecol. Syst. 4:1-23.

—. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. 62(4): 447-502.

Holling, C.S., and G.K. Meffe. 1996. Command and control and the pathology of natural resource management. Conserv. Biol. 10(2):328-337.

Holt, R.D., J.H. Lawton, K.J. Gaston, and T.M. Blackburn. 1997. On the relationship between range size and local abundance: back to basics. Oikos 78(1):183-190.

Ingvarsson, P.K., and S. Lundberg. 1995. Pollinator functional-response and plant-population dynamics — pollinators as a limiting resource. Evol. Ecol. 9(4):421-428.

Jacquemyn, H., R. Brys, and M. Hermy. 2002. Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. Oecologia 130(4):617-625.

Jansson, G., and P. Angelstam. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. Landscape Ecol. 14:283-290.

Jennersten, O. 1988. Pollination in *Dianthus deltoides (Caryophyllaceae*): effects of habitat fragmentation on visitation and seed set. Conserv. Biol. 2(4):359-366.

Jones, J.L., E.O. Garton, A.S. Harestad, M.G. Raphael, and R.A. Powell. 1994. Selection of successional stages by fishers in north-central Idaho. Pages 377-390 *in* S.W. Buskirk, ed. Martens, sables, and fishers: biology and conservation. Cornell Univ. Press, London, England.

Jones, K., R. Ellis, R. Holt, B. MacArthur, and G. Utzig. 2002. A strategy for habitat supply modeling for British Columbia — Draft. Final project report-March 2002. Habitat Modeling Steering Comm., Province of British Columbia, Victoria, BC.

Jules, E.S., E.J. Frost, L.S. Mills, and D.A. Tallmon. 1999. Ecological consequences of forest fragmentation in the Klamath region. Nat. Areas J. 19(4):368-378.

Kareiva, P. 1990. Population dynamics in spatially complex environments: Theory and data. Philos. Trans. Royal Soc. London B-Biol. Sci. 330(1257): 175-190.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373(6512):299-302.

Karr, J.R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. Ecology 63:1975-1978.

Kattan, G.H., H. Alvarezlopez, and M. Giraldo. 1994. Forest fragmentation and bird extinctions — San-Antonio 80 years later. Conserv. Biol. 8(1):138-146.

Kearns, C.A., and D.W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. Bioscience 47(5):297-308.

Keith, D.A., T.D. Auld, M.K.J. Ooi, and B.D.E. Mackenzie. 2000. Sensitivity analyses of decision rules in World Conservation Union (IUCN) Red List criteria using Australian plants. Biol. Conserv. 94(3):311-319.

Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conserv. Ecol. 1.

Keymer, J.E., P.A. Marquet, J.X. Velasco-Hernandez, and S.A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. Am. Nat. 156(5):478-494.

King, A.W., and K.A. With. 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? Ecol. Modeling 147:23-39.

Klausmeier, C.A. 1998. Extinction in multispecies and spatially explicit models of habitat destruction. Am. Nat. 152(2):303-310.

—. 2001. Habitat destruction and extinction in competitive and mutualistic metacommunities. Ecol. Letters 4(1):57-63.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure — a hierarchical framework for the study of heterogeneity. Oikos 59(2):253-260.

Kremsater, L.L., and F.L. Bunnell. 1999. Edge effects: theory, evidence and implications to management of western North American forests. *in* J. Wisniewski, ed. Forest fragmentation: wildlife and management implicatons. Brill, Boston, MA.

Kreuzer, M.P., and N.J. Huntly. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. Oecologia 134: 343-349.

Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. Conserv. Biol. 11:849-856.

Lamberson, R.H., R. McKelvey, B. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conserv. Biol. 6(4):505-512.

Lamberson, R.H., B.R. Noon, C. Voss, and K.S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conserv. Biol. 8(1):185-195.

Lambert, W.D., and C.S. Holling. 1998. Causes of ecosystem transformation at the end of the Pleistocene: Evidence from mammal body-mass distributions. Ecosystems 1(2):157-175.

Lamont, B.B., and P.G.L. Klinkhamer. 1993. Population size and viability. Nature 362(6417):211-211.

Lamont, B.B., P.G.L. Klinkhamer, and E.T.F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii* — a demonstration of the Allee effect. Oecologia 94(3):446-450.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. Am. Nat. 130(4): 624-635.

—. 1988a. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia 75(4): 601-607.

—. 1988b. Genetics and demography in biological conservation. Science 241:1455-1460.

—. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nat. 142(6):911-927.

—. 1994. Risk of population extinction from fixation of new deleterious mutations. Evolution 48(5): 1460-1469.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9(4): 1179-1188.

Laurance, W.F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biol. Conserv. 55(1):77-92.

Lavorel, S., R.H. Gardner, and R.V. O'Neill. 1993. Analysis of pattern in hierarchically structured landscapes. Oikos 67:521-528.

Lawton, J.H., S. Nee, A.J. Letcher, and P.H. Harvey. 1994. Animal distributions: patterns and processes. Pages 41-58 *in* N.R. Webb, ed. Large-scale ecology and conservation biology. Blackwell, Oxford, England.

Leimgruber, P., W.J. McShea, and G.D. Schnell. 2002. Effects of scale and logging on landscape structure in a forest mosaic. Environ. Monit. Assessment 74(2):141-166.

Lennartsson, T. 2002. Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. Ecology 83(11):3060-3072.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15:237-240.

—. 1970. Extinction. Lectures on Mathematics in the Life Sciences 2:75-107.

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symposia in Biologia 22:13-24.

Lomolino, M.V., and D.R. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. Ecology 81(6): 1517-1532.

—. 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecol. Biogeography 10(2): 113-132.

Ludwig, D., B. Walker, and C.S. Holling. 1997. Sustainability, stability and resilience. Conserv. Ecol. 1.

Lundberg, S., and P.K. Ingvarsson. 1998. Population dynamics of resource limited plants and their pollinators. Theoretical Population Biol. 54(1): 44-49.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

Mader, H.J. 1984. Animal habitat isolation by roads and agricultural fields. Biol. Conserv. 29:81-96.

Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. Ecology 75:607-614.

Margules, C., A.J. Higgs, and R.W. Rafe. 1982. Modern biogeographic theory: are there any lessons for nature reserve design? Biol. Conserv. 24(2): 115-128.

May, R.M. 1973. Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton, NJ.

—. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269: 471-477.

McCarthy, M.A., D.B. Lindenmayer, and M. Drechsler. 1997. Extinction debts and risks faced by abundant species. Conserv. Biol. 11(1):221-226.

McClellan, C.H., A.P. Dobson, D.S. Wilcove, and J.F. Lynch. 1986. Effects of forest fragmentation on new- and old-world bird communities: empirical observations and theoretical implications. Pages 305-313 *in* C.J. Ralph, ed. Modeling habitat relationships of terrestrial vertebrates. The University of Wisconson Press, Madison, WI.

McIntyre, N.E., and J.A. Wiens. 1999. Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. Oikos 86(1):129-137.

McNaughton, S.J. 1993. Biodiversity and function of grazing ecosystems. Biodiversity and Ecosystem Function.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. Research Branch, Minist. For. Spec. Rep. Ser. 6.

Menge, B.A., E.L. Berlow, C.A. Blanchette, S.A. Navarrete, and S.B. Yamada. 1994. The keystone species concept — variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64(3):249-286. (Article not seen, citation from Power, M.E., D. Tilman, J.A. Estes, B.A. Menge, W.J. Bond, L.S. Mills, G. Daily, J.C. Castilla, J. Lubchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. Bioscience 46(8):609-620.)

Metzger, J.P., and H. Décamps. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecologica 18(1):1-12.

Meyer, W.B., and B.L. Turner. 1992. Human population growth and global land-use/cover change. Annu. Rev. Ecol. Syst. 23:39-61.

Mikusiñski, M., and P. Angelstam. 2001. Effects of forest loss on the distribution of vertebrates with different degrees of habitat specialization in Europe. Page 30 *in* P. Angelstam and M. Breuss, eds. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA. Available on the web at: http://iufro.boku.ac.at/iufro/iufronet/d8/wu80206/pu80206.pdf. Accessed March 1, 2004.

Mills, L.S., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43(4):219-224.

Moilanen, A., and I. Hanski. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. J. Anim. Ecol. 64:141-144.

—. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7): 2503-2515.

Moilanen, A., A.T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. Am. Nat. 152(4):530-542.

Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: A management perspective. Oikos 84(2):302-305.

Muradian, R. 2001. Ecological thresholds: a survey. Ecol. Econ. 38(1):7-24.

Naiman, R., H. Decamps, and F. Fournier. 1989. Role of land/onland water ecotones in landscape management and restoration. Proposals for collaborative research. UNESCO. Mab Digest No. 4. (Report not seen, citation from Metzger, J.P., and H. Décamps. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecologica 18(1): 1-12.)

Nee, S. 1994. How populations persist. Nature 124: 123-124.

Nee, S., and R.M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. J. Anim. Ecol. 61:37-40.

Nee, S., R.M. May, and M.P. Hassell. 1997. Two-species metapopulation models. Pages 123-147 *in* M.E. Gilpin, ed. Metapopulation biology: ecology, genetics, and evolution. Acad. Press, New York, NY.

Neuhauser, C. 1998. Habitat destruction and competitive coexistence in spatially explicit models with local interactions. J. Theoretical Biol. 193(3): 445-463.

Ney-Niefle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. Conserv. Biol. 14(3):893-898.

Nichols, W.R., ed. 2001. Random house Webster's unabridged Dictionary — second edition. Random

House, New York, NY.

Niles & Associates, I. 1996. EndNote Plus 2.1. Niles & Associates, Inc., Berkeley, CA.

Nisbet, R.M. and W.S.C. Gurney. 1982. Modelling fluctuating populations. Wiley, New York, NY. (Book not seen, citation from Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. Am. Nat. 147(4): 527-541.)

Norton, M.R., S.J. Hannon, and F.K.A. Schmiegelow. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography 23(2):209-223.

O'Neill, R.V., S.J. Turner, V.I. Cullinam, D.P. Coffin, T. Cook, W. Conley, J. Brunt, J.M. Thomas, M.R. Conley, and J. Josz. 1991. Multiple landscape scales: an intersite comparison. Landscape Ecol. 5:137-144.

Orbach, R. 1986. Dynamics of fractal networks. Science 231:814-819.

Orians, G.H. 1975. Diversity, stability and maturity in natural ecosystems. Pages 139-150 *in* R.H. Lowe-McConnell, ed. Unifying concepts in ecology. Centre for Agric. Publishing and Documentation, The Hague, Netherlands.

Ovaskainen, O., and I. Hanski. 2001. Spatially Structured Metapopulation Models: Global and Local Assessment of Metapopulation Capacity. Theoretical Population Biol. 60(4):281-302.

—. 2002. Transient dynamics in metapopulation response to perturbation. Theoretical Population Biol. 61(3):285-295.

Ovaskainen, O., K. Sato, J. Bascompte, and I. Hanski. 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. J. Theoretical Biol. 215(1):95-108.

Pagel, M., and R.J.H. Payne. 1996. How migration affects estimation of the extinction threshold. Oikos 76(2):323-329.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

—. 1969. A note on trophic complexity and community stability. Am. Nat. 103:91-93.

Pakkala, T., I. Hanski, and E. Tomppo. 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. Silva Fennica 36:279-288.

Parker, M., and R. Mac Nally. 2002. Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. Biol. Conserv. 105(2):217-229.

Patterson, B.D., and W. Atmar. 1986. Nested subsets and the structure of the insular mammalian faunas and archipelagos. Biol. J. Linn. Soc. 28:65-82.

Penteriani, V., and B. Faivre. 2001. Effects of harvesting timber stands on goshawk nesting in two European areas. Biol. Conserv. 101(2):211-216.

Perry, G.L.W. 2002. Landscapes, space and equilibrium: shifting viewpoints. Prog. Phys. Geogr. 26(3): 339.

Peterman, R.M., W.C. Clark, and C.S. Holling. 1979. Shifting stability domains in fish and insect systems. Pages 321-341 *in* L.R. Taylor, ed. Population dynamics. Blackwell Scientific Publications, Oxford, England.

Peterson, G.D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems 5(4):329-338.

Petit, S., and F. Burel. 1998. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. Agric. Ecosystems & Environment 69(3):243-252.

Pimm, S.L. 1984. The complexity and stability of ecosystems. Nature 307:321-326.

—. 1986. Community stability and structure. Pages 304-329 *in* M.E. Soulé, ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

—. 1991. The balance of nature? University of Chicago Press, Chicago, IL.

—. 1998. Extinction. Pages 20-38 *in* W.J. Sutherland, ed. Conservation science and action. Blackwell Science, Oxford, United Kingdom. (Article not seen, citation from Ney-Niefle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. Conserv. Biol. 14(3): 893-898.)

Pimm, S.L., and R.A. Askins. 1995. Forest losses predict bird extinction in eastern North America. Proceedings of the National Academy of Sciences

92:347-354. (Article not seen, citation from Ney-Niefle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. Conserv. Biol. 14(3):893-898.)

Pimm, S.L., G. Russell, J. Gittleman, and T. Brooks. 1995. The future of biodiversity. Science 269: 347-350. (Article not seen, citation from Ney-Niefle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. Conserv. Biol. 14(3):893-898.)

Pither, J., and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166-174.

Plotnick, R.E., R.H. Gardner, and R.V. Oneill. 1993. Lacunarity indexes as measures of landscape texture. Landscape Ecol. 8(3):201-211.

Powell, A.H., and G.V.N. Powell. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. Biotropica 19(2):176-179.

Power, M.E., D. Tilman, J.A. Estes, B.A. Menge, W.J. Bond, L.S. Mills, G. Daily, J.C. Castilla, J. Lubchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. Bioscience 46(8): 609-620.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. Ecology 43(3):410-432.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am. Nat. 132(5):652-661.

Pulliam, H.R., J.B. Dunning, and J.G. Liu. 1992. Population-dynamics in complex landscapes — a case-study. Ecological Applications 2(2): 165-177.

Rabinowitz, D. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pages 182-204 *in* M.E. Soulé, ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

Raffaelli, D., S. Hall, C. Emes, and B. Manly. 2000. Constraints on body size distributions: an experimental approach using a small-scale system. Oecologia 122(3):389-398.

Raivio, S. 1992. Bird communities in fragmented coniferous forests: the importance of quantitative data and adequate scaling. PhD Thesis. Univ. of Helsinki, Helsinki, Finland. (Thesis not seen, citation from Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: A management perspective. Oikos 84(2):302-305.)

Ramsey, M., and G. Vaughton. 1991. Self-incompatibility, protandry, pollen production and pollen longevity in *Banksia menziesii*. Australian Journal of Botany 39(5):497-504. (Article not seen, citation from Lamont, B.B., P.G.L. Klinkhamer, and E.T.F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii*— a demonstration of the Allee effect. Oecologia 94(3):446-450.)

Reed, D.H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. Conserv. Biol. 17(1):230-237.

Reed, D.H., J.J. O'Grady, B.W. Brook, J.D. Ballou, and R. Frankham. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biol. Conserv. 113(1): 23-34.

Rempel, R.S., D.W. Andison, and S.J. Hannon. 2004. Guiding principles for developing an indicator and monitoring framework. The Forestry Chronicle 80(1):82-90.

Renjifo, L.M. 1999. Composition changes in a Subandean avifauna after long-term forest fragmentation. Conserv. Biol. 13(5):1124-1139.

Restrepo, C., L.M. Renjifo, P. Marples, and R.O. Bierregaard, Jr. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. *In* W.F. Laurance, ed. Frugivorous birds in fragmented neotropical montane forests: Landscape pattern and body mass distribution.

Reunanen, P., and A. Nikula. 1998. Liito-oravan elinymparistot ja maiseman rakenne Kiollismaalla (in Finnish with Swedish summary). Metsahallituksen luonnonsuojelujulkaisuja Sarja A. (Article not seen, citation from Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: A management perspective. Oikos 84(2):302-305.)

Robbins, C.S., D.K. Dawson, and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl. Monog. 103.

Rodríguez, A., and H. Andrén. 1999. A comparison of Eurasian red squirrel distribution in different fragmented landscapes. J. Appl. Ecol. 36(5): 649-662.

Rolstad, J., and P. Wegge. 1987. Distribution and size of Capercaillie leks in relation to old forest fragmentation. Oecologia 72(3):389-394.

—. 1989. Capercaillie *Tetrao urogallus* populations and modern forestry — a case for landscape ecological studies. Finnish Game Research 46:43-52.

Rykiel Jr., E.J. 1996. Testing ecological models: the meaning of validation. Ecological Modelling 90(3):229-244.

Saari, L., J. Aberg, and J.E. Swenson. 1998. Factors influencing the dynamics of occurrence of the Hazel Grouse in a fine-grained managed landscape. Conserv. Biol. 12(3):586-592.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392(6675):491-494.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5:18-32.

Schemske, D.W., B.C. Husband, M.H. Ruckelshaus, C. Goodwillie, I.M. Parker, and J.G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75(3):584-606.

Schieck, J., K. Lertzman, B. Nyberg, and R. Page. 1995. Effects of patch size on birds in old-growth montane forests. Conserv. Biol. 9:1072-1084.

Schmiegelow, F.K.A., C.S. Machtans, and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation ? An experimental study of short-term community responses. Ecology 78: 1914-1932.

Schmiegelow, F.K.A., and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol. Appl. 12:375-389.

Shaffer, M.L. 1980. Bears: their biology and management. Fifth International Conference on Bear Research and Management 5:133-139.

—. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.

Simberloff, D., and J.L. Martin. 1991. Nestedness of insular avifaunas — simple summary statistics masking complex species patterns. Ornis Fennica 68(4):178-192.

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations — the case of the pool frog (*Rana lessonae*). Biol. J. Linn. Soc. 42(1-2):135-147.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry: second edition. Freeman and Co., San Francisco, CA.

Soulé, M.E. 1987. Viable populations for conservation. Cambridge Univ. Press, Cambridge, England.

Spies, T.A., W.J. Riple, and G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4(3): 555-568.

Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effect of edge permeability and habitat geometry on emigration from patches of habitat. Am. Nat. 129:532-552.

Stauffer, D. 1985. Monte-carlo study of biased diffusion at the percolation threshold. J. Physics A-Mathematical and General 18(10):1827-1829.

Stauffer, D., and A. Aharony. 1992. Introduction to percolation theory. Taylor and Francis, London, England.

Stephens, P.A., and W.J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution 14(10):401-405.

Stephens, P.A., W.J. Sutherland, and R.P. Freckleton. 1999. What is the Allee effect? Oikos 87(1): 185-190.

Summerville, K.S., and T.O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (*Lepidoptera)*. Ecology 82(5):1360-1370.

Sutherland, G.D., A.S. Harestad, K. Price, and K.P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv. Eco. 4.

Sutherland, J.P. 1974. Multiple stable points in natural communities. Am. Nat. 108:859-873.

Swift, T.L., and S.J. Hannon. 2002. Critical threshold responses resident birds to forest cover in east-central Alberta. Page 374 *in* T.S. Veeman, P.N.

Duinker, B.J. Macnab, A.G. Coyne, K.M. Veeman, G.A. Binsted, and D. Korber. Proceedings of the 2002 sustainable forest management network conference—advances in forest management: from knowledge to practice, November 2002, Edmonton, AB.

Swihart, R.K., Z. Feng, N.A. Sladea, D.M. Mason, and T.M. Gehring. 2001. Effects of habitat destruction and resource supplementation in a predator-prey metapopulation model. J. Theoretical Biol. 210(3): 287-303.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68(3):571-573.

Terry, E., B.N. McLellan, and G.S. Watts. 2000. Winter habitat ecology of mountain caribou in relation to forest management. J. Appl. Ecol. 37:589-602.

Thomas, C.D., and W.E. Kunin. 1999. The spatial structure of populations. J. Anim. Ecol. 68(4): 647-657.

Thompson, I.D., and A.S. Harestad. 1994. Effects of logging on American martens, and models for habitat mangement. Pages 355-367 *in* R.G. Powell, ed. Martens, sables, and fishers: biology and conservation. Cornell Univ. Press, Raleigh, NC.

—. 2003. The ecological and genetic basis for emulating natural disturbance in forest management: theory guiding practice. Pages 29-42 *in* A.H. Perera, L.J. Buse, and M.G. Weber, eds. Emulating natural forest landscape disturbances: concepts and applications. Columbia Univ. Press, New York, NY.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75(1): 2-16.

Tilman, D., and J.A. Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363-365.

Tilman, D., C.L. Lehman, and C.J. Yin. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. Am. Nat. 149(3): 407-435.

Tilman, D., R.M. May, C.L. Lehman, and M. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65-66.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72(3):1038-1049.

Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos 90(1):7-19.

Tjernberg, M., K. Johnsson, and S.G. Nilsson. 1993. Density variation and breeding success of the black woodpecker *Dryocopus martius* in relation to forest fragmentation. Ornis Fennica 70:155-162.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecol. Appl. 12(2):354-363.

Turner, M.G. 1989. Landscape ecology — the effect of pattern on process. Annu. Rev. Ecol. Syst. 20: 171-197.

Turner, M.G., R.H. Gardner, V.H. Dale, and R.V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55(1):121-129.

Urban, D.L., R.V. Oneill, and H.H. Shugart. 1987. Landscape Ecol. Bioscience 37(2):119-127.

Väisänen, R.A., O. Jarvinen, and P. Rauhala. 1986. How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests. Ornis Scandinavica 17(3):282-292. (Article not seen, citation from Andrén, H. 1997. Habitat fragmentation and changes in biodiversity. Ecol. Bull. 46:171-181.)

van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

van Langevelde, F., C. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A.K. Skidmore, J.W. Hearne, L. Stroosnijder, W.J. Bond, H.H.T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84(2):337-350.

Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. Am. Nat. 158(3):211-220.

Verboom, J. and K. Lankester. 1991. Linking local and regional dynamics in stochastic metapopulation models. Biol. J. Linn. Soc.

42(1-2):39-55. (Article not seen, citation from Metzger, J.P., and H. Décamps. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecologica 18(1):1-12.)

Venier, L.A., and L. Fahrig. 1996. Habitat availability causes the species abundance-distribution relationship. Oikos 76(3):564-570.

Villard, M.A., K.E. Freemark, and G. Merriam. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an empirical investigation. Pages 474-482 *in* Ecology and conservation of Neotropical migrant landbirds. J.M. Hagan and D.W. Johnson, eds. Smithsonian Institute Press, Washington, DC. (Article not seen, citation from Metzger, J.P., and H. Décamps. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecologica 18(1):1-12.)

Villard, M.A., M.K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. 13(4): 774-783.

Virgos, E. 2001. Role of isolation and habitat quality in shaping species abundance: a test with Badgers (*Meles meles* L.) in a gradient of forest fragmentation. J. Biogeography 28(3):381-389.

Virkkala, R. 1991. Population trends of forest birds in a Finnish Lapland landscape of large habitat blocks — consequences of stochastic environmental variation or regional habitat alteration. Biol. Conserv. 56(2):223-240.

Vos, C.C., J. Verboom, P.F.M. Opdam, and C.J.F. Ter Braak. 2001. Toward ecologically scaled landscape indices. Am. Nat. 157(1):24-41.

Ward, S., and I. Thornton. 1998. Equilibrium theory and alternative stable equilibria. J. Biogeography 25: 615-622.

Waterhouse, F.L., A.S. Harestad, and P.K. Ott. 2002. Use of small streams and forest gaps for breeding habitats by winter wrens in coastal British Columbia. Northwest Sci. 76(4):335-346.

Watkinson, A.R., and W.J. Sutherland. 1995. Sources, sinks and pseudo-sinks. J. Anim. Ecol. 64(1): 126-130.

Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient — initial conditions and mechanisms of competition. Ecol. Monogr. 63(2):199-229.

Weir, R.D., and A.S. Harestad. 2003. Scale-dependent habitat selectivity by fishers in south-central British Columbia. J. Wildl. Manage. 67(1):73-82.

Wellnitz, T., and N.L. Poff. 2001. Functional redundancy in heterogeneous environments: implications for conservation. Ecol. Letters 4:177-179.

Widén, B. 1993. Demographic and genetic effects on reproduction as related to population size in a rare, perennial herb, *Senecio integrifolius (Asteraceae)*. Biol. J. Linn. Soc. 50(3):179-195.

Wielgus, R.B. 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biol. Conserv. 106(3):381-388.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecol. 3(4):385-397.

Wiens, J.A., and B.T. Milne. 1989. Scaling of landscapes in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecol. 3:87-96.

Wiens, J.A., R.L. Schooley, and R.D. Weeks. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78(2):257-264.

Wiens, J.A., N.C. Stenseth, B. Vanhorne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66(3):369-380.

Wilcove, D.S. 1987. From fragmentation to extinction. Nat. Areas J. 7:23-29.

Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 *in* M.E. Soulé, ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA.

Wilson, E.O. 1985. The biological diversity crisis: a challenge to science. Issues in Sci. and Technol. 2(1):20-29.

Wilson, R.J., S. Ellis, J.S. Baker, M.E. Lineham, R.W. Whitehead, and C.D. Thomas. 2002. Large-scale patterns of distribution and persistence at the range margins of a butterfly. Ecology (Washington DC) 83(12):3357-3368.

Wissel, C. 1984. A universal law of the characteristic return time near thresholds. Oecologia 65:101-107.

With, K.A. 1997. The application of neutral landscape models in conservation biology. Conserv. Biol. 11(5):1069-1080.

With, K.A., S.J. Cadaret, and C. Davis. 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80(4):1340-1353.

With, K.A., and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76(8):2446-2459.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78(1):151-169.

With, K.A., and A.W. King. 1997. The use and misuse of neutral landscape models in ecology. Oikos 79(2):219-229.

—. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecol. 14(1):73-82.

—. 1999b. Extinction thresholds for species in fractal landscapes. Conserv. Biol. 13(2):314-326.

—. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biol. Conserv. 100(1):75-88.

Wolff, J.O., E.M. Schauber, and W.D. Edge. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conserv. Biol. 11(4):945-956.

Worthen, W.B. 1996. Community composition and nested-subset analyses: basic descriptors for community ecology. Oikos 76:417-426. (Article not seen, citation from Andrén, H. 1997. Habitat fragmentation and changes in biodiversity. Ecol. Bull. 46:171-181.)

Wright, D.H. 1991. Correlations betwen incidence and abundance are expected by chance. J. Biogeography 18:463-466.

Wu, J.G., and O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. Q. Rev. Biol. 70(4):439-466.

Zschokke, S., C. Dolt, H.P. Rusterholz, P. Oggier, B. Braschler, G.H. Thommen, L. E., A. Erhardt, and B. Baur. 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572. (Article not seen, citation from Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecol. Appl. 12(2):354-363.)

APPENDIX 1

Table 1. Core threshold literature. Cells with dark shading indicate modeling and empirical studies in forests; lighter shading indicates empirical studies set in forest / agricultural, grassland, or microcosm habitats; no shading indicates theoretical studies. The table summarizes numerical results from the core research on thresholds. Because the literature covers such diverse aspects of ecology, readers should be cautious about using this table to generalize across topics. For the major papers reviewed, the table shows the citation (author and date), the research setting (empirical or theoretical), the prior model (for theoretical studies), keywords (based on the topics in this paper), the threshold (amount of habitat remaining), the taxa, and a brief description of the study location, methods, and main results.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Åberg *et al.* (1995)	Empirical	n/a	Fragmentation (gap) thresholds	1. Grouse cross maximum 100 m gap in agricultural landscape, but cross 2 km gap in intensively managed forest landscape	Hazel Grouse (*Bonasa bonasia*)	Comparison of species occurrence in a landscape with a hostile matrix (forest-farmland), with occurrence in a forested landscape. The hostile matrix reduces by a factor of 20 the gap distance over which the Hazel Grouse travels.
Andrén (1994)	Model / empirical	Random sample hypothesis	Fragmentation threshold	10–30%	Summary of studies looking at 35 species of birds and mammals	Random habitat loss (random sample hypothesis) accounted for patterns of species occurrence between 10 and 30% of remaining habitat. When less habitat remained, fragmentation became important. But see Mönkkönen and Reunanen (1999), Andrén (1999), and Bender *et al.* (1998) for discussion of Andrén's (1994) findings.
Andrén (1996)	Model	Random sample hypothesis, statistical power	Fragmentation threshold	1. ~37% 2. ~20% 3. ~12% 4. ~4%	Species lost in following order: 1. area sensitive, poor disperser 2. area sensitive, good disperser 3. less area sen., poor disperser 4. less area sen., good disperser	Used simulation models to estimate the statistical power to reject the random sample hypothesis. Examined the effect of habitat fragmentation (area and isolation effects) on population survival in landscapes with different proportions of suitable habitat. Results vary with habitat requirements and dispersal ability. See Andrén (1994, 1999) and Mönkkönen and Reunanen (1999) for results from empirical data based on therandom sample hypothesis.
Andrén (1999)	Model / empirical	Response to Mönkkönen and Ruenanen (1999)	Fragmentation threshold	n/a	Birds and mammals in forested landscapes	Reply to Mönkkönen and Reunanen (1999). Andrén re-asserts the claim that the findings of Andrén (1994) are significant, based on the result seen after removing the forested landscape type from the dataset—this essentially agrees with Mönkkönen and Reunanen (1999). See Andrén (1994) and Mönkkönen and Reunanen (1999).
Angelstam (2001)[1]	Empirical	n/a	Habitat amount thresholds. habitat specialist, old forest	1a. 0.2 km^2 (patch—single male) 1b. 0.9 km^2 (patch—lek) 1c. 16% (landscape—single male) 1d. 24% (landscape—lek) 2a. 0.8 km^2 (patch—single male) 2b.2.2 km^2 (patch—lek) 2c. 30% (landscape—single male) 2d. 30% (landscape—lek)	1. Black Grouse (*Tetrao tetrix*) 2. Capercaillie (*Tetrao urogallus*)	Boreal Fennoscandinavia, 4 x 4 km plots. Examines the effect of number, size, and landscape proportions of habitat patches for the occurrence and density species studied.

---

[1] Abstract in Angelstam and Breuss (2001a), therefore only limited data available to report here. Paper forthcoming in Angelstam, P. and M. Breuss, eds. 2004. Ecological Bulletins, Volume 51 [In Press].

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Angelstam *et al.* (2001b)[1]	Empirical	n/a	Habitat amount threshold, habitat specialist, old forest	1. 70% old forest 2. 30% old forest	1. Capercaillie (*Tetrao urogallus*), squirrel (*Sciurus vulgaris*); old-forest specialists 1. Moose (*Alces alces*)	Examined the incidence in 5 x 5 km landscapes, of old forest specialists and non-old forest specialists related to forest cover, classified as old or not old, in boreal forests in northern Sweden. In addition to the values given in the adjacent cells, *Martes martes* (old-forest specialist) responded similarly to the response of Capercaillie (*Tetrao urogallus*) and squirrel (*Sciurus vulgaris*), but was more linear. Incidence of *Lynx lynx* was generally low but increased linearly; no results reported for *Vulpes* vulpes, *Lepus montanus* or *Lagopus lagopus*.
Angelstam *et al.* (2002, cited by Angelstam *et al.* 2003)	Empirical	n/a	Habitat quality threshold, dead wood, habitat specialist	Between 10 and 20 m^3 ha^{-1} of dead wood over a 100 ha area	White-backed Woodpecker (*Dendrocopos leucotos*)	Examined relationships between dead wood variables and the presence of woodpecker species in 25 one-km^2 plots in hemiboreal in northeast Poland. Habitat generalists (Black Woodpecker [*Dryocopus martius*] and Great Spotted Woodpecker [*Dendrocopos major*]) were found in all landscape types, whereas habitat specialists (Lesser Spotted Woodpecker [*D. minor*], White-backed Woodpecker, Middle Spotted Woodpecker [*D. medius*], Grey-headed Woodpecker [*Picus canus*] and Three-toed Woodpecker) [*Picoides tridactylus*] were only observed in landscapes without intensive forest management, or where natural forest succession occurred following land abandonment. White-backed Woodpecker was the most area-demanding deciduous forest specialist, and showed the clearest non-linear relationship between dead wood variables and presence.
Angelstam and Jansson (2001)[1]	Empirical	n/a	Habitat quality threshold, habitat amount threshold	Not reported	*Dendrocopos leucotos, Picus canus, Dendrocopos minor, Sitta europea, Parus palustris, Carduelis chloris, Picus viridis, Aegithalos caudatus, Parus caeruleus, Bonasa bonasia, Parus major*	Set in boreal in south-central Sweden. Examined the effect of the composition and structure of the deciduous forest component on the presence of resident bird species having different habitat requirements. Contrasted habitat needs of species with the existence of habitat structures along a gradient of habitat change. Suggests differing planning scales for different species, depending on their habitat requirements.
Bascompe and Rodriguez (2001)	Empirical	n/a	Fragmentation thresholds, landscape parameters	29–35%	Plantae	Study of changes in woody species richness with habitat loss in prairie habitat in Kansas. When matrix covers 65%, threshold decline in species richness; species richness independently, negatively correlated with largest patch size, patch heterogeneity, and number of patches, beyond 65% matrix.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Bascompte and Solé (1996)	Model	Levins' 1969 model, spatially explicit (cellular automaton), with non-equilibrium dynamics	Percolation theory, fragmentation threshold, non-equilibrium dynamics	72% indicates the beginning of a phase transition; postulate this occurs earlier than percolation threshold because small patches become isolated first. Model then confirms 60% percolation findings when the largest patch becomes fragmented.	Landscape structure, demographic properties: colonization (dispersal)	Spatially explicit form of Levin's model differs from spatially implicit models (e.g., Nee and May 1992) in showing that occupancy is not constant throughout habitat loss. Spatially implicit models show a constant occupancy rate as habitat destruction increases; this paper shows that the proportion of unoccupied habitat in a landscape increases as habitat destruction increases, because habitat becomes isolated, reducing patch occupancy. This model agrees with Dytham (1995a, 1995b) and Moilanen and Hanski (1995) in showing that patch occupancy decreases in a threshold way with increasing habitat destruction, hence extinction threshold occurs sooner than spatially implicit models show. Used a range of colonization and extinction probabilities to show that spatial effects matter more (decline to extinction threshold takes place for less habitat destruction) for species with low demographic potential.
Bascompte and Solé (1998)	Model	Levins (1969), May (1994), Kareiva and Wennergren (1995); mean field metapopulation model and spatially explicit cellular automaton model	Predator-prey; dispersal	50–65%	Generic	Spatially implicit and explicit simulations of predator-prey interactions under habitat destruction. Models qualitatively similar, but colonization is a local process in a spatially explicit model, and a global process in a spatially implicit model. Effects on predator and prey similar, but change in colonization rate affects trophic levels differently—predators diminish more rapidly than prey, and, as colonization rate slows, the proportion of predator-occupied sites increases non-linearly; threshold exists in colonization rate, below which predator becomes extinct.
Beier (1993)	Model / empirical	Model parameterized with empirical data	Habitat amount threshold; MVP	2 200 km^2 with immigration	Cougar (Felix concolor)	Santa Ana mountain range of southern California. Model predicts very low extinction risk in 2200 km^2 area, when occasional emigration occurs from other populations.
Bélisle and Desrochers (1997)	Empirical	n/a	Gap thresholds	25 m distance-to-edge threshold 50 m gap-crossing threshold	Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*P. villosus*), Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee (*Poecile artcapillus*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*S. carolinensis*), Red-eyed Vireo (*Vireo olivaceus*); group of woodland passerines.	

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Bender *et al.* (1998)	Model / empirical	Meta-analysis	Patch size, fragmentation threshold	n/a	134 species of birds, mammals, and insects primarily in forest settings, also wetland, marshland, and grassland	Meta-analysis of 25 patch-size effect studies. Main focus of study was to discern the conditions under which patch size had an effect on population density. The authors find no fragmentation threshold resulting from the effects of patch size—this result contrasts Andrén (1994). The authors suggest that their failure to detect a fragmentation threshold might be due to one of two factors: 1. different methods—Andrén uses discrete 'vote count' method to assess if random sample hypothesis predicted population size, and this study used a continuous response variable; and 2. Andrén looked at both patch size and isolation, and this study looked only at patch size, so Andrén's result may be due to isolation effects.
Boswell *et al.* (1998)	Model calibrated with empirical data	Cellular automata (patch occupancy); Britton *et al.* 1996	Fragmentation threshold, keystone species	55%	Army Ant (*Eciton burchelli*)	Neo-tropical forest. Species became extinct before the p_c for eight nearest neighbours (i.e., $p_c = 0.4072$) was reached, as described by percolation theory. This is likely because, although it may not be impossible for a colony to get from one site in a cluster to any other site, it may be very difficult. This result (decline in population prior to percolation threshold) was also demonstrated by Dytham (1995a), With and Crist (1995), and Bascompte and Solé (1996).
Bronstein *et al.* (1990)	Model calibrated with empirical data	n/a	MVP, Allee effect	95 individuals	Fig tree (*Ficus natalensis*)	A stochastic simulation model was calibrated with data from a population in Gabon to determine the Allee threshold. Simulations show that 95 trees is the median critical population size to maintain pollinator populations for four years for *F. natalensis*. At this population size, no gap in flowering sequence occurs, hence wasps avoid extinction. The model was sensitive to the probability of overlap between male and female flowers on separate trees, resulting in a range of 64–294 trees required for pollinator maintenance.
Burke and Nol (2000)	Empirical	n/a	Habitat amount threshold; patch area threshold	500 ha	Ovenbird (*Seiurus aurocapillus*)	A study on forest-breeding songbirds examining the influence of patch size on reproductive success in fragmented upland deciduous forests in south-central Ontario. A 500 ha threshold patch size was required to maintain sufficient core habitat, for the most area-sensitive species, in order for a patch to function as a source (as opposed to a sink) habitat.
Burkey (1989)	Model	Stochastic analogue to discrete logistic growth model	Dispersal	Variable	Generic	Variable threshold in probability of extinction of a patch, depending on amount of fragmentation, expected growth rates of population, and inter-patch migration rates.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Bütler *et al.* (2003a[1], 2003b; cited by Angelstam *et al.* 2003)	Model / empirical	No	Habitat quality thresholds, dead wood	1. Threshold declines occur for probability of occupancy, from 0.95 to 0.10, when snag basal area decreases from: a. 1.3 to 0.6 $m^2\ ha^{-1}$ in the Swiss sub-alpine forests, and b. 0.5 to 0.3 $m^2\ ha^{-1}$ in Swedish boreal forests 2. Using precautionary principle, suggested management targets for snags, of 1.6 $m^2\ ha^{-1}$ (basal area) or 18 $m^3\ ha^{-1}$ (volume) or 14 ≥ 21 cm dbh snags/ha, over an area of 100 ha in sub-alpine forest	Three-toed Woodpecker (*Picoides tridactylus*)	Characterizes habitat thresholds for woodpeckers based on dead wood amounts in forests. Empirical data from sub-alpine spruce (*Picea abies*) forests in Switzerland was compared to a theoretical model based on energy requirements, to derive quantitative snag density requirements based on probability of occupancy in the sub-alpine forests. Swiss results then used to estimate probability of occupancy in boreal forests in south-central Sweden.
Carlson (2000)	Model / empirical	Lande 1987	Fragmentation threshold, rare, habitat specialist, extinction debt	13% suitable habitat (9–17% when 5% range of parameters used)	White-backed Woodpecker (*Dendrocopos leucotos*)	Deciduous old-growth—Fennoscandinavia.
Dale *et al.* (1994)	Model / empirical	Model parameterized with empirical data	Habitat amount threshold-related gap sensitivity; habitat specialists	Non-linear response to habitat change under multiple scenarios of habitat change, for species with large area requirements but small gap-crossing ability.	Scarab beetles (*Scarabinidae* spp.) Euglossine bees (*Euglossa* and *Eulaema* spp.)	Central Amazon. Compared effects of three systems of land change on two classes of species with large area requirements: those with large gap-crossing ability, and those with small gap-crossing ability.
Desrochers and Hannon (1997)	Empirical	n/a	Gap thresholds	70 m—birds 3x less likely to cross open than forest; 100 m—birds 8x less likely to cross open than forest	Black-capped Chickadees (*Parus atricapillus*), Red-breasted Nuthatches (*Sitta canadensis*), Red-eyed Vireos (*Vireo olivaceus*), Golden-crowned Kinglets (*Regulus satrapa*), Yellow-rumped Warblers (*Dendroica coronata*)	Study set in boreal forest and deciduous / rural lowlands in Quebec. Examined the effect of narrow (<160 m) gaps in the forest on movement by songbirds, and whether there was a threshold distance across gaps where birds prefer to move through woodland as opposed to crossing in the open. Find a non-linear response in the probability of an individual or flock to cross gap to respond to Chickadee mobbing calls, with gaps <30 m having little effect on bird movements, but birds three times less likely to cross 70 m gaps, and ~eight times less likely to cross 100 m gaps, compared to similar distances in the forest. Strong difference among species: Chickadees and Yellow-rumped Warblers show strong affinity to forests, Nuthatches show no significant difference in response between clearcuts and open fields.
Doncaster *et al.* (1996)	Model calibrated with empirical data	Lawton *et al.* 1994: eradication threshold from epidemiology; Hanski 1994	Habitat amount threshold, metapopulation	8% suitable habitat	Hedgehog (*Erinaceus europaeus*)	

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Donovan and Lamberson (2001)	Model	Gardner (1999) RULE program	Fragmentation threshold, reproduction	Habitat held constant at 30%	Generic	Incorporated fecundity patterns and area sensitivity of a hypothetical forest-nesting passerine in a model of fragmentation effects on population growth. Habitat amount held constant at 30%, 10 levels of fragmentation from 1 (highly fragmented: 9 036 patches) to 10 (continuous: 90 patches). As landscapes become more continuous (greater number of larger patch sizes), a threshold response of fecundity to patch size causes a threshold increase in population growth. As landscapes become more continuous, area sensitive species respond (seek out and breed in) larger patch sizes, and thus experience greater population growth in fragmented landscapes than do area-insensitive species. Area-insensitive species also nest in larger patches as landscape continuity increases, simply because larger patches become more predominant in the landscape. Because they differentiate less between nesting sites, area-insensitive species experience lower growth at moderate fragmentation than do area sensitive passerines.
Drolet *et al.* (1999)	Empirical	n/a	Habitat amount threshold	55% forest cover at landscape (100 ha) scale	Bay-breasted Warbler (*Dendroica castanea*) absent from landscapes below the threshold amount cover	Studied the landscape- (100 ha) level effects of forest cover and fragmentation on nesting songbird presence in boreal forest north of Quebec City. Although seven of 14 species were significantly correlated with landscape variables, three species responded to forest cover only, but no species responded to landscape configuration (edge and core area) after controlling for other factors. Concluded that harvesting in boreal forest would reduce the use of remnant forest patches by certain species through decrease in habitat amount at the landscape scale, rather than changes in spatial configuration. Demonstrates the importance of landscape context, as all species studied had home ranges <5 ha. Show that maintaining 5 ha patches in largely clearcut landscapes will not necessarily maintain all species possessing this home range requirement.
Dytham (1995b)	Model	Spatially explicit population model; cellular automaton	Competition, habitat amount at extinction	- 65% random habitat loss, superior competitor (inferior disperser) extinct - 45% gradient habitat loss, superior competitor extinct - <25% block or line habitat loss, superior competitor extinct - 25% random habitat loss, superior disperser (inferior competitor) extinct - <25% gradient, block or line habitat loss, superior disperser extinct	Species traits—superior competitor vs. superior disperser	Modeled the effect of different types of habitat removal (random, gradient, block, line) on the habitat amount remaining at extinction for two metapopulations, one characterized by superior dispersal, the other by superior competitive ability. Results confirm the finding of Nee and May's (1992) analytical solution (deterministic model), with respect to the effect on species with different dispersal/competition abilities. Also in agreement with spatially explicit models of Moilanen and Hanski (1995) and Bascompte and Solé (1996), in showing that patch occupancy decreases as habitat loss increases, due to isolation of patches—extinction therefore occurs at a lower level of habitat loss than predicted by Nee and May's (1992) deterministic model for all three spatially explicit models.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Edenius (2001)[1]	Model / empirical	No	Habitat amount threshold, habitat quality	Not reported	Siberian Jay (*Perisoreus infaustus*)	Examined quantitative habitat requirements in boreal forest in northern Sweden, at a range of spatial scales, using radio telemetry and permanent feeding stations. Proportion of forest area and proportion of forest >100 years were significantly ($p<0.05$) greater in home range than in random areas. Greater amount of variation in visits to feeding stations was explained by old forest in a 315 ha area than in a 45 ha area, and incorporating the amount of spruce always increased the amount of variation explained.
Edenius and Sjöberg (1997)	Empirical	n/a	Patch size threshold	5 ha	Avian species in the Swedish boreal forest	Threshold fragment size (<5 ha), below which a species area curve derived by rarefaction indicated that patches were significantly ($p<0.05$) depauperate. Also found a steep species area curve (akin to Helle 1984), leading them to conclude that higher thresholds than Andren's (1999) 30% were likely required in the boreal. Also nested subset pattern.
Eriksson and Kiviniemi (1999)	Model / empirical	n/a	Habitat amount threshold	n/a	18 Scandinavian grassland species	Determined the minimum suitable habitat as described by Hanski et al. (1996) incorporating (extinction debt) into a "quasi-equilibrium" habitat threshold estimate using analysis of site occupancy and recruitment of 18 species of semi-natural grasslands in Scandinavia. Eight of 18 species currently persisted in areas where the suitable habitat is below the extinction threshold—thus an extinction debt.
Fahrig (1997)	Model	Cellular automaton	Fragmentation threshold	20%	Generic	Fragmentation has the greatest effect on population persistence at 20% remaining habitat. Extinction risk increased precipitously when <20% habitat remained on the landscape; above this, the amount of habitat had a much greater effect on extinction probability.
Fahrig (1998)	Model	SEPM	Reproduction, fragmentation threshold	20% landscape level of breeding habitat	Generic	A spatially explicit simulation model that discerns under what conditions fragmentation of breeding habitat affects population survival. Spatial arrangement of habitat relevant only under a narrow range of conditions: 1. average between-generation movement distance of the organism is about 1–3 times the expected nearest distance between breeding sites; 2. the breeding habitat of the organism covers <20% of the landscape; 3. the habitat is permanent; 4. the organism has high breeding site fidelity; and 5. mortality rate outside of the breeding habitat is higher than within breeding habitat areas.
Fahrig (2001)	Model	SEPM (based on Fahrig 1997, 1998)	Reproduction, dispersal, matrix, fragmentation	1–99%, depending on parameter combinations; showed that reproduction had the strongest effect on extinction threshold	Generic	A spatially explicit simulation model that discerns the relative effects of four factors on the habitat threshold: reproductive rate, rate of emigration of the organism from habitat, habitat pattern (fragmentation), and matrix quality. In this study, reproductive rate had the largest potential effect on the habitat threshold, and fragmentation had the least effect.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Fahrig (2002)	Model	SEPM	Fragmentation threshold	5–80%—from previously reported results	Generic	Synthesis of four spatially explicit population models that test the effect of fragmentation on the habitat threshold. All four studies agree that there is an increasing effect of fragmentation on the response variable (e.g., on population size) as habitat loss increases, and that fragmentation increases the extinction threshold—but they differ in the predicted fragmentation effect. Difference is in life-history traits modeled—colonization and extinction in two of the models, and birth, immigration, death, and extinction in the others. Concludes that matrix quality affects the extent to which fragmentation influences the habitat threshold; therefore, in some cases, habitat fragmentation will not mitigate the effect of habitat loss.
Flather and Bevers (2002)	Model	Reaction (reproduction)-diffusion (dispersal) model, (i.e., from bio-diffusion modeling)	Relative importance of habitat area and arrangement, reproduction, dispersal	30–50%	Below this threshold, effects of habitat arrangement became important when species persistence became uncertain due to dispersal mortality	Over a broad range of habitat amounts and arrangements, population size was largely determined by purely by effect of habitat amount; proportion of habitat accounted for >96% variation vs. <1% accounted for by arrangement. As habitat reduced below 30–50% (the threshold indicating persistence probability), habitat arrangement became important predictor of population size.
Frankham (1995, cited by Metzger and Décamps 1997)	Empirical	n/a	Effects of small populations, fragmentation	n/a	*Drosophila melanogaster, D. virilis, Mus musculus*	Threshold between inbreeding and incremental extinction at intermediate fragmentation levels. Paper not reviewed by this author.
Franklin and Forman (1987)	Model	Cellular automaton	Fragmentation threshold, disturbance susceptibility	30–70%	Landscape structural characteristics (e.g., patch size, patch isolation, edge) Thresholds in patch size, and spread of disturbance occur across a gradient of cutting patterns	Model simulated 1 000 ha^2 landscape, with “habitat removal” occurring in 10 ha patches; checkerboard pattern of removal. Cells selected for cutting so that each new cut minimizes the variance in interpatch distance between it and all other cut patches. See Spies et al. (1994).
Gardner *et al.* (1987)	Model / empirical	Cellular automaton	Percolation theory, fragmentation threshold, neutral landscape model	Thresholds in landscape indices depend on the scale of examination	Landscape structural characteristics	Compared spatial metrics in real, forested landscapes in the eastern United States, to predictions from percolation theory. Examined three empirical landscapes with varying levels of forest cover, and determined the number, size and fractal dimension patches for each landscape. Also derived these vales for neutral landscape maps (modeled maps), and compared the results of real to modeled landscapes. Find significantly (P<0.05) fewer patches in empirical than in modeled landscapes. Observe critical thresholds in the number of patches in real landscapes, but at lower levels than they observe in the neutral maps. Suggest that fragmentation in real landscapes results in greater aggregation of remaining habitat than predicted by neutral maps.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Gibbs (1998)	Empirical	Fragmentation index	Fragmentation threshold, habitat amount threshold	1. 50%—fragmentation threshold 2. 30%—precipitous decline seen far below the fragmentation threshold (50%)—habitat amount threshold	1. Red-spotted Newt (*Notophthalmus* v. *viridescens*) drops out 2. Wood Frogs (*Rana sylvatica*), Spotted Salamanders (*Ambystoma maculatum*) decline precipitously	An amphibian study examining the presence / absence of amphibians along a fragmentation and forest cover gradient in Connecticut. One species, red-spotted newt, drops out along the habitat-loss gradient near the threshold point (~ 50% forest habitat remaining) at which fragmentation shifted from being uniformly low to uniformly high. Wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) do not occur below ~ 30% forest habitat. Because wood frogs and spotted salamanders decline at the fragmentation threshold (from ~ 90% to ~ 60% and 80% occurrence in suitable habitat, respectively), but precipitous declines occurred farther along the habitat-loss gradient, either the relative effect of habitat loss was still important below the fragmentation threshold, or the author observed an extinction debt.
Graham (2001)	GIS model parameterized with empirical data	Spatially explicit habitat model	Gap (cost-distance) threshold, habitat quality	800–1000 'cost-distance' units	Keel-billed Toucans (*Ramphastos sulfuratus*)	Habitat quality and gap size were represented by a single value—"cost-distance" in a GIS model used to predict what factors influence movements of Keel-billed Toucans in fragmented tropical forest (Mexico). Threshold value of cost distance units beyond which movements are rare.
Groom (1998)	Empirical	n/a	Patch size and isolation thresholds; Allee	1. 26 m isolation threshold for pollen receipt for tiny (<10 individuals) patches 2. 16 m isolation threshold for seed-set for tiny patches 3. 104 m isolation threshold for pollen receipt for small (11–50 individuals) patches	Lovely clarkia (*Clarkia concinna concinna*)	Survey of lovely clarkia in California. Isolation explains, better than patch size or plant size, the level of seed set and the amount of pollen received. Isolation thresholds are evident, and interact with patch size in such a way that isolation effects increase as patch size decreases. Additionally, a greater number of patch extinctions due to reproductive failure occur in small patches than large, providing weak empirical evidence for Allee thresholds leading to extinction.
Hager (1998)	Empirical	Habitat amount threshold	Habitat amount threshold	n/a—several species were absent from smaller islands	Red-spotted Newt (*Notophthalmus* v. *viridescens*), ringneck snake (*Diadophis punctatus edwarsii*), and gray treefrog (*Hyla versicolor*)	An inventory of amphibians and reptiles in three island archipelagos in Ontario to discern area sensitivity. Communities occurred in nested subsets, and species dropped out along a gradient of habitat area, highlighting area thresholds. Did not attribute the absence of these species to the absence of habitat elements on smaller islands, such as pools. Concludes that area sensitivity explains the species gradient; attributes findings to habitat loss, but does not control for fragmentation (isolation) effects.
Hanski *et al*. (1996)	Model	Levins 1969	Habitat thresholds, metapopulation thresholds; extinction debt	Greater than estimated by Levins' (1969) model	Glanville Fritillary (*Meltiaea cinxia*).	By incorporating the rescue effect, stochasticity, and non-equilibrium (transient) dynamics, describes how Levins' (1969) model underestimates habitat thresholds and minimum viable population of a metapopulation.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Hargis *et al.* (1999)	Empirical	n/a	Habitat amount thresholds at patch and landscape scale	1. ~75%—landscape occupancy threshold in 9 km^2 landscape 2. Landscapes with <100 m between open areas had no martens	American Marten (*Martes americana*)	Study set in the Uinta Mountains of Utah, to discern stand- and landscape-level thresholds for habitat use by evaluating differences in marten capture rates. Landscape had low levels of fragmentation—non-forest cover ranged between 2 and 42%. Significant ($p<0.05$) threshold in patch occupancy whereby martens avoided habitats with <100 m between openings (i.e., those landscapes containing patches with virtually no patch interior). This was true even though small mammal (i.e., prey) species were significantly more numerous in openings. There was also a threshold in landscape occupancy (no martens) when openings covered >25% of the landscape.
Henein *et al.* (1998)	Model parameterized with empirical data	No	Habitat threshold, connectivity, habitat specialist	~30%	Eastern Chipmunk (*Tamias striatus*)	70% habitat loss = critical thresholds for model chipmunks (specialists) having high dependence on native habitat. White-footed mice (Peromyscus leucopus; generalists) did not have threshold response.
Hill and Caswell (1999)	Model	Cellular automaton and spatially implicit patch-occupancy	Habitat amount threshold; fragmentation threshold	- Threshold in habitat varies depending on degree of fragmentation and dispersal ability - Fragmentation increases the amount of habitat required for species to persist	Generic	Compares spatially implicit (patch-occupancy) model with spatially explicit cellular automaton to show that degree of fragmentation and dispersal ability affects the habitat amount at which the habitat threshold occurs.
Hill and Caswell (2001)	Model / empirical	Chain binomial model parameterized with empirical data	Habitat amount threshold, dispersal	- For a given number of patches, expected time to extinction and probability of persistence are sensitive to changes in the number of suitable patches - Threshold value of suitable patches, which varies with ability to disperse, at which the expected extinction time declines abruptly from very high to very low values	Glanville Fritillary (*Meltiaea cinxia*)	Model predicts the quasi-equilibrium distribution of occupied patches, the expected extinction time, and the probability of persistence to a given time as a function of the total number of patches and the number of suitable patches in the landscape. Particularly addresses the problem of a finite (small) number of patches in the landscape, and the effect on the habitat threshold of increasing the ability to disperse (search for suitable patch). Describes method for parameterizing model, and presents an example using Glanville fritillary data.
Jacquemyn *et al.* (2002)	Model parameterized with empirical data	n/a	Non-linear decline in dispersal probability	Dispersal probability declines in the form of a negative exponential from the maximum probability of 40% between the closest patches, to no probability of dispersal between patches 1 000 m apart. Colonization probability decreases to <10% when the distance to the nearest forest patch was >350 m	*Primula elatior*	Investigated the effects of patch size and isolation on colonization probability, population size, and fitness, in a forest / agricultural setting in Flanders, Belgium.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Jansson and Angelstam (1999)	Model parameterized with empirical data	No	Habitat thresholds, fragmentation (gap) thresholds	- Presence probability = 0.8 at 100 m inter-patch distance when total habitat covers 5% of landscape - Presence probability = 0.8 at 500 m inter-patch distance when total habitat covers 15% - threshold declines below these gap thresholds	Long-tailed Tit (*Aegithalos caudatus*)	Study examined thresholds in patch occupancy as a function of habitat amount in the surrounding landscapes. There were distinct thresholds in these landscape variables for the probability of local Long-tailed Tit presence. This study demonstrates that, at higher levels of habitat availability, species can persist with greater spacing of habitat patches. The greater the habitat availability, the lower the threshold of extirpation in relation to habitat isolation and predator-prey interactions.
Keitt *et al.* (1997)	GIS model—spatially explicit habitat model (SEHM)	n/a	Fragmentation threshold, dispersal, connectivity	- At dispersal distances <45 km, landscape variables showed landscape to be half as connected as observed for dispersers with >45 km dispersal capability	Mexican Spotted Owls (*Strix occidentalis lucida*)	A range (0–100 km) of "threshold" dispersal distances represented a range of scales at which to compute connectivity measures. The authors identified a distance (between 40 and 45 km) at which they observed an abrupt change in connectivity (i.e., a percolation threshold). Organisms operating at dispersal distances less than 45 km observed their environment to be almost half as connected as organisms with greater dispersal. This particular study examined the distribution of suitable habitat for Mexican Spotted Owls.
King and With (2002)	Model	RULE (Gardner 1999), NLM	Fragmentation, dispersal	1. <30%–40% 2. >40% 3. < 80%	1. Both landscape structure and dispersal behaviour affected dispersal success 2. Spatial arrangement less important generally, random dispersal (mean-field) adequately predicts 3. Landscape structure important to success of dispersal for weak dispersers unless habitat amount high	NLM with random and fractal maps, three dispersal algorithms (mean-field, nearest-neighbour, and percolation process), range of habitat abundance and fragmentation.
Lamberson *et al.* (1992)	Model calibrated with empirical data	Levins 1969	Habitat amount threshold	20%	Northern Spotted Owl (*Strix occidentalis caurina*)	Levins' 1969 metapopulation model calibrated with demographic parameters from existing population, and adapted to territorial populations; aspatial.
Lamberson *et al.* (1994a)	Model calibrated with empirical data	SEPM; dispersal patterned after Lande (1987, 1988), other species demographics from literature; also modeled stochasticity, and incorporated non-equilibrium dynamics	Dispersal; non-equilibrium dynamics; Allee effect; extinction debt	~18–~30%, depending on assumptions about owl biology (e.g., dispersal search efficiency) and environmental stochasticity	Northern Spotted Owl (*Strix occidentalis caurina*)	Model incorporated Allee effects, stochasticity, non-equilibrium dynamics (ongoing timber harvest) to show a multiple stable state system (the multiple states including population persistence at different levels at landscape equilibrium in harvested and undisturbed habitats, and extinction); variability in survival probability depending on environmental variance; and extinction debt. Also demonstrated that occupancy measures may be misleading—"packing" of owls into suitable habitat in response to habitat change (harvest) resulted in temporarily higher occupancy.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Lamberson *et al.* (1994b)	Model calibrated with empirical data	SEPM	Habitat amount, management application	Cluster size sufficient to support territories for 20–25 owl pairs—beyond this amount, there were diminishing returns in population persistence for owl pairs.	Northern Spotted Owl (*Strix occidentalis caurina*)	In the context of reserve design, examined owl persistence (based on change in occupancy levels) relative to the degree of aggregation of suitable habitat (incorporating habitat amount and aggregation). Agrees with findings of Carroll and Lamberson (1993).
Lamont *et al.* (1993)	Empirical	n/a	Allee, plant pollinator, rare, reproduction, genetics	Patches <200m^2	*Banksia goodie* (woody prostrate species)	Small populations had significantly lower (p=0.004) number of seeds per unit population size, indicating that small populations do not have same conservation value as larger, and there was a threshold below which extinction might be inevitable—(no fertile cones in patches <200 m^2). Among banksias, seed-set is rare or zero in the absence of pollinators (Ramsey and Vaughton 1991), and high levels of out crossing are the norm. Loss of birds is well documented; this might reduce pollination and pollen transfer may increasingly be between siblings as population size is reduced.
Lande (1987)	Model	Levins 1969 metapopulation model modified for territorial organism	Extinction threshold	25–50%	Generic	Levins' 1969 metapopulation model calibrated with demographic parameters, and adapted to territorial populations; aspatial. Provided first theoretical evidence for the presence of an extinction threshold and it also showed that the location of the threshold is influenced by life history and dispersal parameters. High demographic potential (high fecundity and survivorship) have greatest influence on persistence.
Lande (1988a)	Model calibrated with empirical data	Levins 1969	Habitat amount threshold	~ 21% in old forest	Northern Spotted Owl (*Strix occidentalis caurina*)	Levins' 1969 metapopulation model calibrated with demographic parameters from existing population, and adapted to territorial populations; aspatial.
Lennartsson (2002)	Empirical, and model calibrated with empirical data	Stochastic matrix population model (Caswell 2001)	Habitat amount and fragmentation thresholds	1. 45–60% = seed set threshold for herkogamous plants 2. a) 35–55% = viability threshold in large (15 ha) grasslands 2. b) 45–65% = viability threshold in medium sized (5 ha) grasslands 2. c) 55–70% = viability threshold in small (2.5 ha) grasslands	Field gentian (*Gentianella campestris*)	Evaluation of extinction risk of endangered herb experimentally reintroduced in Swedish grasslands. Examined two landscape types (grassland rich = 12–15% semi-natural grassland within 1.5 km; grassland poor = 2–5% semi-natural grassland within 1.5 km). Habitat amount and fragmentation effects confounded, as amount of grassland habitat was used as the measure of fragmentation.
Lundberg and Ingvarsson (1998)	Model	Ingvarsson and Lundberg 1995	Plant-pollinator	Threshold between stable and unstable domains	Plant-pollinator systems	Threshold density below which plant-pollinator systems cannot exist, is a general feature of plant-pollinator systems

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
McIntyre and Wiens (1999)	Empirical	EMS	Habitat amount threshold, fragmentation threshold	20%	Tenebrionid beetle (*Eleodes obsoleta*) movement patterns in a mosaic of buffalograss (*Buchloë dactyloides*)	Study tested the separate effects of spatial pattern and habitat amount in an experimentally fragmented landscape, investigating the hypothesis that sparse but contiguous habitat was functionally equivalent to a greater amount of randomly distributed habitat. They compared two levels of habitat loss (80 and 90%) combined with two levels of habitat arrangement (randomly distributed and contiguous), for darkling beetle populations in buffalograss patches embedded in a sand matrix. The comparison between the habitat amount treatments exhibited greater differences than the comparison between the spatial pattern treatments. However, the two parameters interacted such that spatial pattern mattered at higher amounts (i.e., 20%) of habitat. Two of four landscape parameters (average patch size and average inter-patch distance) exhibited greater differences between clumped and random landscapes in the 20% habitat treatment than they did in the 10% habitat treatment. These two parameters were better predictors of movement responses than the other two parameters, explaining the interaction between habitat loss and fragmentation. The authors suggest that the anomalous result might be because 'the effects of habitat configuration may emerge only after some minimal habitat needs are met.'
McLellan *et al.* (1986)	Model	Habitat fragmentation in model after Moore 1962, Jones 1973	Fragmentation threshold	1. 50% 2. 20%	1. Birds with large area requirements and restricted dispersal 2. Birds with less extensive area requirements and greater dispersal	Early model examining the influence of fragmentation on birds, based on area requirements and dispersal ability.
Mikusiński and Angelstam (2001)¹	Empirical	n/a	Habitat amount threshold	1. 15% 2. 50% 3. 40–70%	1. Black Woodpecker and Red Squirrel 2. Brown Bear, Wolf, Lynx, Moose 3. White-backed Woodpecker	Examined relationships between forest cover and carnivores, herbivorous mammals, and woodpeckers at the regional scale (50 x 50 km grid cell) across Europe. Amount of forest loss had stronger negative effect on large, specialized carnivorous vertebrates than on smaller, herbivorous species. Moose (large herbivorous species) were also negatively affected by forest loss.
Mönkkönen and Ruenanen (1999)	Model / empirical	Response to Andrén (1994)	Fragmentation threshold, landscape context	n/a	Birds and mammals in forested landscapes	Reply to Andrén (1994). The authors re-analyzed Andrén's (1994) dataset, and demonstrate that of the four landscape types Andrén (1994) studied, the random sample hypothesis was sufficient to explain species numbers in forested habitats (i.e., no evidence to suggest fragmentation effect); whereas in the other habitats, non-random patterns prevailed (therefore, effect of fragmentation). The authors highlight the importance of landscape context, and they suggest that the lack of a fragmentation effect in forested landscapes may be related to either or all of: time since change, lack of sharp contrast between habitat and non-habitat (compared to farmland / forest habitat, for example), or temporal change in forested habitats. See also Andrén (1994, 1999), Bender et al. (1998).

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Naiman *et al.* (1989, cited by Metzger and Décamps 1997)	Concept	n/a	Biodiversity	50%	Biodiversity	Biodiversity decreases rapidly when frequency of ecotones increases above 50%. Paper not reviewed by this author.
Pakkala *et al.* (2002)	Model calibrated with empirical data	Hanski and Ovaskainen 2000	Metapopulation, landscape context, scale, habitat amount threshold, habitat quality threshold	Threshold in metapopulation capacity (landscape quality threshold), below which Three-toed Woodpecker won't persist	Three-toed Woodpecker (*Picoides tridactylus*)	Examined metapopulation capacity in boreal landscape in southern Finland. The metapopulation capacity was based on stand characteristics (age, tree species composition), and spatial characteristics. Found that measures of the metapopulation capacity of the landscape were significantly (p<0.05) positively related to the fraction of the landscape that was occupied, and demonstrated a threshold for the occurrence of the woodpecker at the landscape level.
Parker and Mac Nally (2002)	Empirical	EMS	Fragmentation threshold	None observed at >10% remaining habitat	*Elodes* spp.	The authors investigated species richness and abundance at two levels of habitat loss (60% and 90%) and three levels (arrangements) of spatial fragmentation. In this study, no fragmentation threshold was discerned in the EMS, although post-hoc power tests were low (<0.50) for all abundance measures, and the study duration was short (one season). Additionally, the authors propose that 90% habitat loss might not have been sufficient to precipitate threshold declines.
Pearson *et al.* (1996)	Model	NLM	Fragmentation threshold, gaps, dispersal	25%	Generic	P_c shifted from 0.6 to 0.25 when species could move across unsuitable habitat or "gaps".
Penteriani and Faivre (2001)	Empirical	n/a	Stand-level thresholds	70%	Goshawk (*Accipiter gentiles*)	This study of Goshawk nesting patterns in two European areas looked at the effects of harvesting activity and reduction in forest cover on occupancy rate, productivity, and number of young per breeding pair. The authors were particularly interested in the effects of progressive thinning (removing 10, 20, 20, 20% in four passes) and clearcutting activities (removing the final 30% of stand), spaced over 10–15 years; and whether thresholds would occur. Site fidelity was strong if the harvest levels did not exceed 30%. Between the second and third passes (i.e., after removal of 50% of the stand), no nesting pairs remained. The authors concluded that Goshawks can tolerate some levels of timber harvesting within nesting stands, up to a threshold of 30% removal.
Plotnick and Gardner (1993)	Model	NLM	Fragmentation threshold, gaps, dispersal	30%	Generic	For species able to cross gaps of unsuitable habitat, p_c (or h_{crit})=30%; fine-scale fragmentation poses a greater risk to landscape connectivity than the same fragmentation of habitat at a coarser scale
Pulliam *et al.* (1992)	Model parameterized with empirical data	MAP (e.g., Fahrig 1988); BACHMAP	Reproduction, dispersal, matrix	Variability threshold: Increasing reproductive success from 0.5 to 1.5 female offspring resulted in 100% increase in population size, and 25% decrease in juvenile and adult survivorship resulted in 100% and 400% increase respectively, in extinction probability	Bachman's Sparrow (*Aimophila aestivalis*)	A spatially explicit model incorporating landscape change as a function of timber harvest, and avian demographics, was created to discern the relative impacts of dispersal, reproductive success, and survivorship on population size and extinction probability. Sensitivity analysis showed that variation in demographic variables (juvenile and adult survivorship) affects population size more than variation in dispersal ability.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Rodríguez and Andrén (1999)	Model / empirical	No	Fragmentation threshold Patch and isolation size threshold	26% at regional scale 600 m gap threshold 10 ha at patch threshold	Eurasian Red Squirrels (*Sciurus vulgaris*)	Data from six studies in European deciduous and coniferous forest / farmland habitats were used to parameterize and cross-validate models. Note that of the six landscapes studied, only one has forest as the dominant habitat; range of percent cover of forest at the landscape level is 8–69%.
Rolstad and Wegge (1987)	Model / empirical	No	Fragmentation threshold—qualitative change, reproduction, habitat specialist	50%	Capercaillie (*Tetrao urogallus*) leks	Habitat amount threshold (approximately 50% habitat) = qualitative change in relationship between patch parameters and lek use. Below 50% available habitat, fragmentation had negative effects on cock density, and larger patches were required for persistence. Similarly, there was a threshold patch size, which varied with habitat loss, below which lek density, cocks per lek, and total cock density decreased rapidly.
Saari *et al.* (1998)	Empirical	n/a	Habitat amount threshold; Patch size threshold	10 ha	Hazel Grouse (*Bonasa bonasia*)	Patch size threshold for occupancy and brood presence in Finnish landscape mosaic.
Schmiegelow and Mönkkönen (2002)	Model / empirical	Estimated rarefaction curves for old-forest specialists based on existing data	Habitat amount thresholds, rarity, habitat specialist	At 200 sampled pairs, 13 of 19 (68%) of species observed (sharp inflection point), at ~1100 sampled pairs, 90% of species observed in Canadian boreal; these values could be extrapolated to species area requirements	Old-forest specialists	Study to discern thresholds (i.e., the inflection point) in species richness accumulation curves. Used the random sample hypothesis to discern if habitat loss or fragmentation better predicted mature and old-growth forest specialist bird species in Canadian and Finnish boreal forests. Fragmentation threshold not observed. Established benchmark communities based on long-term reference data to establish the expected number of mature and old forest specialists. Concluded that resident old-growth associates exhibited the greatest sensitivity to habitat loss due to their lower abundance.
Shaffer (1980; 1981: general results ~ 50 individuals = MVP)	Model / empirical	Population viability model parameterized with grizzly data	Habitat amount thresholds, MVP	35–70 animals is MVP 700–10 000 km^2 minimum area requirements for corresponding MVP size	Grizzly Bear (*Ursus arctos*)	Model parameterized with data from grizzlies from Yellowstone National Park. This study determined the MVP, defined as the smallest, isolated population having at least a 95% probability of surviving in 100 years. Used two measures to indicate extinction thresholds: 1. no females >4.5 years in population and 2. no individuals remained of the sexes; observes little difference between results using these two measures.
Spies *et al.* (1994)	Model / empirical	Tested Franklin and Forman's (1987) model	Habitat amount thresholds, fragmentation thresholds, edge thresholds	The empirical analysis shows that edge density peaks at 40% removal, somewhat earlier, but close to the 50% prediction of the model. However, there is approximately 30% interior forest remaining at 50% habitat removal in the empirical landscape, versus no interior forest remaining in the simulated landscape.	Landscape analysis	Examined metrics studied by Franklin and Forman (1987) in a 2,589 km^2 landscape in Oregon's Willamette National Forest and adjacent private land, for which Landsat imagery was used to classify landscape into two classes: less than and greater than 60% conifer cover. The cutting pattern in the empirical landscape does not exhibit the patch size and density thresholds suggested by the model, however, a higher cutting rate in some landscapes resulted in higher amounts of edge and lower amounts of interior habitat than occur in landscapes with lower cutting rates. Spies et al. (1994) attribute the lack of patch thresholds to the scale of their sampling and the nonuniform application of staggered-cutting, suggesting that investigation at a finer scale, where relatively rapid cutting occurs, may reveal thresholds. See Franklin and Forman (1987).

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Summerville and Crist (2001)	Empirical	n/a	Fragmentation threshold, rare	1. No fragmentation threshold for common species 2. 60%—over half of rare butterfly species not observed below this habitat amount 3. 40%—no rare butterfly species observed below this habitat amount	Lepidoptera	Community and species responses generally linearly related to amount of habitat remaining (proportional area hypothesis), except for rare species. Suggest that support for thresholds to habitat fragmentation might be difficult to establish, due to the need for a high number of (e.g., 10–15) landscape replicates.
Swift and Hannon (2002)	Empirical	n/a	Fragmentation threshold	1. 20–40% probability of occurrence 2. 40–60% pairing success 3. 20–30% occurrence of mated pairs	1. Red-breasted Nuthatch, White-breasted Nuthatch, Hairy Woodpecker 2. WBN, HW 3. Downy Woodpecker (also showed no threshold change in occupancy)	AB boreal mixedwood, fifty 100-ha sites with forest cover between 5–80%.
Swihart *et al.* (2001)	Model	Extension of Bascompte and Solé (1998) Mean field metapopulation model and SEPM	Predator-prey, specialist	Threshold varied with model assumptions.	Generic metapopulation	Examined the effect of habitat destruction on predator-prey systems. Focus was to discern the effect of allowing predators to consume alternate prey (resource supplementation). Comparison between generalist predators (using resource supplementation) and specialist predators showed that the benefits of resource supplementation to generalist predators increased non-linearly as habitat destruction occurs. Effect of habitat destruction most pronounced for specialist predators, in that extinction occurred at a lower level of habitat loss.
Thompson and Harestad (1994)	Model / Empirical	MVP / Minimum Viable Habitat Analysis	Habitat area, habitat specificity, fragmentation threshold	1. 237 individuals 2. 600 km^2 3. 70–80% 4. 30%, prefer 50–70%,	American Marten (*Martes americana)* 1. MVP 2. Mature and old forest required to maintain a single MVP 3. Landscape threshold in carrying capacity with small patch cutting. When tree removal in patch cuts at 25% removal exceeds 20–30% of landscape, a non–linear decline appears in maximum carrying capacity. 4. Canopy cover required for marten presence in a stand; greater than half of cover provided by mature or old softwoods.	Boreal mixedwood forest—Ontario. Used empirical data on habitat suitability to estimate carrying capacity across successional stages. Combined with minimum viable population analysis to determine landscape thresholds for amount of mature and old forest required to support viable population.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Tilman *et al.* (1994)	Model	Levins (1969), Nee and May (1992), Tilman (1994)	Extinction debt, competition	~ 35% = acceleration of extinction rate with additional habitat loss	Generic, multi-species	Species are hierarchically ordered based on their competitive ability, following the simplified assumption (Nee and May 1992) that superior competitors are inferior dispersers. Species are predicted to become extinct in order from best to poorest competitors, as habitat destruction continues. Rate of species loss is an accelerating curve at higher levels of habitat loss. See Tilman *et al.* (1997)
Tilman *et al.* (1997)	Model	Levins (1969), Nee and May (1982), Tilman (1994); Tilman *et al.* (1994)	Competition, spatial effects	Varies depending on assumptions about dispersal and mortality rates, and pattern of removal of habitat	Generic, multi-species	Further examines Nee and May's (1992) finding that superior competitors are the species most vulnerable to extinction due to habitat loss.Provides analytical solutions for Tilman *et al.* (1994), extends the model to the spatial case. Spatial model robust to the prediction that species with the poorest dispersal relative to mortality are most susceptible to extinction, whether abundant or rare.
Tscharntke *et al.* (2002)	Empirical	n/a	Fragmentation threshold, edge effect	20%	Rape pollen beetles	Agricultural / grassland landscapes in Germany. Increased parasitism edge effect seen below 20% remaining natural grassland habitat.
Turner *et al.* (1989)	Model	Percolation model	Fragmentation threshold	P_c differentiates qualitative threshold	Qualitative disturbance threshold	Propagation of disturbance qualitatively different above and below p_c . Above, disturbances occurring only within a habitat (e.g., a forest parasite) are favoured; below, disturbances having the capacity of spreading through the matrix or originating in the matrix are favoured.
Venier and Fahrig (1996)	Model	No	Reproduction, dispersal	~40%	Species abundance and distribution and breeding habitat availability	Below approximately 40% breeding habitat, threshold response in abundance and distribution. Study is focused on relationships between species abundance and distribution—findings ascribe relationship to movement relative to breeding habitat availability.
Verboom and Lankester (1991, cited by Metzger and Décamps 1997)	Model	No	Fragmentation	Threshold	Threshold when exceeded, reduces local recolonization rate	Paper not reviewed by this author.
Villard *et al.* (1992, cited by Metzger and Décamps 1997)	Empirical	n/a	Fragmentation	Threshold	Threshold when exceeded, reduces local recolonization rate	Paper not reviewed by this author.
Villard (1999)	Empirical	n/a	Habitat amount threshold—stand level forest cover threshold	1. ~10% forest cover for probability of presence 2. ~20% forest cover for probability of presence 3. ~40% forest cover for probability of presence 4. ~50% forest cover for probability of presence	1. Black-and-White Warbler (*Mniotilta varia*) 2. Ovenbird (*Seiurus aurocapillus*) 3. White-throated Sparrow (*Zonotrichia albicollis*) 4. Chestnut-sided Warbler (*Dendroica pensylvanica*)	Survey of 15 forest bird species in 33 landscapes, 6.25 km^2 in area, with forest cover between 3.4% and 66.8% in eastern Ontario. The authors find that spatial configuration and habitat amount are both important predictors of species presence, and interpret forest cover thresholds for two species (Black-and-White Warbler, Ovenbird) based on the slope of the regression line for probability of presence and forest cover. Note that non-linear change for this statistical test is also apparent for Chestnut-sided Warbler and White-throated Sparrow, although the authors do not comment on this. This study does not detect a fragmentation threshold.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
Virgos (2001)	Empirical	n/a	Fragmentation threshold - isolation	<20%	Badger (*Meles meles*)	Below 20% cover, isolation was best predictor of abundance; above 20% cover, habitat quality was best predictor.
Virkkala (1991)	Empirical	n/a	Fragmentation or habitat amount threshold	Somewhere between 64 and 38% of landscape in old forest	Siberian Tit (*Parus cinctus*), Three-toed Woodpecker (*Picoides tridactylus*), Siberian Jay (*Perisoreus infaustus*), Pine Grosbeaks (*Pinicola enuclator*), and Capercaillie (*Tetrao urogallus*)	Landscape-level study of old-forest associates in northern Finland. Species abundance was lower than expected from habitat loss that occurred between the 1940s and 1980s. However, in a nearby nature reserve (>1 000 km^2) comprised of original forest habitat, there was no significant difference in population density during this time. Young (<20 year) forest in the managed landscape increased nine-fold during this period, to 28% in 1980, while old (>120 year) forest decreased by almost half to 38%. Although the concomitant decrease in old forest likely confounds the results, Andrén 1997 inferred from these data that landscape occupation of >40% by young forest and clearcuts in this landscape crossed the fragmentation threshold.
Wielgus (2002)	Model / empirical	PVA; Leslie matrix (post-breeding, age class)	Population size threshold (PVA), habitat amount threshold	8 556–17 843 km^2 to support a minimum viable population of 200–250 bears	Grizzly Bear (*Ursus arctos*)	Based on demographic data for Grizzly Bear populations in British Columbia, Idaho, Montana, and Wyoming. Results are based on a small probability (p<0.05) of decline to a population at a quasi-extinction threshold (i.e., to a level that would be classed as threatened) within 20 years.
Wiens *et al.* (1997)	Model / empirical	No	Fragmentation threshold	<20%	Tenebrionid beetles	Beetles traversing experimental micro-landscapes, constructed as random mosaics of sand and grass, exhibited a strong threshold in several movement parameters (e.g., net displacement) at <20% grass.
With and Crist (1995)	Model / empirical	Model modified from percolation theory	Fragmentation threshold	20–40%	Two grasshoppers: *Xanthippus corallipes* and *Psoloessa delicatula*	Model findings corroborated with findings in grassland micro-habitat.
With and King (1999a)	Model—random and fractal maps	No	Fragmentation threshold, dispersal, gap thresholds	10%	Dispersal	Below approximately 10% remaining habitat, lacunarity (gap) thresholds were found for area-limited dispersers, corresponding to abrupt declines in dispersal success.
With and King (1999b)	Model—NLM with random and fractal maps	Lande (1987) but spatially explicit so habitat distribution and dispersal non-random. Also, modeled reproductive success (R_o) and dispersal (m) separately, whereas combined in Lande as 'k.'	Habitat supply threshold, fragmentation threshold, dispersal, reproduction	Variable, but generally lower than predicted by Lande (1987) model	Dispersal, reproduction	Thresholds generally lower (i.e., at lower amount of habitat remaining) than Lande (1987) predicted, or did not occur—particularly when landscape clumped and reproduction moderate (R_o >0.1). Exception was poor reproducers (R_o =1.01), which were predicted to go extinct sooner, and more precipitously, than found by Lande's (1987) model.

APPENDIX 1 Table 1. Continued.

Paper	Empirical / theoretical (model)	Prior model?	Sub-topic	Threshold (amount of habitat / cover remaining)	Taxa / species trait	Conditions / comments
With and King (2001)	Model—random and fractal maps	No	Fragmentation threshold, edge, reproduction	Habitat amount was: 1.~1% 2.~20% 3.~30% 4.~50–100% 5.~90%	For species with: 1. low edge, no area sensitivity in clumped fractal landscape 2. low edge, low area sensitivity in fragmented random landscape 3.low edge, high area sensitivity in fragmented random landscape 4. high edge, low area sensitivity in clumped, not at all in fragmented landscape 5. high edge, high area sensitivity in clumped, not at all in fragmented, landscape	Modeled various amounts of area and edge with respect to reproductive parameters for area and edge sensitive and insensitive species in a spatially explicit environment, examining how the fragmentation threshold differed, based on these species traits. Explicitly incorporated the effect of patch structure on reproductive success, as well as examining fecundity and survival as separate parameters. Used reproductive output to elucidate source and sink habitats, and to indicate species edge sensitivity. Modeling suggested that sensitivity to edges can be a more important determinant of thresholds in habitat than can sensitivity to area. Reproductive output was highest on aggregated landscapes (i.e., landscapes with low fragmentation), and lowest on landscapes with high fragmentation. Additionally, the effect of edge sensitivity on reproductive output had the greatest influence on whether species persisted in a given landscape, affecting primarily the level at which thresholds in population persistence occurred in random landscapes.
With *et al.* (1997)	Model	NLM	Fragmentation threshold; habitat quality	29–50% for fractal maps 60% for random maps	Generic	Modeled habitat loss in fractal (clumped) and random (fragmented) habitats to deduce the relative importance of habitat amount, distribution, and quality. Habitat abundance mattered most in random habitats, while effects were scale-dependent on fractal landscapes; habitat abundance was most important at fine scales, habitat quality (habitat affinity) mattered most at coarse scales.
With *et al.* (2002)	Empirical	n/a	Species traits; predator-prey, pest, agroecosystems	20%	Ladybugs (Coccinellidae), aphids, clover	Lacunarity (isolation) threshold, exotic species better than native at tracking prey below threshold, prey insensitive to threshold of 20%.

APPENDIX 1

Table 2. List of studies arranged alphabetically, that demonstrate methods of estimating thresholds; or provide good examples of methods for, or guidance on, structuring experiments on habitat thresholds.

Study	Topic / type of threshold	Comments
Andrén (1996)	Spatial thresholds	Method to determine if the spatial effects of habitat loss are influencing populations or species diversity. Based on the random sample hypothesis (null hypothesis) and the statistical power to reject the null hypothesis.
Andrén *et al.* (1997)	Spatial thresholds	Conceptual method using random sample hypothesis to examine population sizes based on different numerical response types in different landscape mosaics, and to relate population size to the proportion of different landscape elements.
Angelstam and Bleckert (2001)[2]	Habitat thresholds at multiple scales	Presents a framework for assessing the status of landscapes in terms of the need for restoration or the potential intensity of forest management. Incorporates ownership status, and stand-scale tree components, “naturalness” of forests, and degree of forest conversion to non-forest use.
Angelstam and Breuss (2001a)	Thresholds; habitat elements, habitat area	Collection of abstracts characterizing work underway in boreal forests on discerning thresholds.
Angelstam and Breuss (2001b)[2]	Thresholds; habitat elements at tree/patch/stand scale	Uses framework of Angelstam *et al.* (2001a) to examine relationships between habitat elements and biodiversity along a gradient of habitat loss across Europe.
Angelstam *et al.* (2003)	Dead wood thresholds	Reviews several studies that use different methods to characterize dead wood targets to maintain focal species (woodpeckers) at a level above where occur threshold declines in probability of occurrence.
Angelstam *et al.* (2001a)[2]	Stand and landscape elements	Developed for the boreal, framework for approaching the study of thresholds for management application at multiple scales, incorporating focal species, habitat elements, and ecosystem function. See Angelstam and Breuss (2001b)
Angelstam *et al.* (2001b)[2]	Habitat thresholds at landscape scale	Links species’ body size, trophic level, and dependency on large trees, nest holes, and dead wood to current species distributions, and the current conditions. Links loss of species to amount, type, and scale of habitat degradation.
Bond (1994)	Plant-pollinator thresholds	Criteria for ranking the vulnerability of plants to extinction, incorporating pollinator specificity, dependence on the plant-pollinator mutualism, and dependence on seeds for dispersal. This model incorporates compensatory mechanisms, enabling a realistic and subjective assessment of extinction risk in plants.
Doak *et al.* (1992)	Scale and dispersal	Approach to incorporating scale in studies of dispersal.
Doncaster *et al.* (1996)	Habitat threshold	Tests Lawton *et al.* (1994), using Principal Components Analysis to determine the attributes of suitable habitat in order to determine unoccupied fraction, and the incidence function of Hanski (1994) to incorporate spatial features of landscape.
Edenius (2001)	Landscape thresholds, habitat specialist	Development of habitat model to examine habitat needs at multiple scales for Siberian Jay (*Perisoreus infaustus*) in boreal forest.
Eriksson and Kiviniemi (1999)	Habitat thresholds	Uses method of Lawton *et al.* (1994) to estimate habitat thresholds for metapopulations of plants, using analysis of site occupancy and recruitment. Also runs the model incorporating non-equilibrium dynamics.
Fahrig (2003)	Habitat vs. spatial effects	Review of the problem of habitat loss as a confounding variable in studies of fragmentation. Suggests a standard for defining fragmentation.
Frank and Wissel (1998)	Spatial thresholds related to dispersal	Relates the dispersal capability of an organism to the distance separating patches, to determine if individuals in separate patches are subject to spatially correlated environmental changes.

---

[2] Abstract in Angelstam and Breuss (2001a), therefore only limited data available to report here. Paper forthcoming in Angelstam, P. and M. Breuss, eds. 2004. Ecological Bulletins, Volume 51 [In Press].

APPENDIX 1 **Table 2.** Continued.

Study	Topic / type of threshold	Comments
Grimm and Wissel (1997)	Structure for designing research to investigate stability properties	Grimm and Wissel (1997) propose answering three questions when designing or examining a study concerned with stability properties. Based on a stated hypothesis about stability, they suggest the following framework for study design: 1) Which stability properties (constancy, resilience, persistence) are being addressed in the stability statement? 2) To what ecological situation does the statement refer? 3) Is the statement anchored in the situation in question, or is there unacceptable generalization by inferring “stability” of the whole system from a certain stability property in a certain ecological situation? They propose an “ecological checklist” containing the following elements, to answer the second question about the ecological setting: a) level of description (individual, population, community); b) variable of interest; c) reference state or reference dynamic (to determine what is a disturbance and whether a system returns to “normal;” “normal” has to be stated); d) what is being perturbed and what are the spatial and temporal characteristics of the disturbance (disturbance as used here does not include natural disturbance); e) spatial scale; and f) temporal scale. The latter two properties are satisfied by a research area large enough in space and time such that the processes that comprise the system can occur.
Hanski and Ovaskainen (2000)	Landscape threshold for metapopulations	A method to estimate the metapopulation capacity of a real landscape, based on spatial configuration of real patches, and properties of specific species. See Pakkala *et al.* (2002) for applied example.
Hill and Caswell (2001)	Habitat threshold	Model predicts the quasi-equilibrium distribution of occupied patches, the expected extinction time, and the probability of persistence to a given time as a function of the total number of patches and the number of suitable patches in the landscape. Particularly addresses the problem of a finite (small) number of patches in the landscape, and the effect on the habitat threshold of increasing the ability to disperse (search for suitable patch). Describes method for parameterizing model.
Keitt *et al.* (1997)	Spatial thresholds	This spatially explicit (GIS) study of habitat shows that the location of a threshold in landscape connectivity depends on the scale at which a species perceives the landscape as connected. Although the results of this study are species- and landscape-specific, they could be easily modified to create a model for studying other species in other landscapes.
Laurance and Yensen (1991)	Edge thresholds	Method to estimate edge thresholds. Model demonstrates that for an edge-sensitive species, there is a critical range of fragment sizes in which the impacts of edge effects increase almost exponentially. This critical range of fragment sizes is relative to forest type, and depends primarily on the distance that edge effects penetrate into remnant patches.
Lawton *et al.* (1994)	Habitat amount threshold	Simple model based on theory from epidemiology for estimating the threshold amount of habitat required for persistence. See also Doncaster *et al.* (1996) and Eriksson and Kiviniemi (1999).
McGarigal and McComb (1995)	Controlling for effects of habitat loss in examining fragmentation	Good example of method to account for the effects of habitat loss in a study of fragmentation.
Rempel *et al.* (2004)	Monitoring habitat threshold	Describes framework for incorporating thresholds into forest management in the context of adaptive monitoring.
Schemske *et al.* (1994)	Minimum Viable Population	Demographic framework for rare plant recovery efforts.
Thomas and Kunin (1999)	Landscape threshold for metapopulation	Suggests shift away from traditional categorization of metapopulation structure, towards understanding the relative importance of individual patches to regional population persistence. Provides method for evaluating patch network.
Tischendorf and Fahrig (2000)	Connectivity	Proposes standard definition for connectivity, and recommends methods for studying connectivity, based on this definition.
Trzcinski et al. (1999)	Controlling for effects of habitat loss in examining fragmentation	Good example of method to account for the effects of habitat loss in a study of fragmentation.
Vos et al. (2001)	Landscape threshold for metapopulation	Ecological profiles represent clusters of species that differ in their sensitivity to fragmentation, based on dispersal capability and habitat area requirements. Empirical data and model simulations are then used to determine the variables that best predict metapopulation viability.