ARE WE CROSSING ECOLOGICAL THRESHOLDS BY SALVAGE LOGGING IN LANDSCAPES DISTURBED BY MOUNTAIN PINE BEETLE?

by

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ABSTRACT

The theory of ecological resilience focuses on ecosystem processes that can breach thresholds and cause a loss of resilience and a switch to an altered trajectory. Using this theory, I propose hypotheses about habitat changes caused by salvage harvesting following disturbance by mountain pine beetle in Canada. Thresholds could be breached in species, soil or hydrological processes because of habitat changes. I summarize three lessons from the literature about the effects of habitat change on thresholds in species processes. Thresholds relate to the amount and quality of habitat essential for species persistence. Thresholds occur across scales according to species' perceptions of the landscape, and can be induced by an accelerated rate of change. Thresholds are breached as a consequence of traits such as reproduction and species interactions. Policy makers can better elucidate the costs and consequences of breaching thresholds by implementing policy for salvage harvesting that supports adaptive management.

Keywords: ecological resilience; ecological threshold; fragmentation; mountain pine beetle; *Dendroctonus ponderosae*; salvage harvest; ecosystem management; precautionary principle; adaptive management

Subject Terms: Forest ecology – Canada; Forest management – Canada; Ecological disturbances – Canada; Insects – ecology; Forest biodiversity – conservation

For my father, who set the bar,
Thomas, who helped me reach for it
and Kai, for whom it matters.

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1.0 INTRODUCTION

1.1 Ecological thresholds and the mountain pine beetle—agent of landscape change

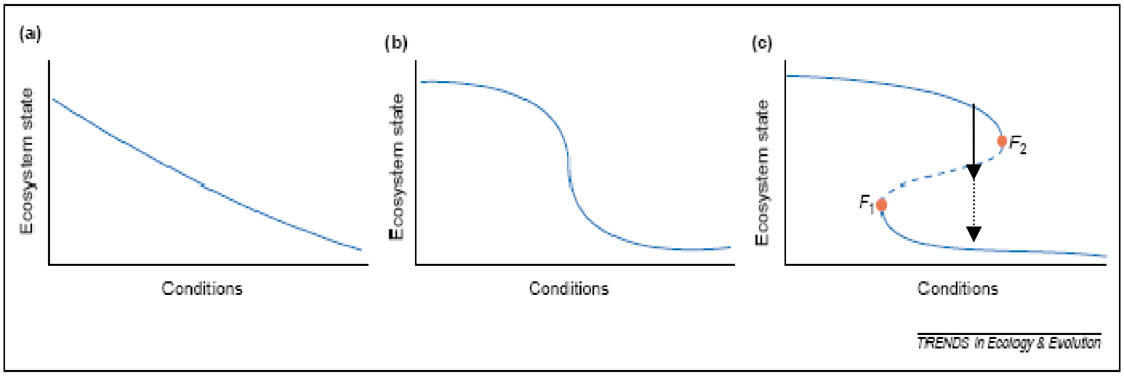
Disturbance by insects is an integral feature of natural disturbance regimes in forests. In some landscapes of western Canada and the north western United States, the mountain pine beetle (MPB; *Dendroctonus ponderosae*) is a primary agent of forest disturbance (Schowalter 2000). Outbreaks in populations of MPB have a pervasive influence on the montane forest ecosystems that contain their primary host, lodgepole pine (*Pinus contorta* var. *latifolia*; Safranyik & Wilson 2006). Ecological thresholds—points of radical change—characterize the population dynamics of MPB within its host ecosystems, causing periodic, epidemic outbreaks that cause high levels of mortality of susceptible trees (Appendix 1; Barryman 2005; Raffa et al. 2008; Scheffer et al. 2001; Scheffer & Carpenter 2003; Walker & Meyers 2004).

In this synthesis, I propose by way of six hypotheses and evidence from the literature, that the perspective of change described by ecological thresholds should further frame our understanding of forest dynamics in managed ecosystems disturbed by MPB. These hypotheses suggest that there is risk that thresholds in other ecosystem properties could be breached in managed forests disturbed by MPB (Andersen et al. 2009). I propose that knowledge about how ecological thresholds are induced should consequently frame our predictions about recovery from the current MPB disturbance (Chapin et al. 2006). I then present and discuss the implications of three lessons from the literature about the threshold response of animal species to changes in forest habitat, one means by which I hypothesize that thresholds in managed MPB ecosystems may manifest.

The concept of ecological thresholds has emerged over the past decade as an applied perspective in resource management (Andersen et al. 2009;

Angelstam et al. 2004b; Bissonette & Storch 2002; Briske et al. 2005; Burkett et al. 2005; Chapin et al. 2006; du Toit et al. 2004; Duinker & Greig 2006; Eiswerth & Haney 2001; Eken et al. 2004; Groffman et al. 2006; Huggett 2005; Lindenmayer & Luck 2005; Scheffer et al. 2001; Scheffer & Carpenter 2003). This concept has a long and pervasive history, evolving in part from the debate about ecological stability. Historically, ecological stability from the perspective of the "balance of nature" or "steady state" paradigm considered only a single, static configuration toward which an ecosystem would develop (Egerton 1973; Perry 2002; Pimm 1991; Wu & Loucks 1995). Although deeply embedded in ecological thinking, this paradigm had a theological, rather than a theoretical or empirical basis, and dissenting perspectives are centuries old (Egerton 1973). In particular, since the late 1960s, research about ecosystem stability has expanded to consider the concepts of ecological resilience—the capacity of an ecological system to absorb perturbation, reorganize and persist (see Section 2.0 for a more detailed discussion of ecological resilience; Holling 1973). The concept of ecological resilience includes the potential for multiple regimes in ecosystems—a regime describes the range of conditions within which the system remains resilient to perturbation (e.g., Augustine et al. 1998; Folke et al. 2004; Scheffer et al. 2001; Scheffer & Carpenter 2003; Sutherland 1974; van Langevelde et al. 2003); and by extension, thresholds of change (Holling 1973; Ludwig et al. 1997; May 1973, 1977; Wissel 1984).

Ecological thresholds separate alternate conditions or regimes in ecosystems or species' populations (Figure 1; Scheffer et al. 2001; Scheffer & Carpenter 2003; Walker & Meyers 2004). Ecological thresholds and regime shifts occur across the globe in managed and unmanaged forest, grassland, Arctic, freshwater and marine ecosystems (Folke et al. 2004; Gunderson 2000; Walker & Meyers 2004). Types of ecological responses include shifts between dominant plant forms in response to grazing or browsing pressure; for example from grasslands to woody vegetation in Australia (Ludwig et al. 1997; Walker et al. 1981), and from floodplains dominated by willow (*Salix* sp.) to domination by alder (*Alnus* sp.) in floodplains in Alaska, with consequent shifts in nitrogen fixation and successional trajectories (Danell et al. 2003). In forests, regime shifts between extensive, mature forest canopy dominated by spruce (*Picea* sp.) and fir (*Abies* sp.), to regeneration dominated by aspen (*Populus* sp.) and birch (*Betula* sp.), can occur through the periodic, landscape scale herbivory of spruce budworm (*Choristoneura fumiferana*) populations in eastern Canada (Holling 1973; Holling 1978; Ludwig et al. 1978). When influenced by human actions, the crossing of thresholds can produce changes that are undesirable, long-lived or irreversible (Wissel 1984), such as losses of diversity or productivity, or biological invasions (Bascompte & Rodríguez 2001; Vitousek et al. 1987; Walker & Meyers 2004; Zimov et al. 1995).



TRENDS in Ecology & Evolution

Figure 1. Three different ways in which an ecosystem variable can respond to a change in conditions. a) the system can change smoothly over a range of conditions, b) the system can change profoundly at a critical level, or c) the system can have more than one regime over a range of conditions. Graphs b) and c) indicate ecological thresholds. c) shows two ways to shift between regimes (Scheffer et al 2001). I) If the system is on the upper branch, but close to the bifurcation point F2, a slight incremental change in conditions may bring it beyond the bifurcation and induce a catastrophic shift to the lower alternative stable state ('forward shift'). II) A perturbation (solid arrow) may also induce a shift to the alternative stable state (dashed arrow), if it is sufficiently large to bring the system over the border of the attraction basin. In both cases, if one tries to restore the state on the upper branch by means of reversing the conditions, the system shows hysteresis. A backward shift occurs only if conditions are reversed far enough to reach the other bifurcation point, F1. Figure text from Figure 2 from Scheffer et al. (2001). Reprinted with permission. Figure 2 from Scheffer and Carpenter (2003). Reprinted with permission.

Changes in system feedback and in the rate of system processes characterize thresholds (Scheffer et al. 2001; Walker & Meyers 2004). Thresholds between regimes arise when key system attributes that change slowly, reach a condition and simultaneously experience an external trigger that can cause either rapid or slow change to the trajectory of a system. For example, the alternate regimes in MPB population dynamics are controlled by the slowly changing variable of host availability—primarily the extent and distribution of mature lodgepole pine trees (Barryman 2005; Raffa et al. 2008; Safranyik & Carroll 2006). For MPB, alternate regimes occur with a rapid change in population dynamics from endemic to epidemic populations, when the extensive availability of mature trees occurs simultaneous to a trigger in climate conditions, such as the absence of severely cold winter conditions.

When the climatic trigger and landscape attributes approach the values associated with threshold changes in MPB population dynamics, the rate and properties of feedback in the system change from a regime dominated by negative feedback that maintains resilience, to the dominance of positive feedback that reduces resilience (Raffa et al. 2008; Walker & Meyers 2004).The alternate regimes are characterized by changes to the conditions of the forests containing the host species lodgepole pine. The endemic regime corresponds to tree mortality at the scale of individual trees or small groups of trees that have low resistance to attack (Raffa et al. 2008; Safranyik & Carroll 2006). Epidemic conditions correspond to widespread tree mortality at stand and landscape scales and consequent shifts in species composition and productivity (Dykstra & Braumandl 2006; Romme et al. 1986; Stone & Wolfe 1996).

Human influence on host availability, the slowly changing attribute of the MPB system, is evident in two ways. First, climate warming has resulted in an expansion of the suitable range of MPB over the past three decades (Carroll et al. 2003; Taylor et al. 2006) and continued range expansion is predicted (Bentz et al. 2001; Logan & Bentz 1999; Logan & Powell 2001). Second, historic forest policy has affected the abundance and distribution of susceptible lodgepole pine trees and ecosystems. A policy of fire suppression over the past hundred years tripled the amount of susceptible lodgepole pine on the landscape over the amount present a century ago (Taylor et al. 2006). Recently, mild winters have failed to bring about the sustained cold necessary to limit the population growth of MPB (Taylor et al. 2006). The occurrence of host availability that is three times more widespread than a century ago, combined with an extended period of relatively mild winters, have occurred simultaneously to remove the negative feedbacks on MPB rate of population growth over a vast area, resulting in the current unprecedented outbreak (Raffa et al. 2008).

Since 1995, epidemic disturbance by MPB in British Columbia has affected 13.5 million hectares of managed forest land and 620 million cubic meters of merchantable lodgepole pine (Walton et al. 2008). This represents 46% of the merchantable lodgepole pine in the province, and MPB may potentially affect 80% of the province's total mature lodgepole pine, the most important commercial tree species in BC (Walton et al. 2008). From historical records, Taylor et al. (2006) estimate that the current disturbance area (covering 135,000 square km of forest) is an order of magnitude larger than in all previous outbreaks. I hypothesize that directional (human) influences altered the disturbance regime and contributed to the magnitude of the current MPB disturbance (Chapin et al. 2006).

1.2 Policy response to MPB disturbance

In 2004, the policy response of the provincial government shifted from trying to control the spread of MPB, to attempting to minimize the impacts of timber losses by facilitating widespread salvage harvesting (Pedersen 2004). Salvage harvesting is the logging of dead or damaged trees and stands following a natural disturbance event. The predominant policy response to the current outbreak is thus large, temporary increases to the rate of cut (allowable annual cut; AAC) in affected landscapes (commonly referred to as 'the uplift'; Table 1 displays the increases to AACs for selected areas). The intent is to implement the uplift over a narrow time frame, in order to maximize the economic value of affected timber[1] (Pedersen 2004). Reflecting the extent of the disturbance itself, the uplift policy allows for a rate of harvest without historical precedent. The provincial government has proceeded with the policy of accelerated harvesting with the intent to continue to maintain non-timber resources such as biodiversity,

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[1] http://www.for.gov.bc.ca/hts/tsr.htm—see AAC determinations for affected Timber Supply Areas

even though pre-existing conservation policy has been waived[1] (Eng 2004; Pedersen 2004; Snetsinger 2005).

Table 1. Uplift increases to allowable annual cuts as of 2007 for some affected Timber Supply Areas.

TIMBER SUPPLY AREA	% INCREASE TO PRE-2004 AAC TO ESTABLISH UPLIFT AAC
Prince George	60
Lakes	111
Quesnel	126
Merritt	53
Okanagan	27
100 Mile House	50
Williams Lake	53
AVERAGE	64

1.3 Ecological effects of salvage harvesting

While salvage harvest addresses socio-economic concerns related to the loss of timber values, it is often at odds with other policy objectives, including the protection of biodiversity (Folke et al. 1996; Schmiegelow et al. 2006). Research about the impacts of salvage harvesting on ecosystems is widespread (e.g., Lindenmayer et al. 2008; Lindenmayer & Noss 2006; McIver & Starr 2001); however, most data focus on salvage harvesting that follows disturbance by fire; there is very little peer-reviewed data available on the impacts of salvage in forests disturbed by MPB (but see Bunnell et al. 2004; Chan-McLeod 2006; Dykstra & Braumandl 2006; Forest Practices Board 2007a, b) or by forest insects generally (but see Foster & Orwig 2006; Schroeder 2007). In the absence of knowledge specific to these ecosystems, we can turn to other systems to help predict possible outcomes of salvage harvesting following MPB disturbance. There are at least three, interrelated lines of evidence that point to the need for a particularly careful assessment of the risk salvage harvesting poses to species persistence and ecosystem recovery in forests disturbed by MPB.

First, there is evidence of direct ecological impacts of salvage harvest in other ecosystems. Whereas natural disturbances are typically an integral component of ecosystem function in forests, salvage disturbance can undermine the ecosystem benefits of major disturbances (Lindenmayer et al. 2004). Salvage harvesting removes or disturbs remnant organisms, organic materials and spatial patterns; these are the biological legacies of disturbance that in part determine the rate and pathway of ecosystem recovery (Franklin et al. 2000; Franklin et al. 1985). The removal of remnant forest patches and individual live or dead trees, downed logs and understory vegetation can negatively affect species that depend on these legacies (Lindenmayer & Noss 2006), and alter successional pathways through the removal of seed sources (Morissette et al. 2002; Nappi et al. 2004). Salvage harvesting can also hinder ecosystem recovery through the alteration of soil and hydrological processes (Foster et al. 1997; McIver & Starr 2000; McIver & Starr 2001). From their literature review of the effects of salvage harvesting on ecosystem processes and biodiversity, Lindenmayer and Noss (2006) conclude that the impacts of salvage harvest have three, interactive effects on ecosystems.

1. *altered stand complexity*
2. *altered ecosystem processes and functions*
3. *altered populations of species and community composition*

Second, two or more cumulative disturbances in quick succession (in a time span that is shorter than the recovery time of the community) can cause a loss of resilience and a switch to an altered regime (Figure 2; Paine et al. 1998; Scheffer et al. 2001). Characteristics of these altered regimes in such circumstances in other ecosystems include the extirpation of species, changes in community composition, species invasions, changes in soil processes, and degraded, less productive states. Salvage harvesting exposes forest ecosystems disturbed by MPB to additional disturbance, and may be particularly deleterious where ecosystem processes or taxa are maladapted to the interactive effects of multiple disturbances (Foster et al. 1997; Lindenmayer et al. 2004; Lindenmayer & Noss 2006; Paine et al. 1998; Schmiegelow et al. 2006). Multiple disturbances in quick succession can alter the processes and pathways of ecosystem recovery; I propose that salvage harvesting in ecosystems disturbed by MPB may be a form of cumulative disturbance that may have deleterious impacts.

Third, recovery from the current disturbance might differ from historic conditions simply due to the magnitude of the current MPB disturbance. Ecosystems may respond differently to large infrequent disturbances than they do to smaller, more frequent disturbance of the same type (Romme et al. 1998; Turner et al. 1998), even in the absence of a management intervention such as salvage harvest. Differences in disturbance extent, frequency and intensity initiate different successional trajectories (Romme et al. 1998; Turner et al. 1998). Romme et al. (1998) pose a conceptual model of disturbance recovery that includes thresholds in ecosystem function because of disturbance extent and intensity (Figure 3). The model proposes that the impact of disturbance on some functions could shift markedly along a gradient of disturbance magnitude, and that threshold changes could occur in process rates and functional responses following large infrequent disturbances. This hypothesis implies that disturbance effects that are relatively benign at smaller scales can be problematic for ecosystem functioning if they are widespread over larger scales. For example, the removal or destruction of seed sources, if it exceeds the dispersal capacity of the species, would change local or regional vegetation composition (line 3 in Figure 3; Drever et al. 2006; Turner et al. 1998). I hypothesize that due to the magnitude of the MPB disturbance, ecosystem recovery may be qualitatively different from the processes of recovery that would follow a smaller epidemic.

The evidence from other ecosystems of the direct effects of salvage harvesting, and the general effects of cumulative disturbance should be considered in view of the potential for a large disturbance event to alter the pathways and processes of recovery. However, in contrast to the type and magnitude of risk posed by extensive salvage harvesting in landscapes recently disturbed by MPB, a compelling assessment of the risk posed by salvage harvest is lacking[1] (Eng 2004; Pedersen 2004; Snetsinger 2005).

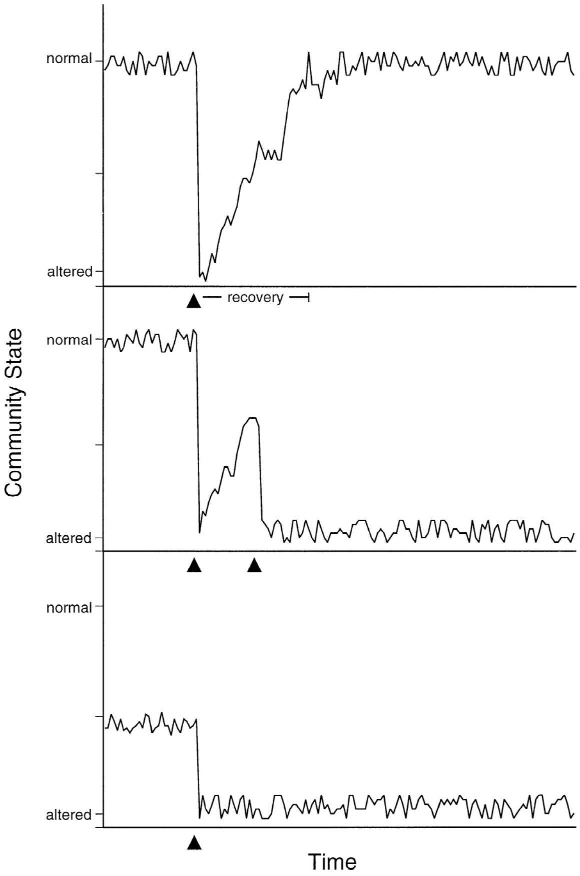


Figure 2. Schematic representation of the effects of large, infrequent disturbances (LIDs) on community state. Top, A normal community is subjected to a single LID and subsequently recovers. Middle, A normal community undergoes a second (or multiple) disturbance(s) before recovery from the first is completed; the combined effects lead to long-term alteration in community state. Bottom, A major disturbance is superimposed on an assemblage already altered by anthropogenic processes or disease; again the combination of stresses leads to long-term alteration of community state. Arrowheads mark the disturbances. Figure 1 from Paine et al. (1998). Reprinted with permission.

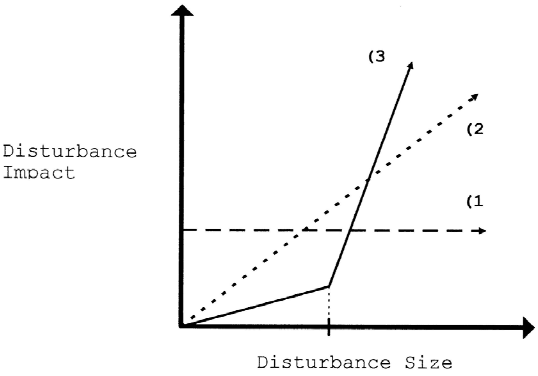


Figure 3. Graphical model of ecosystem-disturbance dynamics showing three general kinds of response of disturbance impact to increasing “size” (extent, intensity, duration or frequency) of disturbance. (1) scale-independent response, (2) continuous response, and (3) threshold response. Figure 1 from Romme et al. (1998). Reprinted with permission.

2.0 ECOLOGICAL RESILIENCE

Ecological resilience is an integrating concept that has developed in part from management models based on natural disturbance regimes (Holling 1973; Holling 1986, 1996; Holling & Meffe 1996; Hunter 1999). Ecological resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change, such that the system retains essentially the same function, structure, identity and feedbacks (Walker et al. 2004). The persistence of the system relates to two aspects: adaptive capacity—the ability of the system to adjust as change occurs to key attributes of the system; and the capacity to self-organize following disturbance—in contrast to a lack of organization or organization forced by external factors (Folke et al. 2004; Gunderson 2000; Holling 1992).

The capacity to self-organize arises in part according to a small set of endogenous plant, animal and abiotic processes, such as natural disturbance. This small set of processes provides structure for and maintains some ecosystems across scales of time and space (Figure 4A; Holling 1986; Holling 1992; Yourke et al. 2002). These processes are hierarchical. The spatial and temporal frequencies of key processes are often separated by an order of magnitude, creating a discontinuous distribution of structure on the landscape (Figure 4A). The nested hierarchy of processes corresponds to a patchy hierarchy of structure; ecological processes shape ecosystem pattern (Kotliar & Wiens 1990; O'Neill et al. 1991; Turner 1989; Wiens 1989).

In forested systems like those recently disturbed by MPB, key, distinct aspects of forest structure occur at definable scales (Figure 4A; Angelstam 1996; Bunnell 1995; Holling 1992). Each aspect of forest structure is a consequence of processes that occur at shared temporal and spatial frequencies (Holling 1992). Types of forest structure range from needles on the scale of centimeters through to trees and stands on scales of meters to kilometers, to landscapes at the scale of tens to thousands of kilometers. At finer scales, dominant processes relate to plant morphology and physiology, such as the annual turnover of needles on conifer trees. At meso scales, disturbance processes dominate, including fire and insects. These processes operating at individual scales—tree, patch and landscape—create cycles of growth, senescence and renewal that occur at multiple frequencies of space and time. These cycles show that there is an interrelationship between process and structure that is mutually reinforcing within and across scales (Gunderson & Holling 2002; Turner 1989). Faster processes operating at smaller scales are constrained by and linked to slower process at larger scales (Gunderson & Holling 2002; Urban et al. 1987).

Holling (1992) proposes that a small set of key processes establishes a persistent template upon which other ecosystem attributes develop. Examining the distribution of birds and mammals according to their body mass in short-grass prairie and boreal forest ecosystems, he demonstrates an example of the relationship between key structuring processes and other ecosystem attributes. Holling (1992) finds that the distribution of these organisms paralleled the discontinuous distribution of process and structure, a relationship that occurred across the two biomes for the groups of birds and mammals in each biome. More recent work has confirmed discontinuous body mass patterns in other systems (Allen et al. 1999; Havlicek & Carpenter 2001; Lambert & Holling 1998; Raffaelli et al. 2000; Restrepo et al. 1997). Through their use of vegetation structure, across the scale hierarchy, the life cycles of organisms link to process rates (Figure 4B). Organisms occupy the forest to meet their daily, seasonal and lifetime needs—nourishment at a fine scale, territory at mid scale, and dispersal and migration at coarser scales. This distribution suggests the association of species rates of process to rates disturbance. I hypothesize that the historic range of natural variability in disturbance regimes is one of a small set of critical structuring processes that maintains resilience in the ecosystems that contain the host species of MPB (*sensu* Holling 1992).

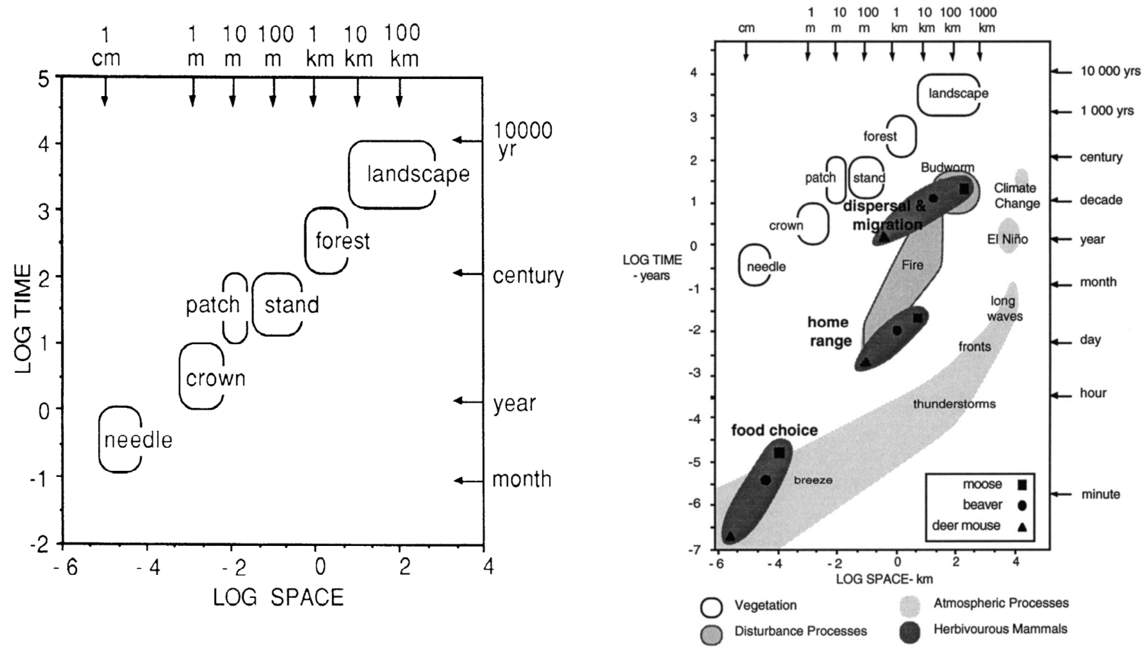
The idea of a small set of key structuring processes in self-organized systems leads to several observations. First, resilience is an emergent property of self-organized systems. Resilience relates to the way in which, within and across scale ranges, there is an interrelationship of structure and process that maintains the system (Elmqvist et al. 2003; Peterson et al. 1998; Peterson 2002). However, resilience is not considered a constant property of the system; resilience varies in an integral way throughout the cycles of growth, senescence and renewal (Gunderson & Holling 2002). Resilience is proposed to be at its lowest point of the cycle immediately following disturbance, when reorganization of the system occurs. During this time, the system is considered most vulnerable to switching to an alternate regime (Gunderson & Holling 2002; Holling 1986; Holling 1992).

Second, there is a range of conditions within which the system is resilient. The dynamic cycle between processes and patterns in forests creates the structure and composition of forests across spatial and temporal scales (Landres et al. 1999; Lertzman et al. 1998; Peterson et al. 1998; Peterson 2002; Turner 1989). The recovery at finer scales that follows disturbance maintains resilience at coarser scales (Kinzig et al. 2006), while organisms distributed across coarser scales maintain resilience at finer scales, for example, through the provision of pollination or seed distribution (Elmqvist et al. 2003; Kinzig et al. 2006; Lundberg & Moberg 2003; Noss 2001; Peterson et al. 1998). A system that retains its resilience can recover from disturbance to the pre-disturbance condition because, although resilience may be at its lowest level immediately following disturbance, resident species have evolved or adapted to persist within the structure and composition that result from natural disturbance regimes (Bunnell 1995; Holling 1992; Hunter 1999). The capacity of species and ecosystems to recover from historic, natural disturbances suggests they should have a tolerance to the replacement of disturbance with harvesting (Bergeron et al. 1999; Bergeron et al. 2002; Bunnell 1995; DeLong & Kessler 2000; Hobson & Schieck 1999; Holling 1992; Hunter 1999). The broad scale policy interpretation is that within the appropriate bounds of disturbance impacts, harvesting can mimic natural disturbance in some meaningful ways and can therefore maintain habitat for many species in forested ecosystems (Bergeron et al. 2002; Schmiegelow et al. 2006). This is a coarse filter approach to conservation in managed landscapes.

However, the central idea in terms of risk to persistence and recovery following disturbance leads to a third observation about self-organized systems. Risk increases when altered rates of disturbance disrupt the capacity to adapt and self-organize, delay recovery and/or change the pathways of recovery (Chapin et al. 2006; Folke et al. 2004; Haeussler et al. 2002). The emphasis on rates of processes emphasizes that factors that cause rates to change may have implications for ecological resilience (Scheffer et al. 2001; Scheffer & Carpenter 2003; Walker & Meyers 2004).

Resilience theory (Folke et al. 2004; Gunderson & Holling 2002; Gunderson 2000; Holling 1973; Holling 1986, 1996; Peterson et al. 1998; Walker et al. 2004; Walker & Meyers 2004) provides an integrated perspective that considers the variables and dynamics of both the management and ecological system to help determine how recovery from disturbance will occur. Resilience theory provides a framework for understanding how change occurs in managed forest ecosystems because it encompasses natural disturbance regimes, adaptability, recovery, thresholds, and the management actions that could influence these attributes (Gunderson & Holling 2002; Holling 1978; Holling & Meffe 1996). Accordingly, the concept of resilience has started to become the basis for the management of natural resources globally (e.g., Bellwood et al. 2004; Hughes et al. 2007), including future forest management in British Columbia (British Columbia Ministry of Forests and Range 2008).

With their explicit focus on management influences, adaptability, recovery and thresholds, the concepts of ecological resilience can inform the policy issues surrounding the current MPB disturbance. Resilience theory can be used to understand the threshold dynamics and different regimes of the ecosystems disturbed by MPB (Barryman 2005; Raffa et al. 2008). Resilience theory provides a framework to understand the association between rates of natural disturbance and the recovery and persistence of species (Holling 1992). Resilience theory



A)

B)

Figure 4. Logarithmic time and space scales of landscape elements and ecosystems of the boreal forest. A). The temporal scale is based on dimensions in years, the spatial scale on dimensions in kilometres. B). As for 4A), showing the relationship between some of the landscape elements and processes that structure the forest. These processes include insect outbreaks, fire, atmospheric processes and the rapid carbon dioxide increase in modern times (Clark 1985). Contagious mesoscale disturbance processes provide a linkage between macroscale atmospheric processes and microscale landscape processes. 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 4A) is Figure 1 from Holling (1992). Reprinted with permission. Figure 4B) is Figure 8 in Peterson et al. (1998). Reprinted with permission.

reveals that exceeding the natural range of rates of disturbance creates risks for ecosystem recovery (Walker & Meyers 2004).

Resilience theory can also help understand how risks to recovery are created or exacerbated (Chapin et al. 2006; Folke et al. 2004; Raffa et al. 2008; Walker et al. 2006). Resilience theory identifies the link between forest policy and MPB disturbance (Barryman 2005; Raffa et al. 2008; Walker & Meyers 2004). A multi-decadal practice of fire suppression altered natural rates of disturbance and increased the area and contagion of trees and forests susceptible to MPB disturbance (Taylor et al. 2006). The current policy response to the ensuing MPB disturbance involves abandoning the management model based on natural disturbance in favour of salvage policy (Schmiegelow et al. 2006) and an increase to the allowable rate of harvest disturbance. These human influences on the system affect a variable that resilience theory identifies as key to the natural process of recovery—rate of disturbance. These influences on rate of disturbance create risks to recovery because management actions that occur outside of the context of natural disturbance regimes by exceeding the rate, extent or severity of a critical process, such as disturbance, increase our uncertainty about the pathways and processes of recovery (Folke et al. 2004; Holling & Meffe 1996; Lindenmayer & McCarthy 2002; Paine et al. 1998; Walker & Meyers 2004). Resilience theory thus provides a unifying framework that explicitly identifies and incorporates the key elements present in issues raised by a policy of salvage harvest of ecosystems disturbed by MPB. However, the utility of this perspective for application to resource management is related to its predictive capacity (Andersen et al. 2009; Chapin et al. 2006; Groffman et al. 2006; Huggett 2005).

Chapin et al. (2006) argue that in systems affected by directional (i.e., human) influences, there are limits to the predictive capacity of existing, steady state hypotheses about recovery. They propose that in a directionally changing world, hypotheses of ecosystem change must incorporate the perspectives of resilience theory, such as the potential to breach thresholds and cause regime shifts in ecosystem attributes in response to ecosystem change. The policy of fire suppression is an example of a directional influence that causes a shift in the variables that control community structure (Chapin et al. 2006; Raffa et al. 2008; Walker & Meyers 2004). In this case, the directional influence alters the amount and distribution of the susceptible host of MPB, lodgepole pine, which in turn affects the natural disturbance regime (Raffa et al. 2008; Taylor et al. 2006). Chapin et al. (2006; p.39) propose seven new hypotheses for predicting change in a directionally changing world, six of which are relevant to the current MPB disturbance. Table 2 summarizes these hypotheses in terms of their relevance to salvage harvesting the current MPB disturbance.

Chapin et al. (2006) hypothesize that in general, threshold changes describing negative impacts should be expected to occur under conditions such as those of the lodgepole pine ecosystems disturbed by MPB. They recognize that the observed dynamics of change will be dictated by the local factors and conditions that characterize individual management issues. The negative impacts suggested by some of these hypotheses are already apparent in ecosystems disturbed by MPB (e.g., hypotheses two and six); while potentially positive effects (hypothesis seven) are negated by the current policy approach.

I hypothesize that salvage harvesting could result in further changes that induce threshold responses in ecosystem attributes. In the case of MPB disturbance, the primary influence of epidemic MPB populations is on the abundance and configuration of habitat types (Chan-McLeod 2006; Shore et al. 2006; but see also Kurz et al. (2008) regarding impacts to carbon storage). These changed habitats are then, via salvage harvesting, reduced in their complexity, with effects on particular species and species assemblages (Lindenmayer & Noss 2006). Applying Chapin et al.'s (2006) hypotheses about change in a directional environment, to form predictions about the potential effects of salvage harvesting suggests that threshold responses could arise through two pathways if salvage harvesting reduces habitat to critical levels. I hypothesize that threshold responses could manifest through changes in species presence or abundance, including species of soil fauna; and/or through changes in other soil properties, and/or through changes to hydrological regimes (Table 2 hypotheses one, two, three and four).

While the literature on threshold responses of species to changes in habitat is abundant, the relevant literature examining threshold responses in water and soil properties to habitat change appears to be sparse. Available soils literature pertains to situations such as fire disturbance (e.g., MacDonald & Huffman 2004) and pollution (e.g., Augustin et al. 2005; Bowman et al. 2008; Gundersen et al. 2006), and to other forest types (e.g., Cowling & Shin 2006; Ren et al. 2007). Potentially applicable studies in similar ecosystems do not discern thresholds in soil properties (e.g., Jerabkova et al. 2006). Thresholds describe regime shifts in groundwater regimes (e.g., Redding & Devito 2008), and hydrological resources in British Columbia are increasingly garnering general attention (e.g., Smerdon et al. 2009). The idea of thresholds in hydrological processes as a consequence of MPB salvage has been explored (Forest Practices Board 2007a). I thus undertook a synthesis of the literature on the threshold response of species attributes to changes in forest habitat (herein called habitat thresholds) to distill the key lessons relevant to the current MPB disturbance and salvage harvest. Table 3 summarizes the six hypotheses from the literature that I have applied to present the case for a closer examination of the potential risks involved in salvage harvesting landscapes disturbed by MPB.

Table 2. Hypotheses for community predictions in a directionally changing world and their relevance to the current MPB disturbance and salvage harvest. Chapin et al.'s (2006) seven hypotheses are displayed in the left column. The right column displays my interpretation of how each hypothesis is relevant to this management problem, and, in underlined, capitalized italics, my interpretation of existing or potential conditions.

HYPOTHESIS	RELEVANCE TO MPB DISTURBANCE AND SALVAGE HARVEST
1. Directional changes in processes that alter critical soil or sediment resources will trigger threshold changes in community structure and dynamics.	Processes related to soil and water resources (e.g., sedimentation) are in part influenced by forest cover and therefore by harvest activities (i.e., road building, removal of forest cover; e.g., Croke & Hairsine 2006; Forest Practices Board 2007a). *POTENTIAL NEGATIVE EFFECT OF HABITAT REMOVAL*
2. Directional changes in the abundance of species that alter soil resource supply or disturbance regime often trigger threshold changes in communities and ecosystems.	1. Species related to soil resources (e.g., decomposers) are in part influenced by forest cover and therefore by harvest activities (i.e., road building, removal of forest cover). *POTENTIAL NEGATIVE EFFECT OF HABITAT REMOVAL* 2. MPB is a species affected by human influence (directional influence). *OBSERVED EFFECT* 3. As a consequence of the current disturbance event, MPB will alter the rate of input to the soil of fine and coarse debris. *POTENTIAL EFFECT*
3. Disturbance events, especially those that are extreme in size, frequency, or severity, often catalyze community change in a directionally changing environment.	Current disturbance extreme is size and severity (Taylor et al. 2006). *POTENTIAL NEGATIVE EFFECT FROM DISTURBANCE ALONE, COMPOUNDED BY HABITAT REMOVAL*
4. Responsiveness to short-term costs and benefits often leads to human actions with unintended long-term human impacts on social-ecological systems.	1. Fire suppression (directional influence) has an unintended impact on disturbance regimes (Taylor et al. 2006). *OBSERVED EFFECT* 2. Salvage harvest to optimize short term economic benefits may have unintended long-term consequences. *POTENTIAL NEGATIVE EFFECT OF HABITAT REMOVAL*
5. Human impacts that occur far from the site of decision making or that are geographically dispersed are often overlooked in policies that affect social-ecological systems.	Not relevant to this management issue.
6. Societal expectations of ecosystem services based on past conditions constrain the capacity of people to adjust their ecological impacts in a directionally changing world.	Current, steady state assumptions prevent society from perceiving the potential for threshold-like change in ecosystem attributes as a consequence of forest policies like salvage harvest. *OBSERVED EFFECT*
7. Institutions that strengthen negative feedbacks between human actions and social-ecological consequences can reduce human impacts through more responsive (and thus more effective) management of common pool resources.	Changing our perception of ecological change to encompass the potential for regime shifts in response to management actions would increase the effectiveness of management agencies. *POTENTIAL POSITIVE EFFECT OF A MANAGEMENT PARADIGM BASED ON ECOLOGICAL RESILIENCE*

Table 3. Six hypotheses from the literature applied to the issue of MPB salvage.

HYPOTHESIS #	HYPOTHESIS	SOURCE
Hypothesis 1	The historic range of natural variability in disturbance regimes is one of a small set of critical structuring processes that maintains resilience in the ecosystems that contain the host species of MPB.	(Holling 1992)
Hypothesis 2	Directional (human) influences altered the disturbance regime and contributed to the magnitude of the current MPB disturbance.	(Chapin et al. 2006; Raffa et al. 2008; Taylor et al. 2006)
Hypothesis 3	Due to the magnitude of the disturbance, ecosystem recovery may be qualitatively different than the processes of recovery that would follow a smaller MPB epidemic.	(Romme et al. 1998; Turner et al. 1998)
Hypothesis 4	Multiple disturbances in quick succession can alter the processes and pathways of ecosystem recovery. I propose that salvage harvesting in ecosystems disturbed by MPB may be a form of cumulative disturbance that may have deleterious impacts.	(Paine et al. 1998; Scheffer et al. 2001)
Hypothesis 5	I propose that while the current MPB disturbance represents a demonstrated type of ecological threshold, the cumulative disturbance caused by salvage harvesting could cause secondary thresholds to be breached in other ecosystems properties.	(Andersen et al. 2009; Barryman 2005; Raffa et al. 2008)
Hypothesis 6	I propose that the ecosystem properties most likely to exhibit threshold changes as a consequence of salvage harvesting involve attributes of species and forest soils.	(Chapin et al. 2006; Lindenmayer and Noss 2006)

3.0 TYPES, DEFINITIONS AND CHARACTERISTICS OF HABITAT THRESHOLDS

The term habitat threshold, in reference to the non-linear response of primarily animal species to changes in habitat, sees multiple applications in the literature. To clarify some of the confusion that arises from different terminology, Table 4 provides definitions and the source references for the types of thresholds discussed in this review.

In the context of changes to forest habitat, the idea of ecological thresholds suggests a critical region of habitat alteration around which previously linear or undetected response in a process, such as species reproduction, changes in such a way as to eventually create an alternate regime in population size (e.g., from a viable population to a small and unviable population). In this situation, when habitat is more abundant than the threshold value, population size fluctuates, but the population remains viable. When habitat declines or degrades toward the threshold region, the probability of extinction increases from near zero to near one (Figure 5; Fahrig 2001, 2002). Threshold responses in the attributes of species to changes in habitat (see Table 4 for definitions) differentiate between incremental changes in habitat that lead to extinction (threshold response), and changes in habitat that simply lead to an incremental decline in population size or diversity and only a small increase to the probability of extinction (non-threshold response) (Figure 5; Fahrig 2001, 2002).

While Figure 5 shows a hypothetical threshold from the literature, this representation is simplified. Regime shifts can occur over a range of conditions in part because they can be induced by external perturbation (demonstrated by the region between the arrow and F2 in Figure 1(c); in the case of habitat thresholds, the conditions on the x-axis in Figure 1(c) are the amount / quality of habitat and the ecosystem state on the y-axis is survival probability; Scheffer & Carpenter 2003).

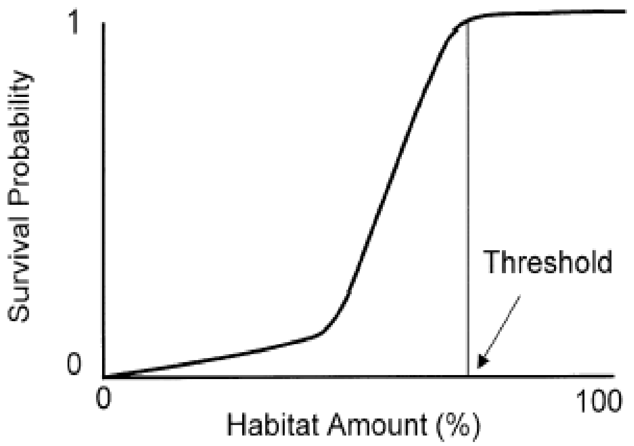


Figure 5. Illustration of the extinction threshold. When habitat amount is reduced to below the threshold the probability of population survival drops precipitously. Figure 1 from Fahrig (2001). Reprinted with permission.

Table 4. Habitat thresholds defined.

TYPE OF THRESHOLD	DEFINITION OF THRESHOLD	SOURCE
Regime shift	An incremental change in conditions that triggers a large shift in a system once past a critical threshold in some ecosystem attribute(s).	(Scheffer et al. 2001; Scheffer & Carpenter 2003)
Extinction threshold	Minimum amount of habitat a species requires for persistence—corresponds to the persistence threshold.	(Fahrig 2002; Lande 1987, 1988a; Ovaskainen et al. 2002; With & King 1999b)
Persistence threshold	Amount of habitat at which the probability of persistence is unlikely—corresponds to the extinction threshold.	(Guénette & Villard 2004)
Occurrence threshold	Amount of habitat at which the probability of occurrence is unlikely.	(Guénette & Villard 2004)
Fragmentation threshold	Proportion of suitable habitat in the landscape at which the loss or decline in population size is greater than expected from the random sample hypothesis.	(Andrén 1994, 1996, 1997)
Biodiversity threshold	1. A saturation point along a logistic curve, beyond which the system destabilizes rapidly as species diversity decreases 2. Loss of key species (keystone or last member of key functional group) that induces threshold response / loss of species that overcomes the damping effect of biodiversity.	1. (Tilman & Downing 1994) 2. (Chapin et al. 2000; McNaughton 1993)
Habitat threshold	The threshold response of species attributes to changes in habitat—generic term that encompasses all types of thresholds defined in this table	General term used in this synthesis

Once populations become small, they are subject to a variety of factors other than changes in habitat quantity or quality which can drive populations toward extinction, including environmental, genetic, and demographic factors (Frankel & Soulé 1981). The demographics of small populations 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 & Ovaskainen 2002). Sources of stochasticity in the demographics of small populations 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 (Allee 1938; Lande 1993, 1994; Shaffer 1981; Wilcove 1987). 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, for example, temporary food shortages.

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 & Sutherland 1999; Stephens et al. 1999). Only processes or mechanisms which lead to reduced individual fitness at low population size or density are classed as Allee effects. These effects are distinct from others which might lead to extinction, such as environmental stochasticity (Stephens & Sutherland 1999; Stephens et al. 1999). Small, isolated populations draw from a restricted gene pool, leading to the establishment of deleterious traits within a population or a decreased ability to adapt to sudden environmental changes (Buza et al. 2000; Hildner et al. 2003; Reed & Frankham 2003; Saccheri et al. 1998; Wilcove 1987).

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 processes, such as mating (Halliday 1978). 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 1988b). Alternatively, an imbalance in the age, size, or sex structure (e.g., too few reproducing females) may reduce reproductive fitness (Berec et al. 2001). Beyond reproductive effects, other mechanisms result in improved fitness with increasing numbers or density. For example, reduced densities decrease the ability of western hemlock (*Tsuga heterophylla*) to acidify soil and sequester water (Ferson & 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. Plant-pollinator systems represent a distinctive form of the difficulty of sexual reproduction, explored further in Section 5.3.3.

Interested readers will find an introduction and review of the general concept of ecological thresholds in several publications (Dykstra 2004; Groffman et al. 2006; Huggett 2005; Lindenmayer & Luck 2005; Muradian 2001; Walker & Meyers 2004). Dykstra (2004) also presents a detailed review of the literature on the threshold response of species to changes in habitat. Guénette and Villard (2004) review the experimental and statistical issues related to detecting habitat thresholds. Other reviews address the thresholds that occur at the ecosystem level; that is, threshold effects in ecosystems in an advanced state of degradation, regime shifts at the community level, and thresholds in social-ecological systems (e.g., Beisner et al. 2003; Muradian 2001; Scheffer et al. 2001; Scheffer & Carpenter 2003; Walker & Meyers 2004 also see the Thresholds Database at www.resalliance.org3). Perrings and Pearce (1994) examine the issue of ecological thresholds and the conservation of biodiversity in an economic context, and present some of the policy implications.

4.0 LITERATURE REVIEW METHODS AND LAYOUT

Research about habitat thresholds occurs across many ecological disciplines. The literature encompasses habitat characteristics, such as spatial structure and habitat amount and quality, and species traits, such as dispersal and reproduction. In this synthesis, I initially hoped to focus on empirical data from BC landscapes. Because of a paucity of local data, the scope broadened to reflect the availability of data. I consequently incorporated studies from North American and European grassland and temperate and boreal forest habitats and from forested habitats in Australia and South America. 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 resulting from MPB disturbance and salvage harvest (e.g., habitat loss and fragmentation).

Bibliographic database searches generated approximately half of the literature reviewed for this synthesis. Search terms were combinations of the terms “threshold”, “forest”, “ecosystem”, “fragmentation”, “extinction” and “habitat”. To minimize gaps in the literature search, names of key authors and bibliographies of key papers 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[2])*
- *Digital Dissertations (1980–present)*
- *Web of Science (1985–present)*
- *Zoological Record (1993–present)*

The resulting literature is primarily about animals, with very little about vascular plants and fungi, and nothing about non-vascular plants and lichens.

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[2] present = March 2007

Dykstra (2004) presented the results from an earlier version of this literature review, which covered the published literature on habitat thresholds between 1969 and 2003. The objective of that review was to interpret and provide data and information to support strategic planning for ecosystem-based management on the north and central coast of British Columbia, Canada (Coast Information Team 2004; Price et al. 2007). For this synthesis, I distilled the key information relevant to MPB disturbance and salvage harvest from Dykstra (2004), and updated those findings by compiling the key literature on habitat thresholds published between 2003 and 2007.

The remaining sections of this synthesis derive primarily from the literature on habitat thresholds. First, I provide a technical summary of three general ecological lessons from the thresholds literature (Section 5.0). These stem from my earlier review, where interested readers will find a more detailed discussion of the literature (Dykstra 2004). The three lessons are a summary of the thresholds literature that is germane to maintaining resilience in populations, primarily of animal species (species persistence), following the salvage harvesting permitted in MPB landscapes (Eng 2004; Pedersen 2004; Snetsinger 2005). Second, I discuss what these lessons imply for the application of retention targets to implement forest policy (Section 6.0). Third, this synthesis concludes with recommendations for policy makers and researchers about how to integrate concepts from resilience theory in general and the theory of habitat thresholds specifically, to improve knowledge and management of disturbance in these ecosystems (Section 7.0).

The fourth and final section associated with the literature on habitat thresholds is a searchable database, available as a separate electronic document (created in Microsoft Office Excel® 2007, back compatible to Microsoft Office Excel® 1997; Appendix 1). Appendix 1 summarizes the primary literature on habitat thresholds published between 1969 and March 2007 (115 papers). For Appendix 1, I briefly summarized the experimental setting and results for each paper and created searchable fields in which I categorized the papers according to the topic areas in Table 5. Appendix 1 also contains complete citation information for each journal paper listed therein.

Table 5. Search categories and category types in Appendix 1, a separate electronic database of the thresholds literature.

CATEGORY	CATEGORY RESPONSE
Geographic location	Forest type, Country
Taxa	Latin species name
Type of study	Empirical (E), modeling (M)
Matrix setting	Forest (F), non-forest (N), model (M), various (V)
Element of habitat structure	Standing dead wood (WLT), coarse woody debris (CWD), old growth (OG), deciduous (DEC), riparian, matrix, patch, gap
Species trait	Reproduction, dispersal, rarity, competition, plant-pollinator, predator-prey, keystone species, habitat specialist, parasitism, various
Habitat remaining at habitat threshold	Habitat amount remaining at threshold response of species
Comments	Short description of study

5.0 THREE LESSONS FROM THE LITERATURE ABOUT THRESHOLDS IN HABITAT

5.1 Lesson 1—Habitat effects caused by harvest removal, like habitat amount, quality and pattern matter, but amount matters most

5.1.1 Species exhibit threshold responses to changes in patch size, cover and quality

Habitat thresholds occur for species at multiple scales due to forest harvesting: at the scale of landscapes and patches, and at the scale of structural elements such as dead and dying trees (Angelstam 1996; Bunnell 1995). The literature demonstrates thresholds at the patch scale attributed to patch size (Burke & Nol 2000; Donovan & Lamberson 2001; Reunanen et al. 2002; Saari et al. 1998), distance to patch edge (Figure 6; Brazaitis & Angelstam 2004), within patch cover (Figure 6; Brazaitis & Angelstam 2004; Guénette & Villard 2005; Penteriani & Faivre 2001; Preston & Harestad 2007; Thompson & Harestad 1994), and opening size (Bélisle & Desrochers 2002; Dale et al. 1994; Desrochers & Hannon 1997; Graham 2001; Jansson & Angelstam 1999; With & King 1999a). Empirical work shows that habitat thresholds related to the requirements of individual species also occur in response to changes in structural habitat elements heterogeneously distributed across landscapes at the patch level. These elements include amount of riparian area (Homan et al. 2004), standing dead wood (Bütler et al. 2004a; Bütler et al. 2004b; Guénette & Villard 2005; Lemaitre & Villard 2005), tree hollows (Ranius & Fahrig 2006) and downed, dead wood (Økland et al. 1996). In these studies, factors at the landscape scale interact with structural factors distributed at the patch scale. Threshold responses of species to changes in habitat occur at coarse (landscape) scales, but relate to structural elements of habitat distributed heterogeneously at fine (patch) scales. For example, Økland et al. (1996) found a link between the presence of several species of saproxylic beetles at a coarse scale (4 km^2) and the amount of standing dead, large diameter, deciduous trees and downed, dead wood distributed among patches in the landscape. The habitat features whose change induces the threshold response of species are the biological legacies of natural processes of disturbance (Franklin et al. 2000; Franklin et al. 1985). Increasingly, models of forest establishment and succession integrate the role played by disturbance in the development of stands (DeLong & Kessler 2000; Franklin et al. 2000; Franklin et al. 2002; Frelich & Reich 1999; Oliver & Larson 1996; Platt & Connell 2003; Turner et al. 1997a; Turner et al. 1997b).

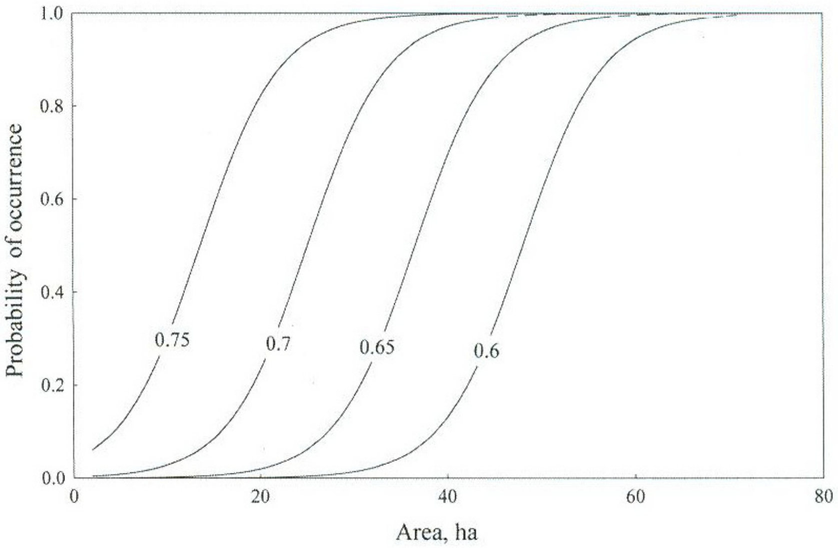

Figure 6. An empirical example of a threshold response in species occurrence to changes in stand area and stand stocking level. Influence of the combined effects of area and stand stocking level on red-breasted flycatcher (*Ficedula parva)* occurrence in forest fragments. This study was undertaken in patches interspersed with cut over areas within large (>2,000 ha) mature deciduous forests, which were themselves surrounded by an agricultural landscape in Lithuania. The x-axis shows the area of the patches, the labels on the curves indicate the stocking level within patches. As patches decline in size, higher stocking is necessary. Other highlights from this study are that the red-breasted flycatcher was absent from edges (did not occur within 50 m of cut over areas), and confined to the interior of forest stands. The probability of the red-breasted flycatcher holding a breeding territory was high if stands were >40 ha, had an average stocking level > than 0.8, and if the shape of the stand tended toward a circle. Figure 3 from Brazaitis and Angelstam (2004). Reprinted with permission from Ecological Bulletins.

Different types and severities of disturbances result in unique remnant conditions (Franklin et al. 1985; Harmon et al. 1986; Keisker 2000; Lundquist 1995; Perry & Amaranthus 1997; Steeger & Hitchcock 1998). At the stand level, for example, different types, rates, and severities of disturbance vary in the residual structures they leave, and set in motion different trajectories of vegetation succession and wood decay (Harmon et al. 1986; Keisker 2000; Lundquist 1995). Some species preferentially select dead and downed trees and other habitat elements (Bull 1983; Bull et al. 1997; Bunnell 1995; Bunnell et al. 2004; Chan-McLeod 2006; Keisker 2000; Machmer & Steeger 1995), thereby linking disturbance and the biological legacies of ecological recovery to unique assemblages of species. Habitat and functional elements in forests, such as dead wood, are attributes whose change in abundance can cause some species to exhibit a threshold response in their presence (Angelstam et al. 2001b; Bütler et al. 2004a; Bütler et al. 2004b; Martikainen et al. 2000; Penttilä et al. 2004).

The literature on the threshold response of species to changes in the physical or environmental characteristics of patches and to specific structural elements within patches demonstrates two inter-connected points relevant to landscapes disturbed by MPB and subject to salvage harvesting. First, these studies suggest the importance of structural habitat elements and overall habitat quality, and the permanence of habitat features within patches and distributed across landscapes. Second, these studies show that species exhibit threshold responses in part as a consequence of their affinity for specific structural elements in forest (e.g., dead standing or downed wood), or their need for other specific physical or environmental characteristics within their habitat (e.g., forest cover, interior forest). The latter finding suggests that in the presence of sufficient other habitat, habitat generalists—those that do not require specific patch qualities, or structural characteristics associated with specific seral (successional) stages—may not exhibit threshold responses to changes in structural elements or other patch characteristics. However, for some species, biological legacies are an important component of ecological resilience, and their removal by salvage has the potential to trigger threshold changes in the persistence of these species.

5.1.2 Species exhibit threshold responses to changes in the amount of habitat at the landscape level

The idea that species have a threshold requirement for amount of habitat—the extinction threshold (Lande 1987, 1988a)—is inherently a landscape-level concept. The concept of habitat thresholds at the landscape level stems primarily from two theoretical approaches. One approach developed the concept and theory of fragmentation thresholds from percolation theory (Gardner & O'Neill 1991; Stauffer 1985; see Table 4 for definitions of types of thresholds). A second theoretical approach—the concept of the minimum viable population (e.g., Beier 1993; Shaffer 1981; Thompson & Harestad 1994), or the minimum viable metapopulation (Hanski et al. 1996)—provides evidence for extinction thresholds derived from the concept of island biogeography (MacArthur & Wilson 1967).

Percolation theory proposes that universal thresholds in habitat occur at the landscape level, caused by fragmentation of habitat. In percolation models, rapid changes in the size, number, and shape of clusters (habitat patches) occur around a critical probability “pc” (proportion of habitat), wherein the largest cluster (patch) just “percolates” (i.e., extends from one edge of the map to another; Gardner & O'Neill 1991; Stauffer 1985). In landscape-level ecological applications, the critical percolation values imply that a sudden change in the connectivity of the landscape occurs at a critical density of clusters (habitat)—the “percolation threshold” (Gardner et al. 1987; Gardner & O'Neill 1991; Gustafson & Parker 1992; Turner et al. 1989; With 1997). The dominant hypothesis from percolation theory relevant to changes in habitat is that the spatial effects of habitat loss will result in threshold changes in spatial metrics, implying a threshold in structural connectivity (Metzger & Décamps 1997). The loss of connectivity associated with percolation (fragmentation) thresholds, if they exist, may relate to a loss of landscape function and influence on population dynamics

(Keitt et al. 1997; Metzger & Décamps 1997; Taylor et al. 2003; Wiens et al. 1997; With & Crist 1995; With et al. 1997).

An early meta-analysis of empirical studies on species decline and loss appeared to corroborate some of the findings of percolation theory. From his review of field data from a variety of landscapes, Andrén (1994) made the influential suggestion that universal thresholds in the response of species to changes in habitat begin to occur in real landscapes when habitat loss is high (once approximately 70% of habitat is lost). At this point, spatial factors begin to have a predominant influence on species—he terms this the “fragmentation threshold.” At the fragmentation threshold, rapid changes occur in the size and isolation of patches at critical proportions of habitat in the landscape; these changes appear to correspond to precipitous declines in the abundance of modeled and empirical species (Andrén 1994, 1996, 1997).

However, at high levels of habitat loss, the results for forested and agricultural landscapes differ, emphasizing how the matrix (i.e., the dominant type of habitat in the landscape) can buffer the influence that spatial factors have on habitat thresholds. Upon re-analysis of the landscapes presented in Andrén (1994), the fragmentation threshold does not occur in the forested habitats set in matrices comprised of other forest seral stages studied by Andrén (1994, 1999; Bender et al. 1998; Mönkkönen & Reunanen 1999). In contrast, when Andrén (1999) removed the forested habitats from the data set, the effect of the fragmentation threshold became more pronounced for island landscapes and for the forested landscapes set in agricultural matrices. This result shows how matrix quality and matrix permeability affect the degree to which even generalist species may exhibit threshold responses to changes in habitat.

Empirical data from forests set in agricultural landscapes generally continue to show that the cumulative effects of ongoing habitat loss lead to landscape structural thresholds, such as lack of connectivity, patch isolation, and threshold amounts of edge habitat in empirical agricultural landscapes. Several studies published since Andrén (1994, 1999), examining forests set in an agricultural matrix, provide further evidence for structural thresholds, such as thresholds in metrics of connectivity, (de Oiveira & Metzger 2006; Leimgruber et al. 2002), fragmentation (Cooper & Walters 2002) and patch isolation (Moore & Swihart 2005). Spatial thresholds are less commonly demonstrated in the context of the threshold response of species to changes such as patch isolation (Radford & Bennett 2004). However, even in agricultural landscapes fragmentation doesn't always have an influence on how species respond to loss of habitat. For example, Holland et al. (2005) find that fragmentation does not have an effect on the minimum habitat requirements for longhorned beetles.

Empirical data from forests in forested matrices likewise show landscape structural thresholds, but not universal fragmentation thresholds *per se*. Several empirical studies of mature forest in an early seral matrix show thresholds in connectivity metrics (Baskent 1999), species response to connectivity (Boswell et al. 1998), metrics of interior forest (Gustafson & Crow 1994; Trani & Giles 1999), edge metrics (Baskent 1999; Spies et al. 1994; Trani & Giles 1999), species response to patch size as a function of isolation (Betts et al. 2006) and species response to opening size (Jansson & Angelstam 1999). However, with few exceptions (Betts et al. 2006; Ecke et al. 2006), the empirical literature does not corroborate the idea of fragmentation thresholds in forested landscapes.

The focus on the idea of "fragmentation thresholds" is due partially to fuzziness in terminology, whereby many fragmentation studies actually measure attributes of habitat loss (Bender et al. 2003; Fahrig 2003). Researchers commonly use a feature of habitat loss, such as patch isolation, as the measure of fragmentation that determines thresholds. However, at the landscape level, habitat amount is the cause of effects such as patch isolation and patch size; isolated and small patches occur most commonly in landscapes with low levels of habitat (Bender et al. 2003; Radford & Bennett 2004). Fragmentation is essentially the breaking up of habitat into smaller pieces while habitat loss causes small patches, patch isolation and other losses of connectivity (Fahrig 2003).

Defining fragmentation in this way shows that habitat loss is the ultimate cause of many of the spatial effects that percolation theory predicts. Research on "fragmentation thresholds" stresses the conclusion that the effects of habitat amount are more important *overall* to habitat thresholds than are the effects of fragmentation (Andrén 1994; Betts et al. 2006; Fahrig 1997, 2001, 2003; Holland et al. 2005; McGarigal & McComb 1995; Trzcinski et al. 1999). Simulation studies that independently assess the effects of habitat loss and fragmentation find that habitat loss generally better predicts landscape connectivity (Goodwin & Fahrig 2002) and population dynamics than does fragmentation (Fahrig 1997, 2002; Flather & Bevers 2002), and that fragmentation affects population survival only under a narrow range of conditions (Fahrig 1998). Recent empirical research, particularly on birds, that has attempted to distinguish species response to the separate effects of habitat loss and spatial factors also demonstrates the overwhelming influence of habitat amount (Angelstam 2004; Betts et al. 2006; Drolet et al. 1999; Fahrig 2003; McGarigal & McComb 1995; Radford & Bennett 2004; Radford et al. 2005; Trzcinski et al. 1999; Villard et al. 1999). Several other studies have examined parameters for both habitat loss and fragmentation (although not controlling for either) and found that habitat amount better predicts species composition (Drapeau et al. 2000; Schmiegelow & Mönkkönen 2002), species presence (Schmiegelow & Mönkkönen 2002), and reproductive parameters (Tjernberg et al. 1993).

Habitat loss alone accounts for the greatest declines in species abundance and presence. Species differ in their requirements for minimum habitat; accordingly, empirical data show that the needs species have for habitat (and consequently their occurrence and extinction thresholds) occur along a gradient of habitat loss (e.g.,Angelstam et al. 2001a; Gibbs 1998; Holland et al. 2005). Manipulation of habitat pattern cannot therefore usually compensate for the loss of habitat because the effects of habitat loss account for the majority of the decline and loss of species in forested systems (Fahrig 1997). It is therefore prudent to keep the perspective that habitat thresholds, even when referred to as fragmentation thresholds, result primarily from loss of habitat.

The focus on fragmentation thresholds is important because it reveals two conditions for which the spatial effects of habitat loss have the relatively greatest effect on habitat thresholds. In analyses of population viability, the response of species to changes in habitat coincides with the minimum amount of suitable habitat required for a particular species to persist in a landscape (Carlson 2000; Hanski et al. 1996; Levins 1969); the “extinction threshold” (Lande 1987, 1988a). In these analyses, minimum requirements for habitat may be relevant at the landscape or patch level, and may involve minimum area and spatial (connectivity) components. Studies of population viability show that the physical aspects of the patch network are particularly important as habitat loss increases (Adler & Nuernberger 1994; Hill & Caswell 1999; Ovaskainen & Hanski 2002; With & King 1999a). The increasing effects of habitat loss (e.g., 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 (Bascompte & Solé 1996; Dytham 1995a, b; Fahrig 2002; Lamberson et al. 1992; Lamberson et al. 1994; Moilanen & Hanski 1995). Analyses of the population size or habitat needs of minimum viable populations thus demonstrate that spatial effects are most relevant to habitat thresholds at high levels of habitat loss. The first important finding from the study of fragmentation thresholds is that the spatial effects of habitat loss primarily influence the requirements species have for minimum amounts of habitat, because habitat requirements are greater in landscapes with dispersed habitat.

Although the empirical evidence for fragmentation thresholds in forested matrices is scarce, the idea of fragmentation thresholds is still pertinent in landscapes disturbed by MPB and subject to salvage. Much empirical data on fragmentation thresholds is set in agricultural landscapes, where the loss of habitat is genuine. Additionally, the models used to study fragmentation thresholds generally use a binary system to classify landscapes simply as habitat or non-habitat, with no re-growth of “harvested” habitat. This type of classification is a good parallel for agricultural landscapes, where the loss of habitat is genuine. Managed forest landscapes are much more complex; habitat value can remain in the harvested area following harvest, and the habitat attributes of cutovers change over time as recovery occurs. Limited rates of cutting moderate the amount of cutover forest on the landscape (Spies et al. 1994). Limited cutting rates allow time for stand recovery, creating a landscape with a matrix of vegetated habitats in different stages of succession, and with a diversity of habitat values, that may prevent most species from responding to fragmentation thresholds in forest habitats.

Thus, studies of forests set in agricultural matrices have limited relevance to forested landscapes; the findings on fragmentation thresholds that occur at and below 30% remaining habitat in agricultural landscapes are generally not applicable to forested landscapes. However, the binary (habitat/non-habitat) models and empirical findings from agricultural landscapes may be a good analogue for forests in notable situations. One situation may apply to species that show affinity to specific forest habitats or habitat features, but are relatively tolerant of habitat loss until it becomes high and spatial factors become predominant. For forest dwelling species in agricultural landscapes, empirical data show that fragmentation thresholds become apparent near or beyond 70% loss of the specific habitat (Andrén 1994, 1999). Recent empirical data in forested matrices shows similar results. Where the overall habitat requirements of species are low, habitat loss may not affect them until or unless it induces strong spatial effects (i.e., fragmentation thresholds; Betts et al. 2006; Ecke et al. 2006). In these situations, habitat loss may induce fragmentation thresholds for certain species: those with low vagility, non-ephemeral habitat, high site fidelity and high mortality in non-breeding habitat areas (Fahrig 1998).

Accordingly, the second important finding to result from the study of fragmentation thresholds is that the threshold response of species to habitat loss can occur in cases where species perceive the matrix to be hostile. For example, species may perceive the matrix to be hostile when factors such as patch isolation prevent individuals from crossing the matrix to re-colonize patches (Moore & Swihart 2005; Radford & Bennett 2004). Although data focused specifically on matrix effects are scarce, available data indicate that the matrix influences thresholds in at least two, interacting ways: due to mortality in the matrix, and matrix effects on the rate of dispersal (Åberg et al. 1995; Fahrig 2001; King & With 2002; Moore & Swihart 2005; Radford & Bennett 2004; With & Crist 1995). Organisms exhibit lower dispersal rates through matrices if they do not perceive the landscape to be functionally connected (King & With 2002)—they are either unwilling or unable to cross the matrix (Taylor et al. 1993). In threshold studies, this lack of functional connectivity expresses as a threshold in the opening distance beyond which individuals won't disperse (Jansson & Angelstam 1999; Moore & Swihart 2005; With & King 1999a), or threshold declines in patch occupancy relative to the amount of habitat at the landscape level (e.g., Betts et al. 2006; Radford & Bennett 2004).

The influence of the matrix depends partly on its extent and quality (i.e., the habitat features it contains). Some research suggests that under most conditions, increasing the quality of the matrix relates to increased movement between patches, buffering a metapopulation against extinction (Vandermeer & Carvajal 2001). However, in an empirical study of goldenrod beetles (*Trirhabda borealis*) in an experimental model system and with simulation models, the influence of matrix elements on landscape connectivity is minor compared to the influence of primary habitat (Goodwin & Fahrig 2002). The amount of matrix matters in part because with lower amount of matrix, species can persist with greater spacing of habitat patches; greater habitat availability results in a greater tolerance to habitat isolation (Betts et al. 2006; Gustafson & Gardner 1996; Jansson & Angelstam 1999; Vandermeer & Carvajal 2001). These studies highlight the importance of habitat retention by showing that the influence of matrix quality depends on patch isolation. Landscape context—the overall amount of habitat as it relates to patch size and inter-patch distance—is important (Betts et al. 2006). However, among the primary factors that influence the extinction thresholds of species (matrix amount and quality, reproductive rates, dispersal—see below) matrix amount and quality are factors that we can directly influence through management actions (Fahrig 2001).

In summary, species exhibit threshold responses to changes in habitat at the landscape level across a gradient of habitat loss. The threshold response of species occurs primarily due to changes in the amount and quality of habitat, and secondarily due to changes in the pattern of habitat (spatial effects). The threshold needs of species for habitat relate to the probability of their persistence in a landscape. The evidence for habitat thresholds at the landscape scale arises from several disciplinary approaches: research on the minimum viable population size, the minimum viable metapopulation size, species minimum needs for habitat (extinction threshold), and other landscape studies that detect thresholds in habitat amount and examine the influence of spatial properties on these threshold responses. These analyses have no *a priori* hypothesis about the level of habitat loss at which species will experience threshold declines; thresholds relate to the life history traits, behaviour and habitat requirements of individual species (see Section 5.3).

Theoretical work derived from percolation theory predicts that universal thresholds will occur as a consequence of the spatial influences of habitat change—fragmentation thresholds. There is only limited empirical evidence for species response to fragmentation thresholds in forested matrices. However, the empirical research set in forests within agricultural matrices, where the loss of habitat is genuine, better demonstrates universal fragmentation thresholds. However, these analyses assume that species have affinity for specific types of habitat; their application in forested matrices is confined to these species. The differences in the findings of empirical research on fragmentation thresholds in agricultural and forested matrices also emphasizes that spatial thresholds predominate where organisms perceive the matrix to be hostile (i.e., they have affinity for certain types of habitat; Fahrig 1998).

Taken together, these results show that habitat retention—by means of the amount of original habitat retained and the maintenance of habitat quality in the matrix—rather than habitat manipulation is the primary means to avoid the threshold response of species that are sensitive to changes in the type of forested habitat. However, for these species, threshold responses can occur across the gradient of habitat loss. For species with affinity for certain types of habitat that are relatively tolerant of the loss of habitat, but experience mortality in the matrix, the aggregation of habitat (and the relevance of fragmentation thresholds in forests) may be increasingly important if the loss of the relevant habitat approaches 70%. The importance of aggregation at lower levels of habitat loss relates to species with strong affinity for continuity in certain types of habitat.

Habitat generalists (e.g., elk (*Cervus elaphus*), moose (*Alces alces*)) and those that prefer large areas of early seral stages (e.g., blue grouse (*Dendragapus obscurus*)) are predicted to experience negligible or positive effects from salvage harvesting. These two categories of species comprise the majority of the terrestrial vertebrate species that are resident in a large portion of the disturbed area (Bunnell et al. 2004). However, data from models and agricultural landscapes suggest that, under accelerated rates of harvest, there is an increased probability to see some species, particularly those associated with late seral stages for reproduction and/or dispersal (e.g., lynx (*Lynx canadensis*), wolverine (*Gulo gulo*)) exhibit threshold responses to fragmentation when the habitat they require for persistence is below 30%, if they don't exhibit extinction thresholds at even lower levels of habitat loss.

5.2 Lesson 2—Dimensional effects like rate and scale of change, and their interactions, matter too

5.2.1 Accelerated rate of harvest can induce fragmentation thresholds for non-generalist species and thresholds in species tolerance to the amount of edge habitat

Rate of harvest can influence species threshold responses to changes in habitat in at least two ways. First, in Section 5.1.2, I proposed that fragmentation thresholds are relevant in situations where species have low vagility, relatively low requirements for specific types of habitat, and for whom the matrix is hostile (Fahrig 1998). For these species, fragmentation thresholds may be relevant at high levels of habitat loss (approaching 70% loss). Situations where cutting rates are high, as may be the case with salvage harvesting in landscapes disturbed by

MPB, may create this landscape context. The influence of matrix habitat on species is a function of the overall amount of habitat in the landscape (e.g., Betts et al. 2006). Landscapes subject to high levels of salvage harvest may therefore have hostile matrices, either because habitat attributes are infrequent, or purely due to matrix extent—the rate of conversion to the matrix. Accelerated rates of harvest for salvage of landscapes disturbed by MPB could result in landscapes covered by widespread cutovers with homogenous habitat values (Klenner 2006). Without the juxtaposition of other successional stages, a homogenized landscape dominated by extensive habitat of the same seral stage limits the habitat values that the matrix can provide (Klenner 2006). In this context, it is reasonable to compare landscapes affected by MPB to those in the modeling work and to empirical landscapes in agricultural settings, and to apply the findings from this work to salvaged landscapes disturbed by MPB. Accelerated rates of harvest may induce threshold responses in non-generalist species across the gradient of habitat loss, and fragmentation thresholds at high levels of habitat loss.

Second, where the rate of harvesting is rapid, thresholds are also much more likely to occur in landscape metrics such as the amount of edge, altering the landscape for species sensitive to changes in edge habitat. Reported thresholds in edge metrics imply that at certain amounts and patterns of habitat removal, the amount of edge can increase dramatically (Baskent 1999; Laurance & Yensen 1991; Trani & Giles 1999). However, forest regrowth normally mitigates edge effects, reducing edge width and increasing forest interior over time. Forest regrowth also normally limits the maximum amount of cutover forest on the landscape, given harvest rates based on a rotation length of 80 yr (Spies et al. 1994). Thus under moderate rates of cutting, the edge effects predicted by models (e.g., Franklin & Forman 1987) may not manifest in real landscapes (Spies et al. 1994). However, the rate of cut can create greater amounts of edge and less interior forest across scales if the cutting rate exceeds the regeneration time required to ameliorate edge effects (Spies et al. 1994). Cutting rate can thus have a greater influence than cutting pattern, on the amount of edge and interior habitat (Spies et al. 1994).

The potential to create an abundance of edge habitat is relevant to species that are sensitive to (avoid) 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 et al. 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).

Species may exhibit threshold responses to changes in habitat based on the amount of edge in a landscape. One spatially explicit model, comparing the relative effects of habitat area and edge sensitivity on reproduction demonstrates that sensitivity to edges can be a more important determinant of thresholds in habitat than sensitivity to area (With & King 2001). In this model, species with high edge sensitivity require a greater amount of habitat (minimum of 50%) at the extinction threshold, compared to the habitat needs of species with low edge sensitivity, and edge sensitivity is a more important determinant of extinction thresholds than sensitivity to area. The finding that sensitivity to edge results in a greater overall demand for habitat is corroborated by a threshold study on birds in Lithuania (Brazaitis & Angelstam 2004). The red-breasted flycatcher showed the greatest aversion to edges of the eight species studied, and demonstrated an occurrence threshold when the characteristics (size, tree density, shape) of its breeding habitat fell below its requirements (Figure 6).

Over a large portion of the landscapes disturbed by MPB and subject to salvage, twelve of 182 identified vertebrate species are sensitive to edge effects (four mammal and eight bird species; Bunnell et al. 2004).

5.2.2 Thresholds are relevant at multiple scales that are consistent with the perceptions that individual species have of the landscape

Although the idea of the threshold amount of habitat—the extinction threshold (Lande 1987, 1988a)—is inherently a landscape-level concept, species scales of perception define landscapes. Beyond the thresholds literature, studies show that species perceive the landscape at a scale consistent with their size, body plan and trophic level (Harestad & Bunnell 1979; Holling 1992; 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 & Wiens 1990). Threshold studies (e.g., Homan et al. 2004) correspondingly show that changes in vegetation structure have a different effect on population processes at different scales (Doak et al. 1992; Pither & Taylor 1998).

Threshold responses may involve multiple scales. 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 induce thresholds in individual and population-level processes in different ways at different temporal and spatial scales (e.g., Homan et al. 2004). Accordingly, species may exhibit threshold responses to the amount and quality of habitat elements at stand scales and the amount and quality of habitat at landscape scales (e.g., Angelstam 2004; Angelstam et al. 2003; Homan et al. 2004), or to the amount of habitat at scales that exceed their dispersal (home) range (Betts et al. 2006; Brazner et al. 2004; Holland et al. 2005; Homan et al. 2004; Ovaskainen et al. 2002; Radford & Bennett 2004).

The threshold response of species to changes in habitat is relevant to the scale at which individual species perceive and respond to landscape structure and change (Bascompte & Solé 1996; Gibbs 1998; Hager 1998; Holland et al. 2005; Homan et al. 2004). Figure 7 and Figure 8 show the results from a study of extinction thresholds of saproxylic longhorned beetles (*Cerambycidae*; Holland et al. 2005). The authors found that each of the 12 beetle species studied demonstrates a characteristic scale of response—the scale at which the species responds most strongly to some aspect of its environment (Holland et al. 2004).

Characteristic scales of response ranged between 20 and 1600 meters. Figure 7 shows that the extinction thresholds also vary among species, and are between 5% and 99% of habitat remaining. Figure 8 displays the relationship between reproductive rate and the extinction threshold and demonstrates two findings. First, when plotted at the characteristic scale of response, lower reproductive rates explain the requirement for more habitat at the extinction threshold (r^2=0.617). (Figure 8 graph (a); see also Section 5.3.1). Second, examining the effect of reproductive rate on the extinction threshold at an arbitrary scale

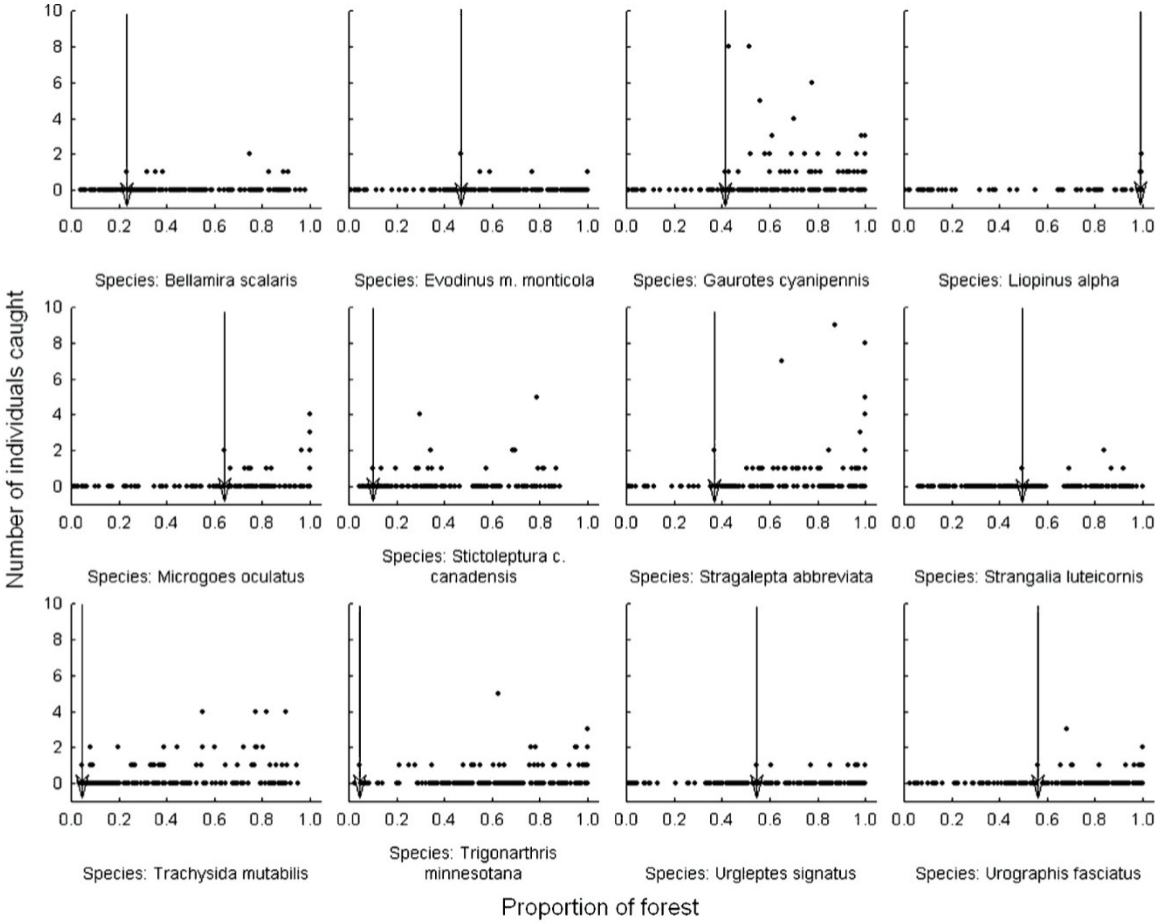

Figure 7. An empirical example showing a range of extinction thresholds for 12 species of saproxylic longhorned beetles (*Cerambycidae* species). The number of individuals caught at the sampling sites was plotted against the proportion of forest cover around the sites. The forest cover was measured at the characteristic scale of response for each species, which varied from 20m to 1600m. The arrows indicate the extinction threshold amount of habitat for each species. Figure 2 from Holland et al. (2005). Reprinted with permission.

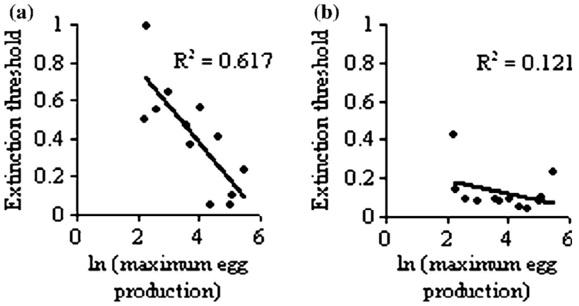

Figure 8. An empirical example showing the relationship between reproductive rates and extinction thresholds. In (a), each of the twelve species had the extinction threshold determined at the spatial scale that it responds most strongly to forest habitat, or the characteristic scale of response to forest habitat (range between 20 to 1600 m). In (b), each of the 12 species had the extinction threshold determined by plotting the abundance against the proportion of forest within 1 km of the sampling site for each species. This relationship is no longer significant when done at this scale. Figure 3 from Holland et al. (2005). Reprinted with permission.

obscures this effect. When plotted at a generic scale for all species (1 km), the relationship between reproductive rate and the extinction threshold is not significant (r^2=0.121; Figure 8, graph (b)).

Not surprisingly, the failure to detect thresholds is occasionally due to a scale mismatch between the scale of investigation and the scale at which thresholds are relevant (Holland et al. 2005; Radford et al. 2005; Spies et al. 1994). Measures of thresholds that aggregate data at landscape scales obscure the effects of thresholds that occur at finer scales, affecting the life history traits of species that perceive the landscapes at these scales (Radford et al. 2005; Spies et al. 1994). Using simulation modeling, Spies et al. (1994) demonstrate the importance of rate of cut by comparing the landscape effects of dispersed patch cuts to the effects at smaller scales, where cutting rates were higher than at the landscape scale. Spies et al. (1994) suggest that, although they did not detect some of the fragmentation thresholds they predicted in their empirical forested landscape, higher rates of cut at finer scales led to more pronounced spatial effects than at the landscape scale. Radford et al. (2005) similarly suggest that measuring species richness at the landscape scale obscures knowledge of the loss of species finer scales. While species may be lost locally due to habitat loss, their presence elsewhere in the landscape, as measured by metrics at coarser scale, obscures the loss at finer scales.

Habitat thresholds studied at the landscape scale, including fragmentation thresholds, are therefore relevant across spatial scales, and not only at the scale at which we traditionally think of landscapes (e.g., tens or hundreds of thousands of hectares). Habitat amount may be even more important at fine scales than at coarse scales to facilitate dispersal (Homan et al. 2004; Ovaskainen et al. 2002; With et al. 1997; With & King 1999b). The emphasis on fine scale thresholds and the coupling of species traits to scale-related thresholds (see Section 5.3) is particularly relevant to the salvage of landscapes disturbed by MPB because existing guidance suggests low retention at fine scales (e.g., 10% - 25% retention in openings <1,000 ha). The extent of landscape change possible under MPB salvage suggests that thresholds are an issue across scales, particularly where the rate of cut is high. If cutovers with little retention predominate at finer scales (e.g., at the scale of patches or aggregated patches), they may induce threshold responses in species for which these scales are relevant (Holland et al. 2005; With & King 1999b).

5.2.3 The rate of change in habitat patches can scale up to induce landscape thresholds

The rate of loss of individual patches matters to the persistence of species at fine and coarse scales (Hanski 1999b). Analyses of population viability reveal that for most species, the spatial influences of habitat loss are predominant at high levels of habitat loss (see Section 5.1.2). A second key finding on extinction thresholds from these studies is that rate of habitat change and the permanence of habitat may be as or more important than are species requirements for habitat area (Fahrig 1992; Hanski 1999a; Keymer et al. 2000). Rates of change are important because the turnover in habitat patches causes population turnover; disappearance of patches increases rates of local extinction by affecting individuals within a patch and decreasing rates of colonization (Hanski 1999a).

There is a threshold rate of change that species can tolerate. The increasing frequency of species extirpation in local patches increases extinction risk at the landscape or metapopulation scale (Hanski 1994; Keymer et al. 2000;

Levins 1969). If the landscape changes too quickly relative to species rates of colonization and extinction (Keymer et al. 2000) or reproductive capacity (Schrott et al. 2005), modeled populations become extinct. This is an example of how regime shift can cross scales (Bodin et al. 2006; Kinzig et al. 2006). Changes at the fine scale—such as patch removal—in forests, can thus scale up, triggering habitat thresholds at coarse scales. Disrupting the rate of a key structuring process such as disturbance (Holling 1992) with accelerated salvage harvesting can thus lead to extirpation of species at patch scales and the extinction of species in landscapes.

5.2.4 Delays in the response of species to changes in habitat constrain our capacity to interpret the implications of current habitat alteration

Complex responses to habitat alteration may result in a time delay between cause and effect (Brown & Kodric-Brown 1977; Hanski & Ovaskainen 2002; MacArthur & Wilson 1967; Tilman et al. 1994). Where habitat alteration results in populations that remain on the landscape but are no longer viable, relic species are considered “extinction debt” (Hanski & Ovaskainen 2002; Ovaskainen & Hanski 2002; Tilman et al. 1994). 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. Extinction debt suggests that a population can survive for some time, even though local extinction occurs (extinction in some patches). Empirical examples exist of species that persist in landscapes even though their habitat requirements are no longer met (Carlson 2000; Petit & Burel 1998); time-lagged declines are also evident (Cooper & Walters 2002).

Extinction debt may occur because habitat change occurs rapidly relative to the response time of organisms (Carlson 2000; Schrott et al. 2005). This may be particularly true of plants; even after habitat loss and fragmentation hinder reproduction and recruitment, plants can persist by way of long-lived life cycle stages, such as dormant seeds and clonal propagules (Eriksson 1996, 1997; Eriksson & Kiviniemi 1999; Lamont et al. 1993).

This longevity and the resilience that it confers to vegetation communities is an advantage in an environment that changes rapidly (Chapin et al. 2004; Chapin et al. 2006; Noss 2001). Because the loss of mature forest habitat in the case of MPB salvage is temporary, such inertia may be important to maintaining species potential on the landscape. For plants and animals, habitat conditions may be temporarily below the threshold level necessary for reproduction and population growth, but species may still occupy remaining habitat patches. If reproductive potential persists, these species may populate future habitats.

Time-lag concepts are important to ecological thresholds because they mean we cannot necessarily expect the results of habitat loss and fragmentation to be apparent until some undetermined and possibly long time afterwards. The notion of delayed response thus imposes serious constraints on our ability to interpret what we see in the present landscape; simply because species occur above or at a threshold amount of habitat does not mean that habitat conditions are adequate to support a viable population. Time lags in response thus mean we can underestimate the risks of extinction (Schrott et al. 2005). Time lags also suggest that occupancy measures have limited utility to estimate extinction thresholds (Ranius & Fahrig 2006). Measures of population viability that focus on rates (e.g., rates of reproduction), rather than states (e.g., occupancy), are an appropriate indicator of the effectiveness of habitat at maintaining viable populations (Angelstam 2004; Guénette & Villard 2004; Ranius & Fahrig 2006).

5.3 Lesson 3—Effects on species' attributes such as life history traits matter

The response species have 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—with their unique combinations of life history and dispersal parameters (Debinski & Holt 2000; Lande 1987; Metzger & Décamps 1997; With & King 2001). Revealing the continued influence of island biogeography, research on the extinction threshold has primarily focused on the characteristics of species that determine extinction and colonization rates of populations (Bascompte & Solé 1996; Bellamy et al. 1996; Fryxell 2001; Keymer et al. 2000; Lamberson et al. 1992; Swihart et al. 2001). Biological and demographic characteristics include species properties such as reproductive traits, dispersal range, inter-specific traits and the degree of habitat specialization or rarity of a species (Bryant 1996; Debinski & Holt 2000; Keitt et al. 1997; Lande 1987; Terry et al. 2000; With & Crist 1995). In turn, how much each of these characteristics is affected by habitat loss is highly species-dependent (Debinski & Holt 2000; With & King 2001). In the following sections, I briefly summarize literature on species traits that primarily influence habitat thresholds.

5.3.1 Reproductive factors have the most influence on extinction thresholds

The distribution and abundance of species responds to the availability of breeding habitat as well as to the amount of habitat more generally (Fahrig 1998; Venier & Fahrig 1996). Consequently, habitat thresholds often relate to components of habitat associated with reproduction (Akçakaya & Raphael 1998; Angelstam 2004; Angelstam et al. 2003; Bütler et al. 2004a; Bütler et al. 2004b; Burke & Nol 2000; Donovan & Lamberson 2001; Fahrig 2001; Homan et al. 2004; Penteriani & Faivre 2001; Saari et al. 1998; With & King 1999b, 2001). The ultimate cause of extinction thresholds is due to a higher mortality than reproductive rate (Fahrig 2002); modeling shows that reproductive traits have the primary influence on the threshold response of species to landscape change (Akçakaya & Raphael 1998; Fahrig 2001; Pulliam et al. 1992; Venier & Fahrig 1996; With & King 1999b, 2001). Differences in reproductive capacity among species further differentiate the species most likely to exhibit threshold responses along the gradient of habitat loss. Empirical data on birds corroborate the theoretical proposition that species with low reproductive rates require more habitat to achieve threshold occupancy levels than do species with high reproductive rates (Vance et al. 2003). Empirical data from 12 species of saproxylic longhorned beetles demonstrate that low rates of egg production explain the requirement for more habitat at the extinction threshold (r^2=0.617; Figure 8; Holland et al. 2005).

Population viability is not synonymous with population abundance (van Horne 1983). Consequently, changes in reproductive capacity may be essential to early detection of impending threshold changes in population size. Comparisons of the impacts of habitat loss on reproductive traits versus other metrics demonstrate that threshold responses in reproductive traits occur at lower levels of habitat loss and fragmentation than for dispersal (Donovan et al. 1997; Pulliam et al. 1992; With & King 1999b) and survival (Pulliam et al. 1992; With & King 2001). Reproductive capacity within a given habitat differentiates between source habitat (in which recruitment of young is sufficient to compensate for mortality; Pulliam 1988) and sink habitat (recruitment doesn't compensate for mortality). Persistence thresholds differentiate source from sink habitat with regard to patch size in modeling (Donovan & Lamberson 2001; With & King 2001) and empirical studies (Burke & Nol 2000). In an empirical study in the Canadian boreal forest, the reproductive capacity of birds displays a threshold response at lower levels of habitat loss than does occurrence (Swift & Hannon 2002). In boreal forests in Sweden, Angelstam (2004) reaches the same conclusion for the proportion of habitat at the landscape level required by black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*). Despite the importance of the variables (e.g., dispersal, see below) tested by spatially explicit population models, reproductive traits tend to be the most important factor influencing habitat thresholds. Reproductive measures are therefore more relevant than are occupancy measures for evaluating and determining the probability of species persistence in changing landscapes (Guénette & Villard 2004).

Reproductive factors thus have the greatest influence on extinction thresholds, 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 the probability of species persistence in a landscape.

5.3.2 Dispersal success depends on matrix quality

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). The degree to which organisms perceive a landscape as fragmented depends on the scale of perception, and at broad scales, is related to dispersal ability (Kotliar & Wiens 1990). Movement by individuals thus determines the scale at which they respond to patchiness and spatial heterogeneity (Fahrig & Paloheimo 1988; Gardner & O'Neill 1991; Keitt et al. 1997; King & With 2002; With & Crist 1995). Since colonization is inherently a landscape-scale process, and habitat loss alters landscape connectivity, most landscape-scale studies of population change emphasize the effect of habitat change and dispersal behaviour on movement factors and colonization rates (Fahrig 2002; Fahrig & Merriam 1994; Keitt et al. 1997; King & With 2002; Lamberson et al. 1992; Lande 1987; McIntyre & Wiens 1999; With et al. 1999; With et al. 1997; With & King 1999a). Dispersal is thus one of the most frequently studied species-specific characteristics thought to determine species response to habitat loss and fragmentation (e.g., Bryant 1996; Gustafson & Gardner 1996; Keitt et al. 1997; Mader 1984; Ovaskainen et al. 2002; Sutherland et al. 2000; Terry et al. 2000).

Both island biogeography and metapopulation models identify patch size and patch isolation as key features associated with extinction, because of their influence on extinction and colonization rates (Levins 1969; MacArthur & Wilson 1967). Differences in the size and isolation of forest patches can account for a large amount of variability in dispersal success, with closer and larger patches having significantly greater exchange of dispersing organisms (see review in Adler & Nuernberger 1994; Gustafson & Gardner 1996). Many modeling studies 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, 2001, 2002; Flather & Bevers 2002; Hill & Caswell 1999; With & King 1999b). Incorporating the spatial arrangement of habitat generally demonstrates that the habitat supply threshold is lower in aggregated than fragmented habitats (Dytham 1995b; Fahrig 2002; Lamberson et al. 1992; Lamberson et al. 1994; Moilanen & Hanski 1995; With & King 1999a). However, the details of the relative importance of patch size and isolation are inconclusive in the threshold literature. A meta-analysis undertaken to determine the universality of fragmentation thresholds finds that patch size has a greater effect on interior and edge species density (negative and positive effects respectively) than on the density of habitat generalists (Bender et al. 1998). The effects of patch size and patch isolation interact; small patches may see higher utilization in landscapes with more habitat than the same size of patch in a landscape with less habitat (e.g., Betts et al. 2006). In addition to modeling evidence (With & King 1999a), there is substantial empirical evidence about movement barriers that result from threshold behavioural responses to opening size in habitat or patch isolation, although studies are generally confined to birds (Bélisle & Desrochers 2002; Betts et al. 2006; Dale et al. 1994; Desrochers & Hannon 1997; Graham 2001; Jansson & Angelstam 1999).

Although the research on dispersal thresholds is largely theoretical, one of the generally consistent findings is that species with poor dispersal capacity appear to be impacted by fragmentation thresholds more detrimentally than species with good dispersal capacity (e.g., Hill & Caswell 2001; Lamberson et al. 1994; Lande 1987; With & King 1999b). Species with large area requirements and low dispersal rates are particularly sensitive to thresholds in habitat loss; these species will exhibit threshold responses to habitat amount at lower levels of habitat loss (Andrén 1996; Hanski et al. 1995; Hiebeler 2000; King & With 2002; McClellan et al. 1986; With & Crist 1995). However, modeling shows that dispersal success in general 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 matters less, although habitat aggregation is always important for weak dispersers, unless habitat availability is very high (≥ 80%). With and Christ (1995) also modeled the effect of dispersal capability, and 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. Accordingly, habitat aggregation appears to mitigate some effects of habitat loss, particularly when habitat loss is high, and particularly for poor dispersers.

However, the matrix can affect species regardless of whether they have poor or good dispersal capacity. Matrix quality interacts with movement by influencing the mortality of dispersing individuals (Fahrig 2001). Although intuitively, it seems as though superior dispersers will fare better than poor dispersers as habitat disappears or changes (King & With 2002), Fahrig (2001) shows that better dispersal led to higher mortality in the matrix, causing habitat thresholds to occur at lower levels of habitat loss (see Gibbs (1998) for a corroborating empirical example). Her finding contrasts with the conclusions of metapopulation work, which suggests that dispersal positively influences the survival of populations because it increases the probability that a patch will be recolonized following patch extinction. Fahrig (2001) reconciles her finding with the results from metapopulation work by showing that dispersal success is partially a function of landscape attributes, rather than simply being a species trait independent of habitat. Fahrig (2001) suggests that good dispersal, observed for species that evolved in habitats with high cover, may, in degraded habitats, leave them vulnerable to mortality in the matrix. Therefore, even superior dispersal may not overcome habitat degradation in the absence of habitat quality, i.e., when mortality is high in the matrix.

The importance of rates and quality of change in habitat are relative to the life history traits of species—higher dispersal rates are an adaptive response to fluctuating habitat availability (Travis & Dytham 1999). This finding from modeling is consistent with the prediction that the majority of vertebrate species that occur in landscapes disturbed by MPB will experience neutral or positive effects from salvage harvesting because the affected ecosystems do not generally represent communities with long-term stability (Bunnell et al. 2004 and references therein). Species in salvaged landscapes disturbed by MPB that prefer contiguous, mature forest habitat, such as northern and southern populations of woodland caribou (*Rangifer tarandus caribou*) and fisher (*Martes pennanti;* Bunnell et al. 2004), may thus respond in a threshold-like way to changes in habitat amount at relatively low levels of habitat loss, while matrix quality will be an important determinant of the persistence of species with less habitat specificity (Bunnell et al. 2004).

5.3.3 Species can be vulnerable to habitat thresholds as a consequence of their interactions with other species

Habitat thresholds can also influence species indirectly, through their interactions with other species, such as competitive interactions. Species may also influence or be influenced by other species as a consequence of their functional role in ecosystems, for example, as interdependent species in plant–pollinator relationships (Ingvarsson & Lundberg 1995; Lamont et al. 1993; Lennartsson 2002), or as keystone species (Boswell et al. 1998; Mills et al. 1993; Paine 1966, 1969).

Inter-specific tradeoffs maintain diversity, resulting in an array of species competing for limiting resources (Tilman 1994). The competitive abilities of these species predispose them to respond differently to habitat loss. The amount of habitat loss at which modeled species experience extinction varies depending on their competitive ability (Dytham 1994; Tilman et al. 1997). As a result, habitat thresholds differ among species, depending on their competitive ability. In general, under the assumption that trade-offs between dispersal and competitive ability structure the co-existence of species in communities, inferior competitors, assumed to have superior dispersal to compensate for their lack of competitive ability, fare better than superior competitors (poor dispersers) as habitat loss increases (Dytham 1994; Moilanen & Hanski 1995; Nee & May 1992; Tilman et al. 1997; Tilman et al. 1994). Where weak competition structures populations, the species with the poorest dispersal capacity are also most prone to extinction (Klausmeier 2001).

Plants possess characteristics distinct from those of animals. Reproductive strategies in plants are 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 by which an increase in number or density of an organism results in an increase in the fitness of individuals or populations (see Section 4.0; Allee 1938; Stephens et al. 1999). 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 (Groom & Pascual 1998; Lamont et al. 1993; 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).

Modeling shows that a threshold number of pollinators is necessary for the long-term persistence of plant populations (Ingvarsson & Lundberg 1995). The threshold number depends on the demographic parameters for both species, and the searching efficiency of pollinators (Ingvarsson & Lundberg 1995), but the existence of the critical threshold is a general feature of plant–pollinator systems (Lundberg & Ingvarsson 1998). Empirical studies show that thresholds in the response of plants to habitat changes are associated with population size (Bronstein et al. 1990), and with landscape factors, such as patch size (Groom 1998; Lamont & Klinkhamer 1993; Lamont et al. 1993; Lennartsson 2002) and patch isolation (Groom 1998).

The degree to which plants are vulnerable to Allee thresholds depends on pollinator specificity, and the degree of dependence seeds for dispersal and plant-pollinator mutualism (Bond 1994). Plants most vulnerable to Allee thresholds are therefore those that are dioecious and self-incompatible, have a single pollinator or propagate only by seeds (Kearns & 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 1996). If plants are more resistant to extirpation or extinction than other organisms, this inertia may scale up, creating community stability (Eriksson 1996). 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). Models that incorporate compensatory mechanisms enable a realistic and subjective assessment of extinction risk in plants.

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). Turner et al. (1998) predict that successional trajectories, following large, infrequent natural disturbances, may differ from smaller, similar disturbances. Remnant patches have particular importance in their capacity to provide sites for colonization and expansion, and the rate of recovery of community composition may be slower in larger compared to smaller disturbances (Turner et al. 1998). Large, contiguous areas above a certain threshold of disturbance (e.g., greater than 20% of the area) or below a threshold level of biodiversity, may thus facilitate invasion by non-native species in salvaged landscapes disturbed by MPB (With 2002, 2004; With & King 2004).

5.3.4 Species can be vulnerable to habitat thresholds as a consequence of rarity

Research demonstrates that thresholds at the patch level appear at lower levels of habitat loss for rare species compared to common species (Penttilä et al. 2004). Studies in experimental model systems show that rare species are disproportionately affected by landscape thresholds (e.g., Summerville & Crist 2001). An empirical study in the Canadian boreal forest also shows that rare species are particularly sensitive to area thresholds (Schmiegelow & Mönkkönen 2002). Species with low abundance demonstrate a need for a greater amount of habitat at the occupancy threshold than species with higher abundance (Edenius & Sjöberg 1997; Schmiegelow & Mönkkönen 2002). Clearly, there are exacerbated risks of extirpation and/or extinction for rare species that are mature and old-growth habitat specialists. Because forest harvesting is specific to certain habitats, e.g., mature and old-growth forests, habitat specialists may be more likely to be affected by harvest regimes than generalists (Schmiegelow and Mönkkönen 2002).Habitat loss also differentially affects rare species, due simply to chance alone (Conner & McCoy 1979).

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).

There are eight vertebrate species resident in a large portion of the area affected by MPB, listed as threatened or rare on provincial and national lists of the population status of species; three of these have habitat needs for late seral forest (northern and southern populations of woodland caribou, wolverine and fisher; Bunnell et al. 2004).

6.0 HABITAT THRESHOLDS AND FOREST MANAGEMENT

6.1.1 Habitat thresholds as policy targets

In a review paper on the utility of the thresholds concept to biodiversity conservation, Huggett (2005) suggests four ways to apply threshold knowledge in practice: three of these applications are relevant to MPB/salvage.

1. *To identify/protect species of conservation risk*
2. *To evaluate tradeoffs between conservation and production*
3. *To set targets for retention and restoration*

The third application, the use of habitat thresholds in forest policy as targets for conservation, is appealing. In order to protect biodiversity, policy established the rate of harvest for salvage harvesting in landscapes disturbed by MPB based on retaining 20% of mature forest habitat at the landscape level[1] (Pederson 2004). At the stand level, policy guidelines recommend retaining between 10% and 25% habitat for openings < 1,000 ha (Eng 2004; Snetsinger 2005). If substantiated by the literature, such generalized targets have the potential to be ecologically meaningful, transparent, simple to implement and risk averse. Although targets to protect habitat and habitat elements are common in resource management, policy driven targets may be inadequate to fulfill their intended objectives. Setting targets driven by political rather than ecological factors invariably results in levels of retention dramatically lower than if ecological factors are considered (Svancara et al. 2005).

Caution is therefore necessary to ensure that the generalized target is appropriate to achieve its intended goal. The findings on patch and landscape level thresholds clearly show that retaining a meaningful amount of habitat is more important overall than is the arrangement of habitat for avoiding the threshold response of species to change. However, two other findings are critical to applying retention targets for biological conservation. First, no generalized targets for the level of habitat that is adequate to protect biodiversity emerge from the literature. Second, maintaining landscapes at fragmentation thresholds poses risks to biodiversity (Chan-McLeod & Bunnell 2004; Homan et al. 2004; Radford et al. 2005). Despite these two conclusions, the literature does suggest critical values for fragmentation thresholds. (Andrén 1994; Fahrig 1998; Gardner & O'Neill 1991; Gustafson & Parker 1992; Turner 1989). In particular, threshold values between 30% and 20% habitat retention appear repeatedly in the literature. However, there are important factors that should deter policy makers from adopting a retention threshold of 30% or lower as a coarse scale target to conserve biodiversity. To understand these factors, policy makers should ask two questions.

1. *Retain 30% or less of what variable, based on what assumptions?*
2. *Retain 30% or less of habitat to achieve what objective?*

The first question is relevant to the simulation modeling that shows that rapid changes occur in the size and isolation of patches at critical proportions of habitat remaining in the landscape. However, these critical values range from 70% to 20% of habitat remaining, depending on the metric and the details of individual models (Andrén 1994; Bascompte & Solé 1996; Boswell et al. 1998; Gardner et al. 1987; Gardner & O'Neill 1991; Gustafson & Parker 1992; Spies et al. 1994; Turner et al. 1989). For example, Fahrig (1998) modeled fragmentation thresholds at 20%. However, she demonstrated that spatial factors had limited influence on population dynamics: 20% applied only to the amount of breeding habitat (as opposed to the amount of total habitat), and only under a narrow set of other conditions for which fragmentation mattered (see Section 5.1.2).

In another example, Andrén (1994) compared thresholds in spatial isolation (modeled at 20% of habitat remaining), to the range of habitat (10% to 30% remaining) at which he interpreted precipitous declines in the density and occupancy of species from the empirical literature (see Section 5.1.2). Andrén (1994) hypothesized that this 20% value represented the fragmentation threshold—the value of habitat loss at which the spatial effects of habitat loss mattered most. However, Andrén’s (1994) finding was not relevant in forested landscapes (Andrén 1999; Mönkkönen & Reunanen 1999). Other factors further limit the applicability of Andrén's (1994) findings as generalized targets in forestry. Only 12% of the studies looked at landscapes greater than 1,000 hectares, and only two looked at landscapes large enough to encompass a set of local populations (i.e., a metapopulation) (Andrén 1994). As well, excluding the forested landscapes, almost half (13 of 27) of the studies in Andrén (1994) employ occupancy measures, which are less pertinent than reproductive measures to the persistence of species (Angelstam 2004; Guénette & Villard 2004).

Targets for habitat retention derived from measures of species occupancy or presence pose risks to species persistence, and raise the second question I posed above: 20% retention of habitat to achieve what objective? One of the surprising results of thresholds work is that species can occupy habitat for a period, even when it is below their extinction threshold (Carlson 2000; Eriksson 1996, 1997; Eriksson & Kiviniemi 1999; Hanski et al. 1996). Species can thus exist, but do not necessarily persist, in landscapes below their habitat requirements, due to time lags in the response of species to habitat change (see Section 5.2.4). Occupancy measures therefore do not address persistence or viability thresholds (i.e., extinction thresholds; Guenette and Villard 2004). If occupancy measures provide the basis for generalized, broad scale targets for habitat retention, ensuing policy is unlikely to ensure the persistence of species.

Targets for habitat retention derived from measures of species richness also need to address the objectives that policy makers intend to meet. Approximately one quarter of the studies that Andrén (1994) cites use measures that describe species richness. Similarly, Chan-McLeod and Bunnell (2004) found thresholds in species diversity at 20% retention; however, even habitat retention above this level did not meet the needs of species dependent on mature forests. Although diversity remained constant above 20%, community composition changed as early-seral replaced late-seral species (Chan-McLeod & Bunnell 2004).

This masking of important changes at the community level is a particularly disturbing example of the maladaptive policy of applying generalized targets, and in particular, purported thresholds in species diversity, as a basis for conservation policy. Measures of species richness are an oversimplified indicator of change, obscuring changes at the community level and ignoring the loss of species that are sensitive to lower levels of habitat loss (Chan-McLeod & Bunnell 2004; Radford et al. 2005). Because thresholds relate to the life history processes and scales of perception of individual species (Holland et al. 2005), thresholds in species richness are unlikely (Lindenmayer et al. 2005; Lindenmayer & Luck 2005; Ranius & Fahrig 2006). The response of species diversity to habitat loss is more likely a smooth curve without thresholds (Lindenmayer et al. 2005; Ranius & Fahrig 2006). Even where thresholds in species richness are reported (e.g., Chan-McLeod & Bunnell 2004; Martikainen et al. 2000; Radford et al. 2005) the evidence is equivocal due to sampling and statistical issues (Ranius & Fahrig 2006). Further, even if statistical and sampling issues are resolved, thresholds in species richness indicate the end point of the process of species decline; habitat thresholds that maintain viable populations of species should therefore be higher than the threshold at which a disproportionate decline in species richness occurs (Radford et al. 2005; Lindenmayer and Luck 2005). Finally, Chan-McLeod and Bunnell (2004), in a paper providing retention guidelines for salvage harvest in landscapes disturbed by MPB, suggest that a retention level of 90% is appropriate to maintain the abundance of species that depend on mature forest. Thus, they make the distinction (Noss 2001; Radford et al. 2005) between the minimal level of retention they believe is necessary for the occurrence of generalist species (20%), and the appropriate level of retention to maintain an optimal population of a species with greater demands for habitat (90%). Similar to the limited capacity to achieve species persistence using generalized thresholds derived from occupancy measures, targets based on thresholds of species richness will likely fail to protect community composition, species that are more demanding of habitat, or even enough habitat for the persistence of some species who utilize the matrix.

The finding from the literature that amount of habitat is more important overall than spatial factors (e.g., Betts et al. 2006) emphasizes the difference between fragmentation thresholds and extinction thresholds, again focusing on the policy objectives of applying generalized targets for retention. Species will respond to a range of threshold values that relate their traits to the landscape context (Andrén 1999; Angelstam & Andersson 2001). Accordingly, extinction thresholds can occur at any amount of habitat loss and cause species to go extinct (Holland et al. 2005). For many species, extinction thresholds occur long before fragmentation thresholds (Andrén 1999; Fahrig 2001; Holling et al. 2005; Ranius & Fahrig 2006). In forests recently disturbed by MPB, in the absence of adequate resources provided by surrounding, live forest, wildlife may adapt to widespread mortality by increasing their territory size to meet their habitat requirements (Chan-McLeod 2006), which would increase the amount of habitat required to maintain species above extinction thresholds. Fragmentation thresholds appear to occur at 20% where the matrix is hostile, and affect community composition and the persistence of individual species. If retaining landscapes at or above fragmentation thresholds is the primary management concern, then 20% is an appropriate retention target. However, a policy target of 20% retention of habitat represents a worst-case scenario in habitat conservation in these landscapes. Managing landscapes at fragmentation thresholds but below the extinction thresholds of many species thus poses risks to ecosystem recovery and function.

Andrén’s (1994) hypothesis that 10%-30% retention of habitat was adequate to prevent precipitous declines in species persistence remained unchallenged for some time before the evidence for forests was debated (Mönkkönen & Reunanen 1999), but in the meantime, policy makers began to apply a 20% target for habitat retention in conservation (Angelstam & Andersson 2001). A retention goal of 20% of habitat is appealing where the challenge of achieving a higher level of retention is not ecologically viable or economically or politically feasible (Lõhmus et al. 2004; Ranius & Fahrig 2006). In European landscapes, long subject to landscape change, amounts of natural forest are below this level. Achieving this target there thus poses an ecological challenge, even though the retention of 20% of habitat is a relatively low target (Angelstam & Andersson 2001; Lõhmus et al. 2004). The application of a 20% threshold for habitat retention has created a policy precedent, and it has become a reference point for ongoing application (e.g., Lõhmus et al. 2004). However, even while proposing these generalized targets, authors acknowledge how tenuous they are (Angelstam & Andersson 2001), and inertia characterizes the development of forest policy, irrespective of the science. For example, Angelstam et al. (2004a) showed that thresholds in species response to changes in habitat occur across a range (10%-50%) of habitat remaining; still, they relate the average of this range (19%) to Andrén's (1994) finding that 10%-30% of retained habitat marks an ecologically relevant threshold response of species to changes in habitat.

Planning for ecosystem-based management in many areas specifies targets for protecting biodiversity primarily aimed at the maintenance of ecological processes or protecting the habitat needs of select taxa. Where the primary objective of management is preservation of biodiversity, research indicates that retention of habitat needs to be much higher than 20% of total habitat to achieve this goal. The use of multiple criteria to establish biodiversity targets has led to recommendations for protection of between 40% and 70% of the total region (Cowling et al. 2003; Noss et al. 2002; Noss et al. 1999). Applying the concept of thresholds to ecosystem-based management on the north and central coast of British Columbia led to the recommendation for protection of 70% of the estimated natural amount of old-growth forests (between 45% and 65% of the total area) at the regional level (Coast Information Team 2004; Price et al. 2007). These targets represent a precautionary approach to forest management, where the primary objective is to minimize harm to biodiversity and ecological processes and function (Raffensperger & Tickner 1999).

Thus, in forests, no general prescriptions emerge from the literature for maintaining habitat conditions above the persistence thresholds of all species. Thresholds occur across a range of habitat conditions, involving interacting and inter-dependent factors such as amount of habitat, habitat configuration, habitat quality, species traits, and disturbance patterns. Using a generalized target, such as 20%, to protect biodiversity in fact poses risks to the conservation of biodiversity for three, interconnected reasons. First, species presence at this level of habitat retention does not assure that habitat is suitable for persistence; only measures of viability such as reproductive success can convey the probability of persistence in a landscape. Second, its basis as a threshold for species richness means that 20% retention of habitat is a threat to biodiversity, because it marks the extirpation of many species from landscapes; the endpoint of their decline. Habitat thresholds to maintain community composition occur at higher levels of habitat retention than indicated by a 20% habitat threshold for species richness. Third, 20% habitat retention corresponds to fragmentation thresholds, while the extinction thresholds of species occur across a gradient of habitat loss. Precautionary approaches to ecosystem-based management in many jurisdictions show that conservation of biodiversity requires between 40% and 70% of the total area of a region.

6.1.2 Uncertainty

The uncertainty around the consequences and costs of exceeding thresholds is high (Perrings & Pearce 1994). While it is evident that threshold responses of species to changes in habitat occur, we currently lack knowledge about what species could respond in a threshold-like way, and where along the gradient of change thresholds could occur, as a consequence (or even in the absence) of salvage harvesting in ecosystems disturbed by MPB. Knowledge about key ecosystem processes or functions, their potential altered regimes and their controlling variables is also poor. Although it is evident from the literature that altered conditions from those known to occur historically in these systems are possible (Forest Practices Board 2007a; Paine et al. 1998; Romme et al. 1998; Turner et al. 1998), we lack conceptual models for what these alternate states might look like. In the absence of historical knowledge about how ecosystems recover from multiple, large disturbances, we must generate and test hypotheses about how recovery will (or will not) occur.

Where agencies are able to quantify the uncertainty associated with different management actions, they can carefully manage ecosystems following MPB disturbance with a reasonable understanding of how management actions will influence ecosystem conditions (Forest Practices Board 2007a). Where data are available, an understanding of the impact of salvage in the context of thresholds should allow the identification of desirable conditions or ecosystem services, of the drivers that affect these conditions and services, and of the factors that cause change in the drivers (Angelstam et al. 2004a; Groffman et al. 2006). This approach quantifies uncertainty using formal methods to analyze risk (Morgan & Henrion 1990). This approach to risk assessment also implies that safe minimum standards are relevant to reduce uncertainty and prevent irreversible losses (Hein & van Ierland 2006; Perrings & Pearce 1994). Safe minimum standards represent one way to specify the maximum amount of risk that management agencies are willing to accept on behalf of the public when confronted with unknown costs.

However, this approach has limitations. In general, it assumes better knowledge about the location and consequences of thresholds than what is available. Risk assessment also assumes that one asks the right question (O'Brian 2000) and that one can reasonably assign probabilities to different states of nature and costs to different ecological outcomes (Schettler et al. 2002). Sources of uncertainty, such as how large infrequent disturbances differ from smaller disturbances of the same type, and how variables interact as a consequence of multiple, large disturbances, may not be easily quantified.

Ecological thresholds involve three sources of uncertainty: statistical, model and fundamental (Schettler et al. 2002). Statistical uncertainty may be quantified if probability distributions can be used to describe a variable. Where a management problem involves multiple, interacting variables, a model is necessary. Models by definition involve simplifying assumptions about relationships and feedbacks between variables, introducing another source of uncertainty. Lack of knowledge about complex systems that extends to novel circumstances, such as ecological outcomes that are poorly understood and their probabilities, creates fundamental uncertainty. Where the dominant form of uncertainty is model or fundamental uncertainty, quantitative risk assessment is an inadequate basis for policy (Schettler et al. 2002). The uncertainty around what are the appropriate mental and statistical models for the multiple, large disturbances in the salvaged ecosystems disturbed by MPB, and the lack of knowledge about the locations of thresholds and outcomes of breaching them indicate that model and fundamental uncertainty are predominant. These sources of uncertainty may, in some cases, exceed the capacity of quantitative risk assessment to provide reliable policy guidance for this issue.

6.1.3 The precautionary principle and adaptive management

The current MPB outbreak and its consequences are, in part, a case of institutional failure—the incapacity of management agencies to adequately manage resources due to the organizational architecture and belief systems that sustain the institutions (Gunderson et al. 1995; Holling & Meffe 1996; Lee 1993a, b). Institutional failure in this case stems from the reliance on traditional management concepts about ecosystem services that derive from the belief that natural systems function according to steady state dynamics. An example of such a concept in British Columbia is the idea of the maximum sustained yield of timber that is integrated into predictive models that forecast timber supply. Because their focus is on controlling disturbance, this concept and its policy permutations have contributed to the institutional failure at managing ecosystems that are host to MPB (Gunderson et al. 1995; Scheffer et al. 2001). The focus on controlling disturbance prevents an appreciation of the value that natural processes have for engendering diversity and renewal, and it is misguided because of the difficulty of managing and predicting stochastic events such as disease outbreaks. More importantly, the focus on controlling disturbance detracts from the fundamental concern to maintain ecological resilience (Scheffer et al. 2001). The institutional failure that contributed to the current epidemic MPB disturbance has also created an opportunity for management agencies to learn, adapt and actualize a management paradigm that captures the fundamental nature of change in forest ecosystems (British Columbia Ministry of Forests and Range 2008; Gaines et al. 1997; Gunderson & Holling 2002; Gunderson et al. 1995).

The precautionary principle is a management approach that addresses the sources of uncertainty inherent in the issues of large-scale salvage of landscapes disturbed by MPB. The precautionary principle has four core components: taking preventative action when faced with uncertainty; shifting the burden of proof from parties who oppose an action to the proponents; exploring a wide range of alternatives to actions that are potentially harmful; and involving the public in decision-making (Raffensperger & Tickner 1999). The components of uncertainty and the burden of proof are central to the precautionary principle in response to more traditional management approaches that forestall protective policy (Myers 2002). For example, for MPB salvage, proponents of salvage would frame the policy response to uncertainty around the need to determine where thresholds are located and what are the outcomes of crossing them, before instituting strict standards (Myers 2002).

Traditional approaches to decision-making ask how much risk is acceptable, whereas a precautionary approach asks how much harm management agencies can avoid. Management agencies exert a large influence over many of the elements that could trigger threshold changes in ecosystems recently disturbed by MPB (Table 2; Chapin et al. 2006; D'Alessandro 2007). Agencies can wield this influence through a management policy that is more risk averse than the existing policy for salvage harvesting. For example, initiating a program of adaptive management (AM) would address the third component of the precautionary principle—to explore a range of alternatives to actions that are potentially harmful (Angelstam et al. 2004a; Lee 1993a; Walters 1986; Williams et al. 2007). AM is a structured approach to decision-making that is robust to many types of uncertainty, and suited to experimentation and hypothesis testing in the context of operational management and research. AM is a heuristic approach that incorporates into policy the knowledge gained from research and monitoring in an operational setting.

The idea that organisms can exhibit a threshold response to changes in habitat can translate to policy targets that pose a low risk to biodiversity conservation. The new paradigm for forest management in BC is to manage to maintain ecological resilience. The extirpation or extinction of species represents a loss of ecological resilience. Habitat thresholds thus pose an approach to maintaining ecological resilience. An approach that is more risk averse than applying a 20% retention threshold could, in the context of a program of adaptive management, focus on generalized targets for extinction thresholds of representative species or ecosystems (Angelstam et al. 2004a). These targets can be ecologically meaningful by managing for traits, or suites of traits of species, or for suites of species associated with different habitat elements in the landscape (Angelstam et al. 2004c; Groffman et al. 2006). Policy targets can also address the ecosystems that are most sensitive to change, or the species that are most demanding of habitat (Fahrig 2001; Jansson & Angelstam 1999; Mönkkönen & Reunanen 1999; Ranius & Fahrig 2006; The Resilience Alliance 2007a, b, c; With & King 1999b).

Alternatively, research to identify thresholds of change could focus on ecological services provided by the disturbed ecosystems, such as soil and hydrological resources (Table 2; Chapin et al. 2006; Groffman et al. 2006; Forest Practices Board 2007). The steps to identifying thresholds in soil or hydrological processes or attributes (including populations or diversity and composition of soil fauna) that occur in response to changes in forest structure or function are similar in scope to detecting habitat thresholds for vertebrate and above-ground invertebrate species (Angelstam et al. 2004a). These steps relate aspects of forest function and/or forest structure that influence soil and hydrological attributes or processes, to changes in the variable(s) of interest. The focus is to determine if, and at what level of habitat change, threshold responses occur in critical soil or hydrological attributes or processes caused by activities associated with salvage harvest of MPB disturbance (Andersen et al. 2008; Chapin et al. 2006; The Resilience Alliance 2007a; 2007b; 2007c).

7.0 SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

7.1 Summary and concluding remarks

In this synthesis I present a set of hypotheses proposed by other authors and myself relevant to the dynamics of change and recovery that could manifest in ecosystems recently disturbed by MPB and subject to salvage harvesting. First, the historic range of natural variability in disturbance regimes is one of a small set of critical structuring processes that maintains resilience in the ecosystems that contain the host species of MPB (*sensu* Holling 1992). Second, directional (human) influences altered the disturbance regime and contributed to the magnitude of the current MPB disturbance (Chapin et al. 2006; Taylor et al. 2006). Third, due to the magnitude of the disturbance, ecosystem recovery may be qualitatively different than the processes of recovery that would follow a smaller MPB epidemic (Romme et al. 1998). Fourth, multiple disturbances in quick succession can also alter the processes and pathways of ecosystem recovery (Paine et al. 1998; Scheffer et al. 2001). Correspondingly, I propose that salvage harvesting in ecosystems disturbed by MPB may be a form of cumulative disturbance that may have deleterious impacts, given the history in these ecosystems; and I present empirical evidence that some species are maladapted to multiple disturbances involving natural and salvage disturbance (Lindenmayer et al. 2004; Lindenmayer and Noss 2006). Fifth, I propose that while the current MPB disturbance represents a demonstrated type of ecological threshold (Barryman 2005; Raffa et al. 2008), the cumulative disturbance caused by salvage harvesting could cause secondary thresholds to be breached in other ecosystems properties (Andersen et al. 2009). Sixth, I propose that the ecosystem properties most likely to exhibit threshold changes as a consequence of salvage harvesting involve attributes of species, forest soils and hydrological systems (Chapin et al. 2006; Lindenmayer and Noss 2006).

Thresholds of change should make us realize that systems under management are capable of producing unexpected, non-linear responses to management actions in surprising circumstances (Holling & Meffe 1996). Thresholds are relevant to the management of ecological systems because they embody the complex and fundamental nature of the potential changes in these systems—loss of resilience. Disturbances that exceed the capacity of species and ecosystems to recover can produce non-linear or threshold changes to ecosystem properties as resilience is lost, which may include drastic and rapid (or slow—or slowly observed) effects on species or ecosystems. Thus, understanding how and when species respond as habitat is disturbed, altered or lost is relevant to maintaining ecological resilience in ecosystems disturbed by MPB and subject to salvage. Given the extent of MPB disturbance and the allowable rate of cut, there are landscapes where the existing and planned loss of mature forest habitat across scales is high, suggesting the relevance of habitat thresholds (Chapin et al. 2006).

There is thus a need to anticipate what may cause species to exhibit threshold responses to salvage harvesting. To help address this information gap, I summarize and discuss the implications for forest policy, three lessons from the literature on habitat thresholds (summarized in Table 6). These lessons are relevant to the type and scale of salvage harvesting permitted in ecosystems disturbed by MPB[1] (Eng 2004; Pedersen 2004; Snetsinger 2005).

The first lesson is that the amount and quality of habitat remaining typically matters more than the spatial pattern of habitat on the landscape. The second lesson is that rate and scale of habitat loss matter too. The third lesson is that critical thresholds emerge from *species interactions with landscape structure*, as opposed to resulting solely from the structure of the landscape itself. The threshold response of species to changes in habitat may be influenced by species interactions such as plant-pollinator relationships, or particular life history traits such as dispersal. However, the ultimate cause of extinction is a higher mortality rate than reproductive rate (Fahrig 2002). Reproductive traits and rates of change are central to species threshold responses to habitat change.

Reproductive traits and rates are central to habitat thresholds for four reasons. First, of all the traits that can exhibit threshold responses, thresholds in reproductive rate have the greatest influence on species persistence (Holland et al. 2005; With & King 1999a; With & King 2001). This emphasizes that the presence or absence of suitable breeding habitat has a primary influence on species persistence. Second, reproductive rates help determine the species that habitat thresholds may primarily affect—those most sensitive to habitat loss appear to have low reproductive rates (e.g., Holland et al. 2005; Vance et al. 2003). Third, studying reproduction reveals changes in the capacity of a species to persist, compared to studying attributes of presence or occupancy, which only reveal that the species exists currently. Fourth, reproductive traits can relate to elements of habitat that are easily studied, such as patch size or patch cover. Reproductive capacity and changes to reproduction should be a primary focus for retention objectives, research and monitoring.

Table 6. Summary of three lessons from the literature about habitat thresholds.

LESSON	INTERPRETATIONS
Lesson 1—Habitat effects caused by harvest removal, like habitat amount, quality and pattern matter, but amount matters most.	i) Species exhibit threshold responses to changes in patch size, cover and quality. ii) Species exhibit threshold responses to changes in the amount of habitat at the landscape level.
Lesson 2—Dimensional effects like rate and scale of change, and their interactions, matter too.	i) Accelerated rate of harvest can induce fragmentation thresholds for non-generalist species and thresholds in species tolerance to the amount of edge habitat. ii) Thresholds are relevant at multiple scales that are consistent with the perceptions that individual species have of the landscape. iii) The rate of change in habitat patches can scale up to induce landscape thresholds. iv) Delays in the response of species to changes in habitat constrain our capacity to interpret the implications of current habitat alteration.
Lesson 3—Effects on species attributes such as life history traits matter.	i) Reproductive factors have the most influence on extinction thresholds. ii) Dispersal success depends on matrix quality. iii) Species can be vulnerable to habitat thresholds as a consequence of their interactions with other species. iv) Species can be vulnerable to habitat thresholds as a consequence of rarity.

Retention of habitat and maintenance of habitat quality across scales is the primary means to avoid most of the negative effects of habitat change on species and to prevent the threshold response of species to changes in habitat. At higher levels of harvesting, aggregation of habitat across scales is the primary means to mitigate some of the spatial effects of habitat loss. Therefore, in salvaged landscapes subject to high levels of habitat loss (e.g., >60% habitat lost), when the effects of the spatial arrangement of habitat becomes most pronounced, aggregation of habitat across scales may be an important tool to mitigate threshold effects in these landscapes. In contrast, a more risk averse approach to salvage in these landscapes would be to maximize retention objectives, maintaining higher levels of habitat across scales.

Our perceptions of how ecosystems change constrain our management actions (Folke et al. 1996; Gunderson 2000; Lindenmayer et al. 2008). A perspective that is equilibrium-centered cannot contemplate the complex types of change suggested by non-linear dynamics. Consequently, with an equilibrium-centered perspective, there is little certainty that management actions will maintain ecosystem resilience. Conversely, by helping avoid long-lived or irreversible change to undesirable states, applying knowledge from resilience theory, such as ecological thresholds, has the potential to reduce uncertainty in management actions by preventing or mitigating drastic declines to the flow of ecosystem goods and services.

Incorporating the ideas of ecological resilience theory in general and ecological thresholds specifically into forest management has the potential to reduce uncertainty surrounding the provisions for forest biodiversity, leading to a management strategy that is risk averse (Angelstam et al. 2004a; Folke et al. 1996). The findings of this review support the opinion of other authors (e.g., Andrén 1999; Lindenmayer et al. 2006) who suggest that generalized targets using thresholds are an insufficient “short-cut” to protect biodiversity. The concept of habitat thresholds nonetheless offers important insights about how change can manifest, or be prevented, in forested ecosystems.

Knowledge of thresholds can help maintain resilience in forested systems by allowing managers to recognize vulnerable species, ecosystems or landscapes, to carefully manage those factors influenced by humans to avoid threshold change, and to build the capacity to manage situations where undesirable changes occur. The idea of thresholds as policy targets can in some instances be cast as an issue of safe minimum standards. Prudent use of quantitative risk assessment would apply this method where data are sufficient and the sources of uncertainty can be reasonably quantified.

Given our inadequate understanding of the locations of habitat thresholds and the unknown consequences of exceeding them, our main basis for policy should derive from our inability to predict losses due to crossing ecosystem thresholds (Perrings & Pearce 1994). The key uncertainties associated with thresholds demand an approach to decision-making that differs from the conventional approach (Folke et al. 1996). It is not that we have the answer wrong to the question of how much habitat is enough; it is that we are asking the wrong question. Managing to maintain a diversity of ecosystem services in the affected ecosystems requires a shift in perspective. The more fundamental question is: what can forest management do to maintain or enhance ecological resilience in affected landscapes? Applying the precautionary principle—casting the management of ecosystems disturbed by MPB around efforts to avoid harm—and implementing this principle through a program of adaptive management provides a renewed opportunity and improved focus to understand the nature, mechanisms and thresholds of ecological resilience in these landscapes.

7.2 Recommendations for forest policy, management and operations

1. Create an environment to develop and implement forest policy that is premised on maintaining or enhancing ecological resilience.
    a. Institute a comprehensive program of adaptive management. Use the current MPB disturbance and salvage harvesting as an

    opportunity to hypothesize, experiment and learn about how to minimize harm in these systems. Incorporate landscapes already subject to salvage into the AM program.

    b. The goal of a program of AM should be to provide adequate funding, support and incentive for forest operations and research to elucidate the response of ecosystem attributes to a range of retention, and to ensure the policy environment is adaptable to new information.
    c. Apply the precautionary principle.
        i. Provide policy and policy guidance to support retention levels according to the habitat requirements of species whose traits make them vulnerable to thresholds in habitat (e.g., rare species, species with low reproductive rates and species with affinity for mature forests).
        ii. Aggregation of habitat is increasingly important to a greater number of species as habitat loss increases, but may becomes critical for habitat specialists in landscapes with >60% habitat loss. Maintain landscapes above this level, and pay attention to configuration early on during the planning of forest harvest activities, as fragmentation depends on both harvest strategy and the initial landscape structure.

2. Improve the knowledge base of decision makers with regard to ecological resilience. Implement a process to disseminate information from structured learning about ecological resilience in general, and this management issue in particular (The Resilience Alliance 2007a, 2007b).
3. Institute a strategic overview of the potential effects of salvage harvesting on fish species (Brazner et al. 2004) and above and below-ground invertebrate and plant species (*sensu* Bunnell et al. 2004).
4. Be ready with mitigating policies to respond to undesirable change.

7.3 Recommendations for forest research

1. Test the hypotheses I propose in this review.
    a. Is natural disturbance one of a small set of key structuring processes in ecosystems disturbed by MPB? For example, do the body mass distributions of birds and mammals demonstrate a discontinuous distribution *sensu* Holling (1992)?
    b. Are there ecosystem functions for which recovery will be different (i.e., breach thresholds) following this large disturbance, compared to a smaller epidemic? For example, will successional trajectories differ? Will soil processes be altered?
    c. Salvage harvesting in ecosystems disturbed by MPB is a form of cumulative disturbance that may have deleterious impacts.
        i. Will multiple disturbances in quick succession alter the processes and pathways of ecosystem recovery in affected ecosystems? For example, will successional trajectories differ? Will soil processes be altered?
        ii. Are some species in affected landscapes maladapted to multiple disturbances involving natural and salvage disturbance? For example, will some species in landscapes that are not subject to salvage have a greater probability of persistence than the same species in landscapes subject to salvage?
    d. Could the cumulative disturbance caused by salvage harvesting prompt secondary thresholds to be breached in ecosystem properties, such as species persistence or soil attributes? For example, will vertebrate species identified as vulnerable to the effects of salvage harvest (Bunnell et al. 2004) exhibit threshold responses? Will rates of decomposition of organic matter exhibit threshold responses in salvaged compared to non-salvaged landscapes?

2. Improve the knowledge base of scientists with regard to ecological resilience. Implement a process to disseminate information from structured learning about ecological resilience in general, and this management issue in particular (The Resilience Alliance 2007c).
    a. Use this process to scope the potential for threshold changes to occur in populations of species, including soil fauna, and in soil processes.
    b. Use this process to better quantify potential successional trajectories.
    c. Use this process to better quantify / qualify issues of invasion by non-native plant species.
    d. Consider focusing a monitoring program on the study of species with short generation times; traits that make them vulnerable to habitat thresholds; or on suites of traits of species; or suites of species associated with different habitat elements in the landscape (Angelstam et al. 2004c; Groffman et al. 2006).
3. Consider scale issues relentlessly to determine the characteristic scale(s) of response of species proposed for study (e.g., Holland et al. 2004; 2005). Habitat thresholds at the landscape scale are relevant across spatial scales, consistent with the perceptions that species have of the landscape. Habitat thresholds may affect species at multiple scales, including scales that exceed their home range.

APPENDIX 1 KEY HABITAT THRESHOLDS LITERATURE: CD-ROM DATA

The CD-ROM attached forms a part of this work.

I created data files in Microsoft (MS) Office Excel® 2007. Data files can be opened with MS Office Excel® 1997-2007.

Data Files:

- Searchable database of key habitat thresholds literature_MS07.docx (view in MS Office Excel® 2003-2007)
  723 KB
- Searchable database of key habitat thresholds literature_MS97.doc (view in MS Office Excel® 1997-2003)
  811 KB

Table 1. Search categories and category types in Appendix 1.

CATEGORY	CATEGORY RESPONSE
Geographic location	Forest type, Country
Taxa	Latin species name
Type of study	Empirical (E), modeling (M)
Matrix setting	Forest (F), non-forest (N), model (M), various (V)
Element of habitat structure	Standing dead wood (WLT), coarse woody debris (CWD), old growth (OG), deciduous (DEC), riparian, matrix, patch, gap
Species trait	Reproduction, dispersal, rarity, competition, plant-pollinator, predator-prey, keystone species, habitat specialist, parasitism, various
Habitat remaining at habitat threshold	Habitat amount remaining at threshold response of species
Comments	Short description of study

REFERENCES

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**:265-269.

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology **45**:41-75.

Akçakaya, 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 Conservation **7**:875-894.

Allee, W. C. 1938. The social life of animals. W.W. Norton & Co., New York, N.Y.

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.

Andersen, T., J. Carstensen, E. Hernandez-Garcia, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: approaches to identification. Trends in Ecology & Evolution **24**:49-57.

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

Andrén, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos **76**:235-242.

Andrén, H. 1997. Habitat fragmentation and changes in biodiversity. Ecological Bulletins **46**:171-181.

Andrén, H. 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. Oikos **84**:306-308.

Angelstam, P. 1996. The ghost of forest past – natural disturbance regimes as a basis for reconstruction for biologically diverse forests in Europe. Pages 287-337 in R. M. Degraaf, and R. M. Miller, editors. Conservation of Faunal Diversity in Forested Landscapes. Chapman and Hall, London.

Angelstam, P. 2004. Habitat thresholds and effects of forest landscape change on the distribution and abundance of black grouse and capercaillie. Ecological Bulletins **51**:173-187.

Angelstam, P., and L. Andersson. 2001. Estimates of the needs for forest reserves in Sweden. Scandinavian Journal of Forest Research. Supplement **3**:38-51.

Angelstam, P., A. Bjärvall, R. Franzén, and G. Mikusiński. 2001a. 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, editors. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA, Stockholm, Sweden.

Angelstam, P., S. Boutin, L. Fahrig, G. Mikusiñski, and I. Storch. 2001b. Response variables for analyses of habitat thresholds at the landscape scale. Page 12 in P. Angelstam, and M. Breuss, editors. Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. Report to MISTRA, Stockholm, Sweden.

Angelstam, P., et al. 2004a. Targets for boreal forest biodiversity conservation - a rationale for macroecological research and adaptive management. Ecological Bulletins **51**:487-509.

Angelstam, P., M. Dönz-Breuss, and J.-M. Roberge. 2004b. Targets and tools for the maintenance of forest biodiversity - an introduction. Ecological Bulletins **51**:11-24.

Angelstam, P., J. M. Roberge, M. Dönz-Breuss, I. J. Burfield, and G. Ståhl. 2004c. Monitoring forest biodiversity - from the policy level to the management unit. Ecological Bulletins **51**:295-304.

Angelstam, P. K., R. Butler, M. Lazdinis, G. Mikusinski, 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**:473-482.

Augustin, S., A. Bolte, M. Holzhausen, and B. Wolff. 2005. Exceedance of critical loads of nitrogen and sulphur and its relation to forest conditions. European Journal of Forest Research **124**:289-300.

Augustine, D. J., L. E. Frelich, and P. A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecological Applications **8**:1260-1269.

Barryman, A. A. 2005. Outbreak thresholds, bark beetles, Pacific Northwest, USA & Canada. Threshold example in Resilience Alliance and Santa Fe Instittue Database. Thresholds and alternate states in ecological and social-ecological systems. Available at http://www.resalliance.org/index.php?id=183. Resilience Alliance and Santa Fe Institute.

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

Bascompte, J., and R. V. Solé. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology **65**:465-473.

Baskent, E. Z. 1999. Controlling spatial structure of forested landscapes: a case study stowards landscape management. Landscape Ecology **14**:83-97.

Bawa, K. S. 1990. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics **21**:399-422.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology **7**:94-108.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376-382.

Bélisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology **17**: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**:64-71.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. Nature **429**:827-833.

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**:517-533.

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

Bentz, B. J., J. A. Logan, and J. C. Vandygriff. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. The Canadian Entomologist **133**:375-387.

Berec, L., D. S. Boukal, and M. Berec. 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. American Naturalist **157**:217-230.

Bergeron, Y., B. Harvey, A. Leduc, and S. Gauthier. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. Forestry Chronicle **75**:49-54.

Bergeron, Y., A. Leduc, B. D. Harvey, and S. Gauthier. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica **36**:81-95.

Betts, M. G., G. J. Forbes, A. W. Diamond, and P. D. Taylor. 2006. Independent effects of fragmentation on forest songbirds: An organism-based approach. Ecological Applications **16**:1076-1089.

Bissonette, J. A., and I. Storch. 2002. Fragmentation: is the messge clear? Conservation Biology **6**:14.

Bodin, O., M. Tengo, A. Norman, J. Lundberg, and T. Elmqvist. 2006. The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. Ecological Applications **16**:440-451.

Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **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. Proceedings of the Royal Society of London Series B-Biological Sciences **265**:1921-1925.

Bowman, W. D., C. C. Cleveland, L. Halada, J. Hresko, and J. S. Baron. 2008. Negative impact of nitrogen deposition on soil buffering capacity. Nature Geoscience **1**:767-770.

Brazaitis, G., and P. Angelstam. 2004. Influence of edges between old deciduous forest and clearcuts on the abundance of passerine hole-nesting birds in Lithuania. Ecological Bulletins **51**:209-217.

Brazner, J. C., D. K. Tanner, N. E. Detenbeck, S. L. Batterman, S. L. Stark, L. A. Jagger, and V. M. Snarski. 2004. Landscape character and fish assemblage structure and function in western Lake Superior streams: General relationships and identification of thresholds. Environmental Management **33**:855-875.

Briske, D. D., S. D. Fuhlendor, and E. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology & Management **58**:1-10.

British Columbia Ministry of Forests and Range. 2008. Future Forests Ecosystems Initiative 2007/08-2009/10 strategic plan, Victoria, British Columbia.

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**:2145-2156.

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

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

Bütler, R., P. Angelstam, P. Ekelund, and R. Schlaepfer. 2004a. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-alpine forest. Biological Conservation **119**:305-318.

Bütler, R., P. Angelstam, and R. Schlaepfer. 2004b. Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*. Ecological Bulletins **51**:219-232.

Bull, E. L. 1983. Bird response to beetle-killed lodgepole pine. Murrelet **65**:94-96.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the Interior Columbia Basin. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Bunnell, F. L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia - patterns and implications for conservation. Conservation Biology **9**:636-644.

Bunnell, F. L., K. A. Squires, and I. Houde. 2004. Evaluating effects of large-scale salvage logging for mountain pine beetle on terrestrial and aquatic vertebrates. Mountain Pine Beetle Initiative Working Paper 2004-2. Natural Resources Canada, Canadian Forest Service, Victoria, BC.

Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications **10**:1749-1761.

Burkett, V. R., et al. 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecological Complexity **2**:357-394.

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

Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (*Dendrocopos leucotos*). Forest Ecology and Management **131**:215-221.

Carroll, A., S. Taylor, J. Régnière, and L. Safranyik. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223-232 in T. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions. Information Report BC-X-399. Canadian Forest Service, Natural Resources Canada, Kelowna, British Columbia.

Chan-McLeod, A. A. 2006. A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management. BC Journal of Ecosystems and Management **7**:119-132.

Chan-McLeod, A. A., and F. Bunnell. 2004. Potential approaches to integrating silvicultural control of mountain pine beetle with wildlife and sustainable management objectives in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions. October 30-31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, B.C.

Chapin, F. S., T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio **33**:361-365.

Chapin, F. S., M. D. Robards, H. P. Huntington, J. E. Johnstone, S. E. Trainor, G. P. Kofinas, R. W. Ruess, N. Fresco, D. C. Natcher, and R. L. Naylor. 2006. Directional changes in ecological communities and social-ecological systems: a framework for prediction based on Alaskan examples. American Naturalist **168**:S36-S49.

Chapin, F. S., et al. 2000. Consequences of changing biodiversity. Nature **405**:234-242.

Coast Information Team. 2004. The scientific basis of ecosystem-based management. Province of British Columbia, Vancouver, British Columbia.

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

Cooper, C. B., and J. R. Walters. 2002. Independent effects of woodland loss and fragmentatinon brown treecreeper distribution. Biological Conservation **105**:1-10.

Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. Biological Conservation **112**:191–216.

Cowling, S. A., and Y. Shin. 2006. Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO2 within a region of Amazonia. Global Ecology and Biogeography **15**:553-566.

Croke, J. C., and P. B. Hairsine. 2006. Sediment delivery in managed forests: a review. Environmental Reviews **14**:59-87.

D'Alessandro, S. 2007. Non-linear dynamics of population and natural resources: the emergence of different patterns of development. Ecological Economics **62**:473-481.

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. Conservation Biology **8**:1027-1036.

Danell, K., R. Bergstrom, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. Forest Ecology and Management **181**:67-76.

de Oiveira, F. J. B., and J. P. Metzger. 2006. Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. Landscape Ecology **21**:1061-1073.

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

DeLong, S. C., and W. B. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management **131**:93-106.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling **3**:481-538.

Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology **11**:1204-1210.

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 Biology **41**:315-336.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064-2075.

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

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. Ecological Monographs **70**:423-444.

Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:2285-2299.

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

du Toit, J. T., B. H. Walker, and B. M. Campbell. 2004. Conserving tropical nature: current challenges for ecologists. Trends in Ecology & Evolution **19**:12-17.

Duinker, P. N., and L. A. Greig. 2006. The impotence of cumulative effects assessment in Canada: ailments and ideas for redeployment. Environmental Management **37**:153-161.

Dykstra, P. R. 2004. Thresholds in habitat supply: a review of the literature. B.C. Ministry Sustainable Resource Management Ecosystem Eonservation Section, and B.C. Ministry. Water, Land and Air Protection Biodiversity Branch, Victoria, BC. Wildl. Rep. No. R-27. [online] URL: http://wlapwww.gov.bc.ca/wld/documents/techpub/r27_thresholds.pdf.

Dykstra, P. R., and T. F. Braumandl. 2006. The influence of the mountain pine beetle on stand dynamics in Canada's Rocky Mountain national parks.

Working Paper 2006-15. Natural Resources Canada, Victoria, British Columbia.

Dytham, C. 1994. Habitat destruction and competitive coexistence - a cellular-model. Journal of Animal Ecology **63**:490-491.

Dytham, C. 1995a. Competitive coexistence and empty patches in spatially explicit metapopulation models. Journal of Animal Ecology **64**:145-146.

Dytham, C. 1995b. The effect of habitat destruction pattern on species persistence: a cellular model. Oikos **74**:340-344.

Ecke, F., P. Christensen, P. Sandstrom, and B. Hornfeldt. 2006. Identification of landscape elements related to local declines of a boreal grey-sided vole population. Landscape Ecology **21**:485-497.

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**:425-431.

Egerton, F. N. 1973. Changing concepts of the balance of nature. Quarterly Review of Biology **48**:322-350.

Eiswerth, M. E., and J. C. Haney. 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. Ecological Economics **38**:259-274.

Eken, G., et al. 2004. Key biodiversity areas as site conservation targets. Bioscience **54**:1110-1118.

Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment **1**:488-494.

Eng, M. 2004. Forest stewardship in the context of large scale salvage operations: an interpretation paper, B.C. Min. For., Res. Br., Victoria, B,C. Tech Rep. 019. <http://www.for.gov.bc.ca/hfd/pubs/docs/Tr/Tr019.htm>.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos **77**:248-258.

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

Eriksson, O., and K. Kiviniemi. 1999. Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. Biological Conservation **87**:319-325.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biology **41**:300-314.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. The Journal of Wildlife Management **61**:603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling **105**:273-292.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation **100**:65-74.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications **12**:346-353.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487-515.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**:50-59.

Fahrig, L., and J. Paloheimo. 1988. Determinants of local population size in patchy habitats. Theoretical Population Biology **34**: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 Museum Bulletin **471**:129-132.

Flather, C. H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist **159**:40-56.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution and Systematics **35**:557-581.

Folke, C., C. S. Holling, and C. Perrings. 1996. Biological diversity, ecosystems, and the human scale. Ecological Applications **6**:1018-1024.

Forest Practices Board. 2007a. The effect of mountain pine beetle attack and salvage harvesting on streamflows. Forest Practices Board Special Investigation. Forest Practices Board, Victoria, British Columbia.

Forest Practices Board. 2007b. Lodgepole pine stand structure 25 years after mountain pine beetle attack. Forest Practices Board Special Report. Forest Practices Board, Victoria, British Columbia.

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. BioScience **47**:437-445.

Foster, D. R., and D. A. Orwig. 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. Conservation Biology **20**:959-970.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and evolution. Cambridge University Press, Cambridge, U.K.

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

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. Conservation in Practice **1**:8-17.

Franklin, J. F., J. A. MacMahon, F. J. Swanson, and J. R. Sedell. 1985. Ecosystem responses to the eruption of Mt. St. Helens. National Geographic Research **Spring**:198-216.

Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management **155**:399-423.

Frelich, L. E., and P. B. Reich. 1999. Neighborhood effects, disturbance severity, and community stability in forests. Ecosystems **2**:151-166.

Fryxell, J. M. 2001. Habitat suitability and source - sink dynamics of beavers. Journal of Animal Ecology **70**:310-316.

Gaines, M. S., J. E. Diffendorfer, R. H. Tamarin, and T. S. Whittam. 1997. The effects of habitat fragmentation on the genetic structure of small mammal populations. Journal of Heredity **88**:294-304.

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 Ecology **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, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, N.Y.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology **13**:263-268.

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

Graham, C. H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology **15**:1789-1798.

Groffman, P., et al. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems **9**:1-13.

Groom, M. J. 1998. Allee effects limit population viability of an annual plant. American Naturalist **151**:487-496.

Groom, M. J., and M. A. Pascual. 1998. The analysis of population persistence: An outlook on the practice of viability analysis. Pages 4-27. Conservation biology, Second edition. Chapman and Hall, Inc., New York, NY.

Guénette, J.-S., and M.-A. Villard. 2004. Do empirical thresholds truly reflect species tolerance to habitat alteration? Ecological Bulletins **51**.

Guénette, J.-S., and M.-A. Villard. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. Conservation Biology **19**:1168-1180.

Gundersen, P., I. K. Schmidt, and K. Raulund-Rasmussen. 2006. Leaching of nitrate from temperate forests - effects of air pollution and forest management. Environmental Reviews **14**:1-57.

Gunderson, L., and C. S. Holling, editors. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C.

Gunderson, L. H. 2000. Ecological resilience - in theory and application. Annual Review of Ecology and Systematics **31**:425-439.

Gunderson, L. H., C. S. Holling, and S. S. Light. 1995. Barriers broken and bridges built: a systhesis in L. H. Gunderson, C. S. Holling, and S. S. Light, editors. Barriers and bridges to the renewal of ecosystems and institutions. Columbia University Press, New York, NY.

Gustafson, E. J., and T. R. Crow. 1994. Forest management alternatives in the Hoosier National Forest. Journal of Forestry **92**:28-29.

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

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

Haeussler, S., L. Bedford, A. Leduc, Y. Bergeron, and J. M. Kranabetter. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Pages 307-327. Exchange Centre Scientific Literature.

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

Halliday, T. 1978. Vanishing birds: their natural history and conservation. Hold, Rinehart and Winston, New York, N.Y.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology **63**:151-162.

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

Hanski, I. 1999b. Metapopulation ecology. Oxford University Press, Oxford, U.K.

Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. American Naturalist **147**:527-541.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology **16**:666-673.

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

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

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Pages 133-302 in A. MacFadyen, and E. D. Ford, editors. Advances in ecological research: volume 15. Academic Press, Orlando, FL.

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

Hein, L., and E. van Ierland. 2006. Efficient and sustainable management of complex forest ecosystems. Ecological Modelling **190**:351-366.

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. Conservation Genetics **4**:233-240.

Hill, M. F., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. Ecology Letters **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**:321-331.

Hobson, K. A., and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects after 30 years. Ecological Applications **9**:849-863.

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. BioScience **54**:227-233.

Holland, J. D., L. Fahrig, and N. Cappuccino. 2005. Fecundity determines the extinction threshold in a Canadian assemblage of longhorned beetles (Coleoptera: Cerambycidae). Journal of Insect Conservation **9**:109-119.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holling, C. S. 1978. The spruce-budworm/forest-management problem in C. S. Holling, editor. Adaptive environmental assessment and management.

International Series on Applied Systems Analysis. John Wiley & Sons, New York.

Holling, C. S. 1986. The resilience of terrestrial ecosystems: local surprise and global change in W. Clark, and R. Mund, editors. Sustainable Development of the Biosphere. Cambridge University Press, Cambridge.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Holling, C. S. 1996. Engineering resilience versus ecological resilience. Pages 31-43 in P. C. Schulze, editor. Engineering within ecological constraints. National Academy Press, Washington, D.C.

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology **10**: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**:183-190.

Homan, R. N., B. S. Windmiller, and J. M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications **14**:1547-1553.

Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation **124**:301-310.

Hughes, T. P., et al. 2007. Adaptive management of the great barrier reef and the Grand Canyon world heritage areas. Ambio **36**:586-592.

Hunter, M. L., editor. 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press.

Ingvarsson, P. K., and S. Lundberg. 1995. Pollinator functional-response and plant-population dynamics - pollinators as a limiting resource. Evolutionary Ecology **9**:421-428.

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 Ecology **14**:283-290.

Jerabkova, L., C. E. Prescott, and B. E. Kishchuk. 2006. Effect of variable-retention harvesting on soil nitrogen availability in boreal mixedwood forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:3029-3038.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London B-Biological Sciences **330**:175-190.

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

Keisker, D. G. 2000. Types of wildlife trees and coarse woody debris required by wildlife of north-central British Columbia. Research Branch, Ministry of Forests, Victoria, BC.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology **1**.

Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernandez, and S. A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist **156**: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? Ecological Modeling **147**:23-39.

Kinzig, A. P., P. Ryan, M. Etienne, H. Allison, T. Elmqvist, and B. H. Walker. 2006. Resilience and regime shifts: assessing cascading effects. Ecology and Society **11**.

Klausmeier, C. A. 2001. Habitat destruction and extinction in competitive and mutualistic metacommunities. Ecology Letters **4**:57-63.

Klenner, W. 2006. Retention strategies to maintain habitat structure and wildlife diversity during the salvage harvesting of mountain pine beetle attack areas in the Southern Interior Forest Region., B.C. Min. For. Range, S. Int. For. Reg. Kamloops, B.C. Exten. Note 04. <http://www.for.gov.bc.ca/hfd/Pubs/RSI/FSP/EN/RSI_EN04.htm>.

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**:253-260.

Lamberson, R. H., R. McKelvey, B. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology **6**: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. Conservation Biology **8**: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**:157-175.

Lamont, B. B., and P. G. L. Klinkhamer. 1993. Population size and viability. Nature **362**: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**:446-450.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist **130**:624-635.

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

Lande, R. 1988b. Genetics and demography in biological conservation. Science **241**:1455-1460.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911-927.

Lande, R. 1994. Risk of population extinction from fixation of new deleterious mutations. Evolution **48**:1460-1469.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications **9**:1179-1188.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation **55**:77-92.

Lee, K. N. 1993a. Compass and gyroscope: integrating science and politics for the environment. Island Press, Washington, DC.

Lee, K. N. 1993b. Greed, scale mismatch, and learning. Ecological Applications **3**:560-564.

Leimgruber, P., W. J. McShea, and G. D. Schnell. 2002. Effects of scale and logging on landscape structure in a forest mosaic. Environmental Monitoring and Assessment **74**:141-166.

Lemaitre, J., and M.-A. Villard. 2005. Foraging patterns of pileated woodpeckers in a managed Acadian forest: a resource selection function. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:2387-2393.

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

Lertzman, K. P., J. Fall, and B. Dorner. 1998. Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. Northwest Science **72**.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240.

Lindenmayer, D. B., P. J. Burton, and J. F. Franklin. 2008. Salvage logging and its ecological consequences. Island Press, Washington, D.C.

Lindenmayer, D. B., J. Fischer, and R. B. Cunningham. 2005. Native vegetation cover thresholds associated with species responses. Biological Conservation **124**:311-316.

Lindenmayer, D. B., D. R. Foster, J. F. Franklin, M. L. Hunter, R. F. Noss, F. A. Schmiegelow, and D. Perry. 2004. Ecology - salvage harvesting policies after natural disturbance. Science **303**:1303-1303.

Lindenmayer, D. B., and G. Luck. 2005. Synthesis: Thresholds in conservation and management. Biological Conservation **124**:351-354.

Lindenmayer, D. B., and M. A. McCarthy. 2002. Congruence between natural and human forest disturbance - an Australian perspective. Forest Ecology and Management **155**:319-335.

Lindenmayer, D. B., and R. F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology **20**:949-958.

Logan, J. A., and B. J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology **28**:924-934.

Logan, J. A., and J. A. Powell. 2001. Ghost forest, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist **47**:160-173.

Lõhmus, A. K., K. Kohv, A. Palo, and K. Viilma. 2004. Loss of old-growth, and the minimum need for strictly protected forests in Estonia. Ecological Bulletins **51**:401-411.

Ludwig, D., D. D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. Journal of Animal Ecology **47**:315-322.

Ludwig, D., B. Walker, and C. S. Holling. 1997. Sustainability, stability and resilience. Conservation Ecology **1**.

Lundberg, J., and F. Moberg. 2003. Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. Ecosystems **6**:87-98.

Lundberg, S., and P. K. Ingvarsson. 1998. Population dynamics of resource limited plants and their pollinators. Theoretical Population Biology **54**:44-49.

Lundquist, J. E. 1995. Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA. Forest Ecology and Management **74**:37-48.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MacDonald, L. H., and E. L. Huffman. 2004. Post-fire soil water repellency: persistence and soil moisture thresholds. Soil Science Society of America Journal **68**:1729-1734.

Machmer, M. M., and C. Steeger. 1995. The ecological roles of wildlife tree users in forest ecosystems. Page 54. Ministry of Forests, Province of British Columbia, Victoria, BC.

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29**:81-96.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of *Coleoptera* in mature managed and old-growth boreal forests in southern Finland. Biological Conservation **94**:199-209.

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

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269**:471-477.

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 J. Verner, M. L. Morrison, and C. J. Ralph, editors. Modeling habitat relationships of terrestrial vertebrates. The University of Wisconson Press, Madison, WI.

McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs **65**:235-260.

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

McIver, J. D., and L. Starr, editors. 2000. Environmental effects of postfire logging: literature review and annotated bibliography. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

McIver, J. D., and L. Starr. 2001. A literature review on the environmental effects of postfire logging. Western Journal of Applied Forestry **16**:159-168.

McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361-383 in E. D. Schulze, and H. Mooney, editor. Biodiversity and Ecosystem Function. Springer-Verlag, Berlin.

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

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

Moilanen, A., and I. Hanski. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. Journal of Animal Ecology **64**:141-144.

Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos **84**:302-305.

Moore, J. E., and R. K. Swihart. 2005. Modeling patch occupancy by forest rodents: Incorporating detectability and spatial autocorrelation with hierarchically structured data. Journal of Wildlife Management **69**:933-949.

Morgan, M. G., and M. Henrion. 1990. Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis. Cambridge University Press, Cambridge, UK.

Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **32**:2169-2183.

Muradian, R. 2001. Ecological thresholds: a survey. Ecological Economics **38**:7-24.

Myers, N. 2002. The precautionary principle puts values first. Bulletin of Science, Technology and Society **22**:210-219.

Nappi, A., P. Drapeau, and J. P. L. Savard. 2004. Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? Forestry Chronicle **80**:67-74.

Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology **61**:37-40.

Noss, R. F. 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology **15**:578-590.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology **16**:895–908.

Noss, R. F., J. R. Strittholt, K. Vance-Borland, C. Carroll, and P. Frost. 1999. A conservation plan for the Klamath-Siskiyou ecoregion. Natural Areas Journal **19**.

O'Brian, M. 2000. Making better environmental decisions: an alternative to risk assessment. MIT Press, Cambridge, MA.

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 Ecology **5**:137-144.

Økland, B., A. Bakke, S. Hågvar, and T. Kvamme. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation **5**:75-100.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. John Wiley & Sons, Inc., New York, NY.

Ovaskainen, O., and I. Hanski. 2002. Transient dynamics in metapopulation response to perturbation. Theoretical Population Biology **61**:285-295.

Ovaskainen, O., K. Sato, J. Bascompte, and I. Hanski. 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. Journal of Theoretical Biology **215**:95-108.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-75.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist **103**:91-93.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535-545.

Pedersen, L. 2004. Expedited timber supply review for the Lakes, Prince George and Quesnel timber supply areas: public discussion paper. British Columbia Ministry of Forests and Range, Victoria, British Columbia.

Penteriani, V., and B. Faivre. 2001. Effects of harvesting timber stands on goshawk nesting in two European areas. Biological Conservation **101**:211-216.

Penttilä, R., J. Siitonen, and M. Kuusinen. 2004. Polypore diversity in managed and old-growth boreal *Pica abies* forests in southern Finland. Biological Conservation **117**:271-283.

Perrings, C., and D. Pearce. 1994. Thresholds effects and incentives for the conservation of biodiversity. Environmental and Resource Economics **4**:13-28.

Perry, D. A., and M. P. Amaranthus. 1997. Disturbance, recovery, and stability in K. A. Kohm, and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C.

Perry, G. L. W. 2002. Landscapes, space and equilibrium: shifting viewpoints. Progress in Physical Geography **26**:339.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems **1**:6-18.

Peterson, G. D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems **5**: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. Agriculture Ecosystems & Environment **69**:243-252.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, IL.

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

Platt, W. J., and J. H. Connell. 2003. Natural disturbances and directional replacement of species. Ecological Monographs **73**:507-522.

Preston, M. I., and A. S. Harestad. 2007. Community and species response by birds to group retention in a coastal temperate forest on Vancouver Island, British Columbia. Forest Ecology and Management **243**:156-167.

Price, K., R. Holt, and L. Kremsater. 2007. Representative forest targets: informing threshold refinement with science: a review paper for RSP and CFCI. February 5, 2007 Draft. Province of British Columbia, Vancouver, British Columbia.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652-661.

Pulliam, H. R., J. B. Dunning, and J. G. Liu. 1992. Population-dynamics in complex landscapes - a case-study. Ecological Applications **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, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

Radford, J. Q., and A. F. Bennett. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. Biological Conservation **117**:375-391.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependend birds. Biological Conservation **124**:317-337.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience **58**:501-517.

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**:389-398.

Raffensperger, C., and J. Tickner, editors. 1999. Protecting public health and the environment: implementing the precautionary principle. Island Press, Washington, DC.

Ranius, T., and L. Fahrig. 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scandinavian Journal of Forest Research **21**:201-208.

Redding, T. E., and K. J. Devito. 2008. Lateral flow thresholds for aspen forested hillslopes on the Western Boreal Plain, Alberta, Canada. Hydrological Processes **22**:4287-4300.

Reed, D. H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. Conservation Biology **17**:230-237.

Ren, H., Z. A. Li, W. J. Shen, Z. Y. Yu, S. L. Peng, C. H. Liao, M. M. Ding, and J. G. Wu. 2007. Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China. Science in China Series C-Life Sciences **50**:277-284.

Restrepo, C., L. M. Renjifo, and P. Marples. 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern and body mass distribution. Pages 171-189 in W. F. Laurance, and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL.

Reunanen, P., A. Nikula, M. Mönkkönen, E. Hurme, and V. Nivala. 2002. Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. Ecological Applications **12**:1188-1198.

Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems **1**:524-534.

Romme, W. H., D. H. Knight, and J. B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? American Naturalist **127**:484-494.

Saari, L., J. Åberg, and J. E. Swenson. 1998. Factors influencing the dynamics of occurrence of the Hazel Grouse in a fine-grained managed landscape. Conservation Biology **12**: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**:491-494.

Safranyik, L., and A. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3-66 in L. Safranyik, and B. Wilson, editors. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Victoria, British Columbia.

Safranyik, L., and B. Wilson, editors. 2006. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Victoria, BC.

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

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution **18**:648-656.

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**:584-606.

Schettler, T., K. Barrett, and C. Raffensperger. 2002. The precautionary principle: proctecting public health and the environment in M. McCally, editor. Life support: the environment and human health. MIT Press, Cambridge, MA.

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

Schmiegelow, F. K. A., D. P. Stepnisky, C. A. Stambaugh, and M. Koivula. 2006. Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conservation Biology **20**:971-983.

Schowalter, T. D. 2000. Insect ecology: an ecosystem approach. Academic Press, San Diego, CA.

Schroeder, L. M. 2007. Retention or salvage logging of standing trees killed by the spruce bark beetle *Ips typographus*: consequences for dead wood dynamics and biodiversity. Scandinavian Journal of Forest Research **22**:524-530.

Schrott, G. R., K. A. With, and A. T. W. King. 2005. On the importance of landscape history for assessing extinction risk. Ecological Applications **15**:493-506.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience **31**:131-134.

Shore, T., L. Safranyik, B. Hawkes, and S. Taylor. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. Pages 95-114. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Canadian Forest Service, Natural Resources Canada, Victoria, British Columbia.

Smerdon, B. D., T. E. Redding, and J. Beckers. 2009. An overview of the effects of forest management on groundwater hydrology. BC Journal of Ecosystems and Management **10**:22-44. www.forrex.org/publications/jem/ISS50/vol10_no21_art24.pdf.

Snetsinger, J. 2005. Guidance on landscape- and stand-level structural retention in large-scale mountain pine beetle salvage operations. British Columbia Ministry of Forests and Range, Victoria, British Columbia

Spies, T. A., W. J. Riple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications **4**:555-568.

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

Steeger, C., and C. L. Hitchcock. 1998. Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. Journal of Wildlife Management **62**:1349-1358.

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

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

Stone, W. E., and M. L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetatio **122**:1-12.

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

Sutherland, G. D., J. S. Richardson, and F. L. Bunnell. 2000. Uncertainties linking Tailed Frog habitat and population dynamics with riparian management. Pages 477-483 in L. M. Darling, editor. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb. 1999. BC Ministry of Environment, Lands and Parks, Victoria, B.C.

Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist **108**:859-873.

Svancara, L. K., R. Brannon, J. M. Scott, C. R. Groves, R. F. Noss, and R. L. Pressey. 2005. Policy-driven versus evidence-based conservation: A review of political targets and biological needs. Bioscience **55**:989-995.

Swift, T. L., and S. J. Hannon. 2002. Critical threshold responses of resident birds to forest cover in east-central Alberta. Page 374. Abstracts of the sustainable forest management network conference - advances in forest management: from knowledge to practice, 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. Journal of Theoretical Biology **210**:287-303.

Taylor, M., K. Suckling, and J. Rachlinski. 2003. Critical habitat significantly enhances endangered species recovery. Available online at: www.biologicaldiversity.org/swcbd/programs/policy/ch/index.html.

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

Taylor, S. W., A. Carroll, R. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67-94. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Canadian Forest Service, Natural Resources Canada.

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

The Resilience Alliance. 2007a. Assessing and managing resilience in social-ecological systems: a practitioner's workbook. Volume 1, version 1.0. The Resilience Alliance.

The Resilience Alliance. 2007b. Assessing and managing resilience in social-ecological systems: a practitioner's workbook. Volume 2 supplementary notes to the practitioners workbook, version 1.0. The Resilience Alliance.

The Resilience Alliance. 2007c. Assessing resilience in social-ecological systems: a scientist's workbook. Resilience Alliance.

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

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology **75**: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. American Naturalist **149**:407-435.

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

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.

Trani, M. K., and J. Giles, Robert H. 1999. An analysis of deforestation: Metrics used to describe pattern change. Forest Ecology and Management **114**:459-470.

Travis, J. M., and C. Dytham. 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings of the Royal Society of London B, Biological Sciences **266**:723-728.

Trzcinski, M., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications **9**:586-593.

Turner, M. G. 1989. Landscape ecology - the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171-197.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems **1**:511-523.

Turner, M. G., V. H. Dale, and E. H. Everham. 1997a. Fires, hurricanes, and volcanoes: comparing large disturbances. Bioscience **47**:758-768.

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**:121-129.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997b. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411-433.

Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1987. Landscape ecology. Bioscience **37**:119-127.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

van Langevelde, F., et al. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology **84**:337-350.

Vance, M. D., L. Fahrig, and C. H. Flather. 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. Ecology **84**:2643-2653.

Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. American Naturalist **158**:211-220.

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

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. Conservation Biology **13**:774-783.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science **238**:802-804.

Walker, B., L. Gunderson, A. Kinzig, C. Folke, S. Carpenter, and L. Schultz. 2006. A handful of heuristics and some propositions for understanding resilience in social-ecological systems. Ecology and Society **11**:13. [online] URL:http://www.ecologyandsociety.org/vol11/iss11/art13/.

Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social–ecological systems. Ecology and Society **9**:5. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5/.

Walker, B., and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: a developing database. Ecology and Society **9**:3. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art3.

Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semiarid savanna grazing systems. Journal of Ecology **69**:473-498.

Walters, C. 1986. Adaptive management of renewable resources. Macmillan, New York.

Walton, A., J. Hughes, M. Eng, A. Fall, T. Shore, B. Riel, and P. Hall. 2008. Provincial-level projection of the current mountain pine beetle outbreak: update of the infestatoin projection based on the 2007 provincial aerial overview of forest health and revisions to the "model" (BCMPB.v5). Ministry of Forests and Range, Province of British Columbia, Victoria, British Columbia.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

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

Wilcove, D. S. 1987. From fragmentation to extinction. Natural Areas Journal **7**:23-29.

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2007. Adaptive Management: The U.S. Department of the Interior Technical Guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.

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. Conservation Biology **11**:1069-1080.

With, K. A. 2002. The landscape ecology of invasive spread. Conservation Biology **16**:1192-1203.

With, K. A. 2004. Assessing the risk of invasive spread in fragmented landscapes. Risk Analysis **24**:803-815.

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

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

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

With, K. A., and A. W. King. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology **14**:73-82.

With, K. A., and A. W. King. 1999b. Extinction thresholds for species in fractal landscapes. Conservation Biology **13**:314-326.

With, K. A., and A. W. King. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biological Conservation **100**:75-88.

With, K. A., and A. W. King. 2004. The effect of landscape structure on community self-organization and critical biodiversity. Ecological modelling **179**:349-366.

Wu, J. G., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology **70**:439-466.

Yourke, R., B. Walker, C. S. Holling, L. Gunderson, C. Folke, S. Carpenter, and W. A. Brock. 2002. Toward an integrative synthesis. Pages 419-438 in L. Gunderson, and C. S. Holling, editors. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C.

Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. C. Iii, J. F. Reynolds, and M. C. Chapin. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. The American Naturalist **146**:765-794.