

How much is really enough?

How much is really enough?: Informing old growth targets with threshold science

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Abstract

The government of British Columbia has stated that the application of ecosystem-based management to the temperate rainforests of British Columbia will be science-based. This paper reviews threshold studies to determine whether science can provide guidance about the level of old forest retention necessary to conserve ecological integrity—a core goal of ecosystem-based management. We summarise empirical, landscape-level studies that describe thresholds in species' occupancy or life-history in relation to amount of suitable habitat. Thresholds began to be detected when habitat declined below about 60% of total area, although a few species crossed above that amount. Below 60% the number of species or communities crossing thresholds increased linearly; nearly two-thirds reached thresholds before their habitat dropped to 30%. Uncertainties include difficulty in identifying suitable habitat, plus the lack of long-term, reproductive studies in intact ecosystems. However, no alternative approach for setting precautionary old forest retention targets appears to exist. We conclude that existing targets of maintaining 70% of the natural levels of old forest in any ecosystem (i.e. 34 – 68% actual old forest) pose a low risk to ecological integrity, and that interim targets of maintaining 30% of the natural level of old forest may pose high risk.

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Introduction

British Columbia's government has chosen to implement ecosystem-based management in BC's coastal temperate rainforests. Similar decisions have been made world-wide as the importance of ecological systems to human wellbeing is recognised. Ecosystem-based management focuses on maintaining ecological integrity. As a result, science is asked how to maintain ecological integrity with high certainty, and more specifically - "how much old forest is enough?".

Much of the literature about "how much is enough?" has centred on thresholds – points where ecological function shifts rapidly. The original threshold literature focused on dramatic shifts in whole ecosystems (Holling 1973). These shifts are typically unpredicted and rapid, and recovery can be extremely difficult (Scheffer et al. 2001).

Detection of threshold responses through research inherently requires that an ecosystem has been pushed past a threshold: it is more difficult to identify management guidelines that **prevent** thresholds being crossed. Threshold identification for any ecosystem *a priori* requires that similar ecosystems have been studied for long enough, at appropriate scales, and with sufficient replicates, to allow prediction. These conditions are rarely met. A large, relatively intact ecosystem, such as the B.C. temperate rainforest poses tremendous difficulties for studies of ecosystem function.

How then can science inform management? Here, we examine thresholds in species abundance or presence as habitat decreases. This approach is based on two assumptions: that species' thresholds predict ecosystem thresholds; and that habitat loss predicts species' thresholds.

Support for the first assumption varies among species. There is good evidence that loss of species can impact ecosystem function (Power et al. 1996, Ellison et al. 2005). Other species may be functionally redundant in the short-term or under stable conditions but may contribute to ecological resilience at other times (Ehrlich & Walker 1998, O'Connor & Crowe 2005). In addition to the importance of particular species, diversity itself may affect function and resilience. In general, reviews conclude that (1) some minimum number of species is necessary to maintain local ecosystem function while conditions

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are stable; (2) larger numbers are necessary to maintain resilience when conditions change; (3) we don't know which species impact which functions in different ecosystems; (4) even rare species can play important roles (Loreau et al. 2001, Lyons et al. 2005).

There is excellent evidence for the second assumption: habitat loss is the primary cause of extinctions, extirpations and population declines (Fahrig 2002, UN Millennium Ecosystem Assessment 2003¹). Specific responses of any species to habitat loss depend on the extent, intensity and duration of the change. A shift in disturbance regime that significantly changes the spatial or temporal distribution of seral stages can represent habitat loss, particularly when seral stages include different species compositions and structural elements that develop over long time periods.

Some populations decline linearly as habitat decreases; other populations show a threshold response, where the **rate** of decline increases due to effects beyond simple habitat amount (abundance threshold in Fig. 1). In this latter case, populations change from one condition to another across a small change in habitat amount. A second type of threshold, the extinction threshold, defines the habitat amount where populations decline to zero.

Abundant evidence supports the existence of habitat thresholds: studies of minimum viable populations, metapopulations, theoretical percolation modeling, and studies of landscapes with different characteristics and species with different traits, all reveal thresholds. Proximate and ultimate mechanisms leading to thresholds include changes in life-history and disruption of genetic and evolutionary processes (Frankham 1995), changes in ecological interactions (Kareiva 1987, Lennartsson 2002), patch isolation (Franklin & Forman 1987, Kareiva & Wennergren 1995) and stochastic disturbance of small sub-populations (Harrison & Bruna 1999). Any of these mechanisms can push population decline beyond the rate predicted based on habitat loss alone.

Thresholds are relevant to understanding what constitutes significant ecological change because beyond a threshold probability of extinction increases, potential to regain abundance decreases (Mönkkönen & Reunanen 1999) and the risk to community structure, resilience and ecosystem function

¹ Available at: <http://www.millenniumassessment.org>

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increase (Fahrig 2001, Guénette & Villard 2004, Walker & Myers 2004). Linear population declines can also be ecologically significant; unfortunately, it is often difficult to interpret the significance of any particular level of decline because there is no detectable, dramatic change (Ludwig 1993). In essence, thresholds are useful because they mark significant ecological change.

There is no consensus on how much habitat is required to avoid either abundance or extinction thresholds, beyond an agreement that amount will vary among organisms and across ecosystems (Bender et al. 1998, Lindenmayer & Luck 2005). Because of variability among species, and because of the impossibility of examining all species, several authors have suggested using habitat thresholds relevant to those regionally-occurring species most sensitive to habitat loss to set management targets (Jansson & Angelstam 1999, Mönkkönen & Reunanen 1999, Fahrig 2001). In the coastal temperate rainforests however, no research into habitat thresholds exists for any species and choosing the most sensitive species is conjecture. Faced with little regionally-relevant information, we searched for an alternative approach suited for precautionary guidance. We looked for studies on thresholds where loss of suitable habitat in any landscape is shown to affect a population or community, following Andrén (1994).

Context

British Columbia's coastal temperate rainforests are characterised by low natural rates of stand-replacing disturbance—with return intervals in the order of millennia (Daniels & Gray 2005). Gap-phase dynamics dominate, and structural elements develop over centuries (Gavin et al. 2003). Habitat loss is primarily a shift in seral stage and stand structure, as ancient forests with complex structure are converted to younger, more uniform forests by logging. Because old forest dominates natural coastal landscapes and because it is the seral stage most at risk in the region, retention targets have been recommended for old forest (CIT 2004).

Initial recommendations suggested a low-risk target of 70% of natural levels of old forest regionally, by ecosystem type (equating to 34% - 68% of old forest depending upon natural disturbance frequency; CIT 2004). However, because the low-risk targets were perceived by some as overly cautious

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and difficult to achieve, interim targets of 30% of natural levels of old forest (14 – 29% of total forested area) were applied to 98% of the landbase, with the low-risk 70% target applying only to rare ecosystems.

Methods

Study selection

We searched the published scientific literature on habitat thresholds, filtering papers to compile a set of studies that described empirical, landscape-level thresholds in species' occupancy or life-history in relation to amount of suitable habitat. Because of the dearth of studies, we were not able to focus analyses on organisms specific to coastal British Columbia. Published papers on species thresholds are likely highly biased towards sensitive or easily-studied species. The former bias is acceptable when the goal is precautionary, though it is important to realise that patterns may not be representative of the range of species. The latter bias is less desirable, but unavoidable.

We found a variety of documented threshold types. Studies of individual species examined population trends over time, changes in reproductive parameters, abundance and patch occupancy over space. Studies of communities described patterns of species' extinctions. We grouped thresholds into the two broad types shown in Fig. 1, similar to the Type II and Type III thresholds described by Guénette and Villard (2004): abundance thresholds are defined as the level of habitat loss associated with a rate change in the abundance, or probability of occurrence, of a species. We also included in this class the few studies that showed reproductive parameter changes at a certain level of habitat loss. Extinction thresholds are defined as the level of habitat loss associated with the loss of a species from remaining suitable habitat. This threshold does not necessarily represent extirpation. We assume, however, that if similar losses occurred across the landscape, extirpation would result. Within this type, we included community thresholds, which show where species richness drops faster due to increased rate of local species extirpations.

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We focused on empirical studies because they examine real landscapes and communities, capturing complexities that are missing from models. We included empirical tests of models, but excluded model-based predictions, even when the models were based on empirical data.

We focused on landscape-level thresholds because these thresholds are most closely linked to questions about habitat amount. We excluded studies on specific requirements within habitat patches, and studies that looked at thresholds in patch size or isolation. Because species response varies with scale and life history (e.g. Holland et al. 2005), we considered "landscapes" at the scale relevant to each organism.

Variation in the suitability of habitat patches can mask effects of habitat amount at landscape scales (Hagan & Meehan 2002, Lichstein et al. 2002). Hence, we excluded studies without clear definitions of "suitable" habitat. We did not, however, require that studies performed detailed multivariate analyses of habitat structure and composition.

Finally, we excluded studies with apparent internal inconsistencies.

Threshold definition

Ecological thresholds are rarely sharp because most relationships are multivariate. Deciding objectively where to pinpoint a threshold on a gentle curve is difficult. In addition, many studies lack continuous data, providing additional interpretative challenges. Reviewed papers used a wide range of approaches, including visual inspection of graphs and simple documentation of habitat amount at which organisms were absent, a variety of linear and non-linear regression techniques and non-parametric optimisation of differences. It was not possible to re-analyse data across studies using a single technique: first, different analyses are appropriate for different types of data (e.g. binary vs. continuous); second, studies often did not provide sufficient information. Hence we have generally accepted the values provided, although in some cases, we have interpolated thresholds off curves, or generated our own curves from data provided.

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When analysing binary data most researchers use logistic regression. This technique is well-accepted and has been compared favourably to other modeling methods (Manel et al. 1999). However, logistic regression models probability of occurrence for each habitat amount, but does not pinpoint the threshold, necessitating subjective choice of a particular probability of occurrence. Some studies use 50% to represent “probably present” (e.g. Reunanen et al. 2004); others use 90% to represent the point at which occurrence starts to decline more rapidly (e.g. Angelstam 2004). When defining thresholds from studies presenting logistic regressions, we have chosen the upper point to represent an “abundance threshold” (Fig. 2). This point is essentially equivalent to a Type II threshold, where an organism is always present above a threshold and sometimes absent below (Guénette & Villard 2004). In most cases, this point is also very close to the maximum change in the rate of decline (maximising second derivative). More recently, studies with binary data have employed techniques that optimise threshold location to maximise the correct assignment of zeros and ones, including non-parametric binomial change point (Homan et al. 2004) and receiver-operator characteristic analysis (Guénette & Villard 2004).

Thresholds in continuous data can be detected using split regression. This technique estimates separate regression lines for different portions of the data and chooses a breakpoint—or threshold—that accounts for the most variance. Some studies combined presence/absence data into classes (e.g. proportion of presences per 10% habitat class; Gibbs 1998, Homan et al. 2004), losing some information, but allowing analyses that require continuous data. We used threshold values listed based on split regression analyses.

Studies of extinction thresholds most often provide the habitat amount at which an organism is no longer present in a patch, or has been extirpated from a landscape. These thresholds do not generally require special analysis techniques. They are equivalent to Type III thresholds, where organisms are always absent below a certain habitat amount and sometimes present above. Some studies examine complete sigmoidal curves; most examine only a portion of the relationship.

Some species were considered by more than one study. Within a threshold type (abundance or extinction), we used the mean value among studies for each species. Some studies examined several

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species, finding thresholds for some and linear declines for others. We only included species with a detected threshold. When thresholds were presented as ranges we selected the value apparently most relevant to landscape for that species, or else used a mean value.

We noted suitable and unsuitable (or "matrix") habitat for each study, to allow comparison of thresholds in hostile and less hostile matrices. We included changes in seral stage (e.g. old forest patches within a harvested forest matrix, or unmown grass in mown grass) in a "non-hostile" category. We included changes in ecosystem type (e.g. forest patches within agricultural fields or sub-urban development) in a "hostile" category, assuming that forestry and mowing were less hostile than shifts in ecosystem type. We did not attempt to define hostility in relation to the life history characteristics of particular species.

Results

Twenty papers (out of hundreds discussing thresholds) met our criteria (see tabular summary: www.veridianecological.ca/links). These studies demonstrated habitat loss thresholds in a variety of species, including one plant, two groups of butterflies, two beetles, a group of parasitoids, three amphibians, eleven birds and three mammals, as well as communities of woody plants, mites and birds.

Traditional meta-analysis, plotting response strength against an indicator variable (in this case % of habitat) is inappropriate for these data because we expect that different species will respond differently; i.e., we have no *a priori* reason to assume response strength will increase as habitat amount decreases. Instead, we examined a cumulative frequency plot of the number of organisms or communities with threshold values within each 10% class of remaining habitat.

Thresholds began to be detected when habitat declined below about 60% of total amount (Fig. 2). Few species crossed thresholds above 60% (butterflies in a grassland experiment, red-spotted newts in ponds along a rural-urban gradient, and American martens in managed forests; Summerville & Crist 2001, Gibbs 1998, Hargis et al. 1999). Below 60%, the number of species or communities crossing thresholds increased linearly for both abundance and extinction thresholds. More than one-third of

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species or communities crossed thresholds above 50%; nearly two-thirds reached thresholds before their habitat dropped to 30% of total amount.

Variation among species was considerable. Out of 15 species or communities exhibiting extinction thresholds, six crossed a threshold at or below 20% of total habitat and six species or communities crossed a threshold between 51 and 60%. The three studies that detected community thresholds found a wide range of thresholds (10%, 35% and 53% of total habitat).

We compared mean threshold values across taxa, threshold types and matrix hostility (recognising the limitations of low power, unbalanced design and varied studies). While our confidence in these patterns is low, we present them as hypotheses for future investigation. Thresholds varied among taxonomic groups (taxon effect: $F_{4,27} = 2.5$, $p = 0.07$; analysis of variance with taxon, threshold type and matrix hostility as main effects, no significant interactions). Birds accounted for this variation, crossing thresholds at lower levels of remaining habitat than other groups (birds: $25 \pm 5\%$ total habitat; other taxa: $45 \pm 5\%$ total habitat; $F_{1,27} = 7.4$, $p = 0.01$; orthogonal contrasts). Analysis for other taxonomic groups is hindered by the low number of studies for some of the groups.

Matrix hostility had no detectable effect on threshold value (mean abundance threshold: hostile matrix $39 \pm 5\%$ [$n = 12$]; non-hostile matrix $42 \pm 11\%$ [$n = 7$]; mean extinction threshold: hostile matrix $28 \pm 6\%$ [$n = 7$]; non-hostile matrix $40 \pm 10\%$ [$n = 8$]; effect of matrix hostility: $F_{1,27} = 1.4$, $p = 0.2$). These findings were limited by the lack of studies within our review comparing matrices. The single paper that compared hostile and non-hostile matrices (Radford & Bennett 2004) found a strong effect of matrix hostility on an isolation threshold.

Studies reported that thresholds vary across spatial scales in unpredictable ways, even within species. For example, wood frogs were more sensitive to the amount of forested habitat near their ponds (thresholds at 88% within 30m versus 44% within 1km), while spotted salamanders were more sensitive to the amount over larger landscapes (thresholds at 32% within 30m versus 51% within 1km; Homan et al. 2004). Similarly, gentian population extinction thresholds varied with the size of the field containing

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habitat patches (35 – 55% threshold in 15 ha fields versus 55 – 70% threshold in 2.5 ha fields; Lennartsson 2002).

Discussion

Our review indicates that more than one-third of species or communities crossed thresholds before their habitats dropped to 50%; nearly two-thirds reached thresholds before their habitat dropped to 30%. Few species had thresholds above 60%. Although we focused on empirically-detected thresholds, similar thresholds are predicted by theoretical work; highest thresholds modelled show that physical connectivity in simple landscapes is easily maintained with habitat amounts above 60%, but that below this threshold connectivity depends upon a variety of other factors (e.g. Gardner and O'Neill 1991, Stauffer & Aharony 1992). More ecologically realistic models predicted thresholds from 30 – 50% (e.g. With et al. 1997, Boswell et al. 1998, Fahrig 2002).

As with any review, uncertainty arises from trying to integrate the results from disparate studies. Threshold studies vary from tightly-controlled experimental studies on invertebrates in micro-habitats to observations of changes in abundance of vertebrates over decades of managed landscapes. The crucial link is that all studies considered thresholds related to the amount of habitat, where the definition of "habitat" was relevant to the species of interest. Studies in ecosystems with higher levels of natural disturbance may find fewer thresholds than those in relatively constant ecosystems. Timeframe is also relevant - a study in third-rotation forests may detect little change in species' abundance as sensitive species may have already been extirpated.

Other uncertainties apply to threshold studies as a group. First, most studies are short-term whereas it can take generations—many years in long-lived organisms—to respond fully to habitat loss (e.g. Tilman et al. 1994, Hanski & Ovaskainen 2002). Community disassembly can occur long after initial loss of rare species, showing that effects on ecosystem function may take even longer to detect (Gonzalez & Chaneton 2002).

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Second, most studies measure species occurrence, although presence does not guarantee persistence (Guénette & Villard 2004). In models, reproductive traits influence persistence most (e.g. Fahrig 2001, 2002; With & King 2001) and limited empirical studies have found reproductive thresholds at higher habitat amounts than occurrence thresholds (Angelstam 2004, Guénette and Villard unpublished data cited in Guénette & Villard 2004).

The third uncertainty arises from how thresholds are expressed. Almost all reviewed studies measured absolute amount of habitat available, rather than amount relative to that expected under natural disturbance. Consider two hypothetical species: the first lives in a common habitat that covers 85% of the landscape and the second lives in an uncommon habitat that covers only 15% of the landscape. The first species crosses a threshold at 30% and the second at 12%. These thresholds, however, are not easy to compare: the second species cannot experience a threshold at any amount above 15%. Rather than comparing 30% and 12%, these thresholds could be calculated as a percent of naturally occurring habitat (i.e. 35% for the first species and 80% for the second). Conclusions about sensitivity would then be reversed. We attempted to assess thresholds as expressed as a proportion of natural habitat; unfortunately, only two studies included sufficient data (Carlson 2000, Jansson & Angelstam 1999). Abundance thresholds for these studies increased from 13% of total habitat to 50% of natural and from 14% to 47%, and an extinction threshold increased from 10% to 33%. Consideration of change from natural habitat levels could change threshold values considerably, particularly for organisms using naturally-rare habitat.

Fourth, most studies did not address the relative hostility of suitable and unsuitable habitat. Modelling and empirical studies find that thresholds are generally clearer and higher where habitat changes from "good" to "bad" (black and white) than when habitat changes introduce shades of grey. Andrén (1994) found that empirical research in forest/agricultural settings demonstrated clearer fragmentation thresholds than studies in forest/forest settings. Contrary to expectations, and contrary to Andrén's analyses, we found no suggestion that the surrounding habitat matrix type affected thresholds.

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Our classification of matrix hostility was necessarily simplistic: changes in seral stage may have been perceived as hostile by some organisms.

The first two uncertainties suggest that longer-term studies, and studies of reproductive processes, might detect more and higher thresholds than those included in the review. The third uncertainty suggests that a better metric for comparison might increase threshold numbers. The fourth points out the complexities of habitat definition and of cross-scale effects.

Applying the results to management

In a discussion of the application of threshold science to management, Lindenmayer and Luck (2005) offer three cautions: (1) there is no convincing evidence pointing to a single threshold value, (2) concentrating on a single threshold ignores the declines that occur above that value, as a simple function of habitat loss, (3) uncritical focus on the amount of habitat cannot account for non-random land-use processes, specifically that the most productive parts of a landscape are modified first.

Our review demonstrates the first caution—variability among thresholds—clearly. This finding is unsurprising. Species perceive landscapes at different scales, have different dispersal and reproductive strategies and different levels of habitat specificity. In general, responses at higher habitat amounts are likely for poor dispersers, habitat specialists and rare species (e.g. Gibbs 1998, Summerville & Crist 2001, Gonzalez & Chaneton 2002, With et al. 2002).

Given the wide range of thresholds, can our analyses shed light on which species to choose as a regionally-occurring species most sensitive to habitat loss? We found that birds generally responded less to habitat loss than other taxa, perhaps because of higher dispersal ability or lower sensitivity to matrix quality. Although birds are frequently studied their lack of sensitivity as a group may make them poor indicators of landscape-level thresholds. Rare species are most likely to show thresholds (Gonzalez & Chaneton 2002, Summerville & Crist 2001), however rare species generally don't meet statistical requirements, and most were eliminated from our analyses. This difficulty poses challenges for any species-based management: the most sensitive species may be hardest to study.

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The American marten was the only species reviewed that is native to coastal British Columbia. As predators, martens are potentially functionally important and to date are the only potential candidate for a sensitive, regionally-occurring species. Three independent studies of martens (none coastal) suggest a high threshold—around 70%—within regenerating clearcuts or natural openings (Hargis et al. 1999, Chapin et al. 1998, Potvin et al. 2000). Martens, however, can persist in landscapes with higher levels of harvesting, with retained structure, or following recovery over time (Buskirk & Ruggiero 1994, Chapin et al. 1997). This discrepancy reflects the real-world complexities of examining habitat requirements for individual species – habitat can sometimes be made useful, or not, by relatively subtle changes in attributes or configuration.

Lindenmayer and Luck's (2005) second consideration includes two elements. First, targets are usually derived from the point where the rate of species loss increases rather than from the most sensitive species. Second, providing a single number as a target, while easy to manage, enforce and monitor, should not be the goal of ecosystem-based management. As a solution to the first element, they suggest that management focus should be "the point where most species are able to maintain viable populations for many generations" rather than "the point where a substantial number of species are lost from the landscape". This suggestion is consistent with using the threshold for the most sensitive organisms, and challenges any suggestion to use community-level thresholds. Using community thresholds is tempting as they represent detectable ecological consequences. However, the approach is particularly risky because community thresholds represent the endpoint of many extinctions, and because population decline and species loss may be masked as other species compensate (Bender et al. 1998, Mönkkönen & Reunanen 1999, Lindenmayer et al. 2005). The second element suggests that thresholds do not provide a panacea and that research, monitoring and adaptive management are critical to improving knowledge. Adaptive management is widely touted as a central piece of implementing ecosystem-based management. However, to our knowledge, adaptive management has not yet been used to test hypotheses relating to 'how much is enough' at landscape scales.

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Our approach of creating a cumulative distribution of thresholds allows managers to select a point that reflects their tolerance for the risk of losing species. The goal stated for coastal British Columbia is to maintain all species across the region, consistent with Lindenmayer and Luck (2005). Our review suggests that maintaining representative habitats at 60% of total habitat has a high certainty of meeting this goal. Although no studies reviewed were in coastal ecosystems, there is no reason to assume that coastal forest organisms need less suitable habitat than organisms elsewhere. Indeed, because of the low rate of natural disturbance, coastal forest dwellers may be more sensitive than organisms living in more changeable ecosystems. In particular, there may be more dispersal-limited species occupying old forests.

Lindenmayer and Luck's (2005) final caution suggests that thresholds cannot simply be applied over landscapes without consideration for ecosystems of differing type and productivity and at differing levels of risk. They suggest that attention should be paid to habitat quality, not merely quantity. This caution applies well to forestry in coastal British Columbia. Analyses of risk to different ecosystems consistently show that productive forests have been preferentially harvested. Because of this concern, the targets in coastal British Columbia are designed to be applied to ecosystem types separately. This approach prevents combining unproductive and productive old forest and then protecting only the unproductive.

Additionally, targets in coastal British Columbia are applied as a proportion of the natural amounts of old forest. The risk associated with an absolute level of habitat loss is hypothesised to vary among ecosystems because these systems, and the species within them, have evolved with different levels of disturbance (Bunnell 1995).

A complicating factor in setting old forest retention targets is that other seral stages provide some habitat values. Younger forests are less hostile to most organisms associated with old forests if structural attributes of old forests have been retained. As stands mature, the effects of habitat loss soften, although regenerated forests classified as "old" at 250 years will differ from the much older old-growth forests of today.

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Conclusion

Few empirical studies have examined landscape-level habitat thresholds, none in coastal British Columbia. Nonetheless, these studies provide the best information available to answer the questions posed. Our review suggests that maintaining more than 60% of suitable habitat poses low risk to most species. In coastal British Columbia, the habitat of interest is old forest. While we are uncertain as to how the risk to ecological integrity increases as old forest levels drop below 60%, our review suggests that risk is no longer **known** to be low below that point. Planned ecosystem-based management guidelines for old forest on the coast call for 70% of the amount of old forest that would exist under natural disturbance conditions for each ecosystem (CIT 2004), translating into 34 – 68% of the total forested area per ecosystem. We conclude that our review provides no evidence to change these planned guidelines if the goal is to maintain low risk to ecological integrity. Current “interim” legislation applies a target of 30% of natural (14 – 29% of total) to ecosystems covering the vast majority of the area. Our review suggests that this target likely poses a high risk to some species, with an unknown impact on ecosystem function.

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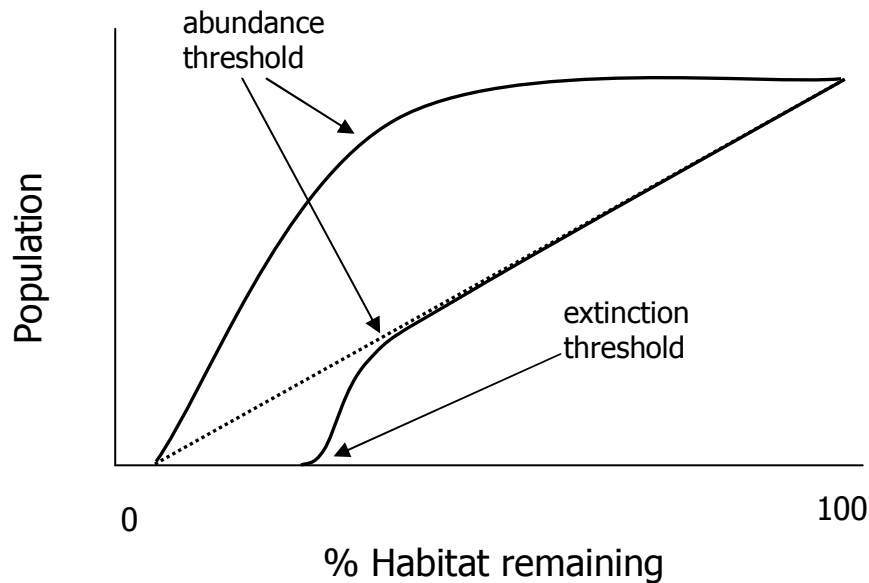
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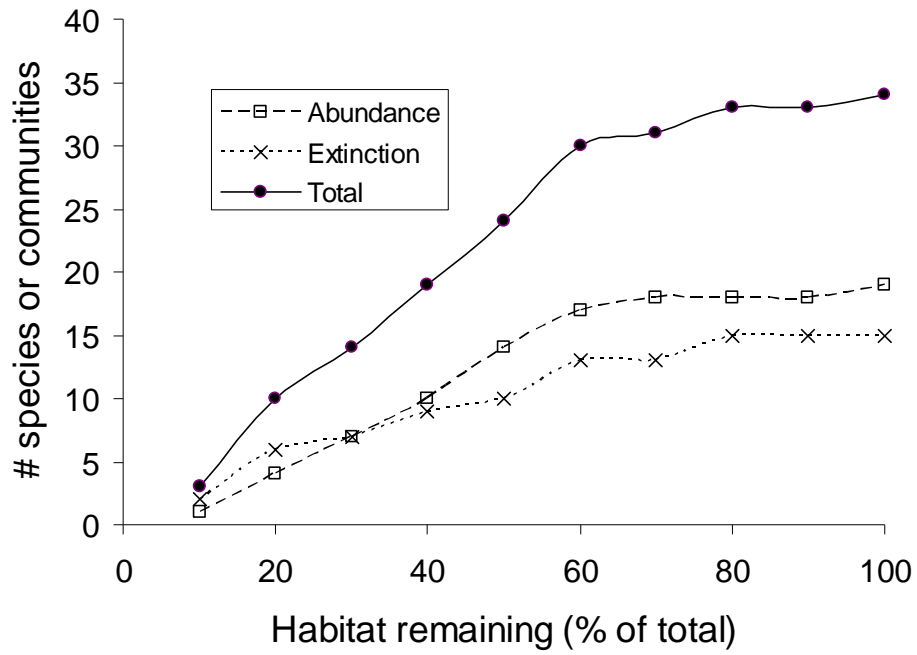
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Figure Legends

Figure 1. Population decline as a function of the amount of habitat. The dotted line shows a population decreasing proportionally to habitat. The solid lines show thresholds: the upper line shows a species initially insensitive to habitat loss; the lower line shows a species that initially declines in proportion to habitat and then declines rapidly to zero while some habitat remains. Modified from Fahrig 2003.

Figure 2. Cumulative frequency distribution of published abundance and extinction thresholds for species and communities as a function of the percent of total habitat remaining (10% classes; points joined for readability). For example, two species crossed extinction thresholds between 5 – 15%, four more between 15 -25%. The solid line is the sum of the extinction and abundance curves.