

Representative Forest Targets: Informing Threshold Refinement with Science

A review paper written for RSP and CFCI

REVISED VERSION

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Disclaimer

This report was commissioned by the Ecosystem-Based Management Working Group (EBM WG) to provide information to support full implementation of EBM. The conclusions and recommendations in this report are exclusively the authors', and may not reflect the values and opinions of EBM WG members.

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Background

It has been several years since the Coast Information Team wrote an EBM Handbook and Science Compendium (available at www.citbc.org) that discusses approaches to meeting ecological ecosystem-based management (EBM) objectives on coastal forests in BC. Since that time, a number of major decisions have been made: new protected areas for the North and Central Coast regions have been identified which removes some of the uncertainty around the protected element of EBM; agreement has been reached to implement 'full EBM' by 2009; interim EBM objectives have been set, including reduced old forest targets for different ecosystems, and discussions regarding how stand and landscape values should mesh in planning are on-going. However, the transition from the interim to full EBM remains unclear. It is therefore timely to review the science literature and attempt to provide additional clarity around a number of these key issues. The specific objectives of the paper are to provide:

- an introduction and background on habitat loss (Section 1),
- a scientific update on habitat thresholds, primarily at the landscape level (Section 2). Additional discussion of landscape and stand level trade-offs is also included,
- a summary of the original CIT recommendations in relation to the coarse-filter retention targets, and an understanding of how a 'percent of natural' target translates into actual retention targets (Section 3),
- recommendations relating to refinement of the coarse filter retention targets, based on this latest review of the science and uncertainties (Section 4).

This paper was written as background for a workshop held in February 2007. As a result of that workshop some edits were suggested which have been incorporated into this final version of the workshop paper.

In addition, the group came to a number of conclusions based on the science presented at the workshop. These conclusions are provided at

http://www.forrex.org/program/con_bio/PDF/Workshops/Forest_Workshop/OGwkshp_summary_report.pdf.

Acknowledgements

We thank all participants of the workshop for providing a response to the paper. See http://www.forrex.org/program/con_bio/forest_wrkshp.asp?AreaPkey=17 for full list of participants.

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1. Introduction

Ecosystem-based management has been identified as the desired management regime for the Central and North coasts of British Columbia (CIT 2004). This decision steps up the ecological goals of management to include 'maintaining ecological integrity' (CIT 2004). Similar decisions have been made world-wide as people have recognised the fundamental underpinning of ecological systems to human wellbeing. As a result, science is now asked for guidance on broader ecological issues: "how to maintain ecological integrity with high certainty" has replaced "what are the minimum requirements to maintain specified ecological values".

Much of this guidance has centred on the search for 'thresholds' – points where ecological function shifts rapidly. The original threshold literature focused on dramatic shifts in whole ecosystems (Holling 1973), and we know that ecosystems can undergo rapid shifts into alternative states. Examples are well documented in oceans, lakes, dry and wet ecosystems across the world (Scheffer et al. 2001; Scheffer and Carpenter 2003). In each of these examples, a phenomenal ecosystem shift occurs as a result of the initial gradual change in abundance of individual species or physical factor¹. Once underway, effects cascade through the ecosystem. This move to an alternative stable state is typically unpredicted and rapid, and recovery is extremely difficult (Scheffer et al. 2001).

Detecting this type of ecosystem threshold responses requires that an ecosystem has been pushed past a threshold. The difficulty arises when the desire is to identify suitable management guidelines that **prevent** thresholds being crossed, rather than to explain observed phenomena. Threshold identification for ecosystems *a priori* requires that whole ecosystems are studied for long enough time periods, at appropriate scales, and with sufficient replicates, to allow prediction. These conditions will be met very rarely, likely for a limited suite of ecosystems.

How then can science be used to identify suitable management regimes that avert shifts and maintain ecosystem functions? Work has again sought thresholds: thresholds in species abundance or presence as habitat decreases have been considered as potential indicators of ecological shifts.

The link between species and ecological function

Species differ in the strength of their functional role in communities. Some species can be described as strong interactors (Soule et al. 2003), meaning that their loss results in high levels of impacts throughout the ecosystem. Such species include foundation species, that have a high impact simply because they are prevalent or provide structural elements (e.g. trees; Ellison et al. 2005), and keystone species, that have a higher functional impact than expected from their biomass (reviews in Power et al. 1996, Lyons et al. 2005, Muradian 2001). Either type of species can play a wide variety of roles, including being ecosystem engineers (e.g. beavers), species that control other dominant species (e.g. top predators, or diseases), key resource providers (e.g. salmon), or mutualists (e.g. species closely dependent on one another). Well-known examples of the types of impacts resulting from loss of a highly interactive species include loss of the kelp forest ecosystem resulting from removal of sea otters and subsequent increased grazing pressure from sea urchins (Riedman and Estes 1990), or loss of top terrestrial predators in central US that has released ungulate populations and led to significant impacts on riparian ecosystems (Ripple et al. 2003).

It has been suggested that species without obvious functional roles may be effectively ecologically redundant (Walker 1992). This original paper has been interpreted by some to mean that the loss of individual species may not be of importance. However, the author clarified his intended message - that species with clear, obvious higher functional significance should be the primary target of conservation efforts, but that apparently redundant species are also important - in two subsequent papers (Walker 1995 and Ehrlich and Walker 1998). Because species respond differently to changes in environmental conditions, some species may be functionally redundant in the short-term or under stable conditions but play an important role at other times (Ehrlich and Walker 1998, O'Connor and Crowe 2005, Lyons et al. 2005). These species thus potentially contribute to ecological resilience, allowing an ecosystem to absorb higher levels of disturbance before undergoing a functional shift (Holling 1973). This idea that redundant species contribute to resilience has

¹ E.g. Changes in: nutrient loading in lakes, predatory fish on reefs, elephant abundance in woodlands, primary vegetation cover in deserts, fish abundance in oceans.

been made decades previously by Ehrlich and Ehrlich (1981) who equated species to rivets on an airplane wing. In their analogy, loss of a single rivet may not affect the plane, but the redundancy of rivets contributes to robustness of the plane, and loss of some (specific but unknown) rivets may be fatal. Observers tend to consider that only the final remaining species to be lost are critical when in fact all species added to resilience (Gunderson 2000).

In addition to the importance of particular species to ecological integrity, diversity itself may be important to function and resilience (Loreau et al. 2001). For example, carefully controlled experiments of synthesised ecosystems found that primary productivity increased with plant species diversity (Loreau et al. 2001; Tilman 2001). Intact communities may also be more resilient in the face of changing conditions: for example, plant communities with experimentally reduced diversity were more susceptible to colonisation by invasive species (Lyons and Schwartz 2001), and a full suite of native bee species were necessary for pollination during years of low abundance (Kremen et al. 2002). Real-world experiments have also suggested that maintaining a high level of functioning requires a high proportion of biodiversity; observed extinctions (in the arctic and in Argentinean floral diversity) have resulted in an unduly rapid loss in functional diversity (Petchey and Gaston 2002).

In addition, changes in biodiversity have been seen to have significant impacts on ecosystem and landscape processes on a day to day basis, and also during extreme events such as unusual disturbance events. Ecosystem processes, in turn, determine services such as clear water and air (Chapin et al. 1998).

We know that species loss is linked to shifts in ecosystem function and resilience.

The link between habitat loss and species loss

The ecological effects of habitat availability on species are well documented: both population size (Fahrig 2002) and species richness (Preston 1962) decrease as habitat availability decreases, and habitat loss has been identified as the primary cause of species' extinctions, extirpations and population declines (IUCN 2006; UN Millennium Ecosystem Assessment 2003²). Habitat loss is identified as the main threat to 85% of all species described in the IUCN's red list³, and is identified as the underlying cause of loss of species world-wide (Global Environment Outlook – UNED 2000).

What is meant by 'habitat loss' can vary extensively - it can refer to the complete removal of ecological values from an area (putting up a parking lot), or it can mean a subtle change in plant community composition that removes a vital food source for a particular butterfly. A change from the natural disturbance regime that results in a significant change in the spatial or temporal distribution of seral stages would also be classified as habitat loss, particularly when seral stages include different species compositions and structural elements that develop over long time periods.

In each case, one or more species lose the opportunity to occupy former habitat. The extent to which a particular species is affected by habitat loss depends on both the amount of the former habitat that is affected and the life history of the species. Where habitat loss occurs over part a species' range, population declines occur; loss of larger portions of the range can lead to extirpation. Extinction can follow if all of a species' distribution is affected. Life-history traits also alter how a species responds to habitat loss: isolated species, small populations, predators, and specialists are amongst the traits that tend have an increased likelihood of seeing a population level change as a result of habitat loss (Laurance 1991; Angermeier 1995; Davies et al. 2000).

We also know that habitat loss is the primary driver of species loss.

So which species?

As outlined above, functional or highly interactive species should be first on the list of those of concern. However, given the knowledge that apparently redundant species may also play important roles in ecosystem resilience, it is important to consider the sensitivity to habitat loss of all species. Species at high trophic levels, with low reproductive rates, low dispersal rates or very specific habitat requirements are all more likely to be impacted by habitat changes (Gibbs 1998; Fahrig 2001; Srivastava and Vellend 2005). Again, an important

² Available at: <http://www.millenniumassessment.org>

³ <http://www.iucnredlist.org/>

message seems to be that species with a diversity of life history traits are relevant to assess, because different species will react in different ways.

Any species may be relevant. However, some are particularly sensitive and should be the focus of study if conservative targets are of interest.

In summary, the literature suggests that many if not most species are functionally important and act a variety of ways. Reviews of recent research conclude that a) some minimum number of species is necessary to maintain local ecosystem function while conditions are stable; b) a larger number is necessary to maintain resilience when conditions change; c) we don't know which species impact which functions in different ecosystems; d) even rare species can play important roles (Loreau et al. 2001, Lyons et al. 2005).

Although we know that habitat loss drives species' decline, and that changes in abundance and presence can impact ecological function and resilience, an important question remains: how much habitat is needed to minimise the risk of changes that potentially impact ecological function? In this review, we summarise the existing set of scientific data that relate to habitat thresholds of individual species, and we make conclusions that relate back to management decisions already in the political arena in BC.

In conclusion we are interested in thresholds in ecosystem function and resilience, but focus our analysis on thresholds in species' responses to habitat change because

- individual species are important in their own right as part of 'biodiversity';
- species interact with other species; hence changes in single species can cause shifts in ecosystem function;
- species react differently to changes in their environment; hence changes in apparently redundant species can change ecosystem resilience;
- management is able to focus on species and habitats more easily than on ecosystems;
- it is not feasible to study loss of ecosystem functionality, particularly in a large, relatively intact ecosystem such as the coastal temperate rainforest of BC.

2. What does the science say?

In this section, we review available science on the influence of habitat loss and thresholds on ecological elements. A review has already been undertaken that focuses on defining and examining the science of thresholds (Dykstra 2004), but that work was not fully incorporated into the original CIT handbook development (as it was a draft in progress at that time). We reassess the utility of thresholds, examine newer papers and attempt to draw some summaries about what current science says relating to when habitat changes have significant ecological impacts. We address two factors a) the question of when habitat change begins to have measurable ecological impacts on populations and communities at the landscape scale, and b) how stand level retention may meet habitat requirements for some species.

The section has two main sections (landscape level information and stand level information), followed by a summary of composite findings for both scales. Details of the review of scientific papers for each scale are included in Appendices 1 and 2 respectively.

2.1. Landscape Level Review: 'How much is enough'?

2.1.1. Background

As outlined above, there is consensus that habitat loss, which includes both the amount and pattern of remaining habitat, causes declines in populations and loss of species, sometimes following a time-lag. These declines can have a wide range of cascading impacts throughout ecosystems. However, there is no consensus on how much total habitat is required to avoid either extirpation or population changes that have significant

impacts to ecological function, beyond an agreement that amount will vary among organisms and across ecosystems (Bender et al. 1998, Lindenmayer and Luck 2005).

How populations decline: Some populations decline linearly as available habitat decreases; other populations show a threshold response, where the **rate** of decline in survival or reproduction increases due to effects beyond simple habitat amount (Figure 1). In this latter case, population changes from one condition (e.g. viability) to another (e.g. extinction) across a small change in habitat amount.

Abundant evidence exists for the existence of thresholds (see Dykstra 2007), studies of minimum viable populations, studies of metapopulations, theoretical percolation modeling, and studies of real landscapes with different characteristics and species with different traits, all reveal thresholds where habitat loss affects populations.

Why thresholds: Manager and planners have been interested in thresholds for their potential ability to predict where small changes in habitat amount can have large ecological effects. Thresholds have been the focus of much attention in the academic literature because they suggest that factors in addition to simply habitat loss are in play. Much work has investigated the existence of "fragmentation" thresholds: the amount of habitat on a landscape where pattern becomes important. Fragmentation is not the only type of threshold, however: proximate and ultimate mechanisms of decline leading to 'threshold' responses include changes in life-history such as reproductive rate and disruption of genetic and evolutionary processes (Frankham 1995), changes in ecological interactions (e.g. predator-prey relationships, pollination, parasitism; Kareiva 1987, Lennartsson 2002, Kruess and Tschardtke 2000), isolation of patches (Franklin and Forman 1987, Kareiva and Wennergren 1995) and stochastic disturbance of small sub-populations (Opdam 1991, Harrison and Bruna 1999). Any of these mechanisms can push population decline beyond the rate predicted based on habitat loss alone.

Thresholds are relevant to understanding significant ecological change because beyond a threshold, the probability of extinction increases, the potential to regain former abundance decreases (Monkkonen and Reunanen 1999) and the risk to community structure, resilience and ecosystem function increase (Fahrig 2001, Muradian 2001, Guenette and Villard 2004, Walker and Myers 2004). In essence, thresholds mark significant ecological change.

We focus on studies where thresholds have been demonstrated because these are known points where significant ecological change has occurred, where species may suddenly become extirpated from a previous apparently secure level and where recovery may start to be difficult.

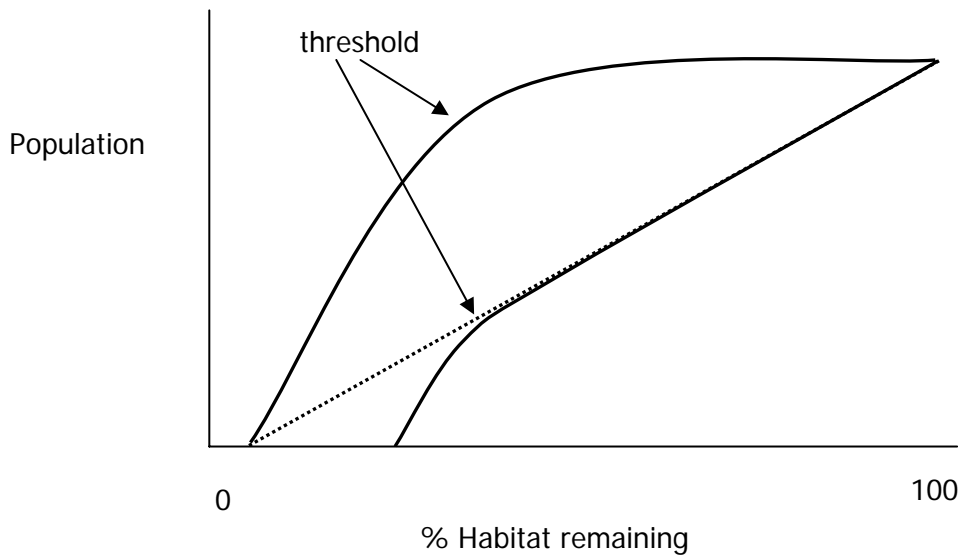


Figure 1. *Population decline as a function of the amount of habitat. The dotted line shows a linear decline. The solid lines show thresholds that make prediction of a species' trajectory difficult and increase the risk of maintaining habitat amounts less than the threshold level. Modified from Fahrig 2003.*

Linear abundance declines: Linear population declines can be equally significant: clearly a population can decline sufficiently in a linear trend that it has a high probability of extirpation or loss of functioning. Unfortunately, it is often difficult to interpret the significance of any particular level of linear population decline because there is no detectable, dramatic change in the population (Ludwig 1993). As a result, although many studies demonstrate linear decline of populations with loss of habitat, it is difficult to pin-point any ecologically significant habitat level before the population drops to zero.

Benchmark habitat amount: A key factor for interpreting science findings from other studies is in gaining an understanding of the context of habitat loss in a particular area. In particular, it is crucial to understand the benchmark from which the loss is being measured. Ecosystems and communities have been changing due to human industrial activities at different rates and over different timeframes in different ecosystems. A study based in northern Europe, where forests are in a third rotation, may detect little change in species' distribution or abundance as sensitive species may already have declined or been extirpated. Measuring population decline of remnant species, likely less-sensitive generalists, as habitat declines from 10 to 5% of natural levels cannot be used to detect, or refute, any thresholds that resulted in extirpation of the sensitive species.

2.1.2. Methods

Papers Reviewed: 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 the amount of suitable habitat. We first reviewed the subset of relevant studies listed by Dykstra (2004) in her review of habitat thresholds, and then extended this list to include more recent references. Because of the dearth of studies, we were not able to focus analyses on organisms of specific relevance to coastal BC, but instead looked for patterns across a wide range of organisms living in a range of habitats. The following section describes the filtering process in more detail.

Habitat thresholds: Because we could not detect points of ecological significance from linear declines, we conservatively included only studies where thresholds were observed. Papers described a variety of

thresholds. Studies of individual species examined population trends over time, and changes in reproductive parameters, abundance and patch occupancy over space. Studies of communities described patterns of species' extinctions. We grouped thresholds into two broad types (Figure 2), respectively similar to the Type II and Type III thresholds described by Guénette and Villard (2004):

Abundance thresholds: the level of habitat loss associated with a rate change in the abundance, or probability of occurrence, of a species. We included in this class the few studies which also showed reproductive parameter changes at a certain level of habitat loss. For consistency, we defined the threshold as the amount of habitat corresponding to the highest change in the rate of decline (i.e. maximising the second derivative) as the curve drops from maximum occupancy. This point occurred at about 90% of maximum occupancy.

Extinction thresholds: the level of habitat loss associated with the loss of a species from remaining suitable habitat. This threshold does not necessarily represent extinction from the landscape, although some studies document 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 numbers of species drop faster due to increased rate of local species extinctions. Community thresholds thus represent the end point of multiple extinctions.

Although these two sets of thresholds appear quite different, they both represent a rate change, and therefore, as outlined above, represent a significant ecological change.

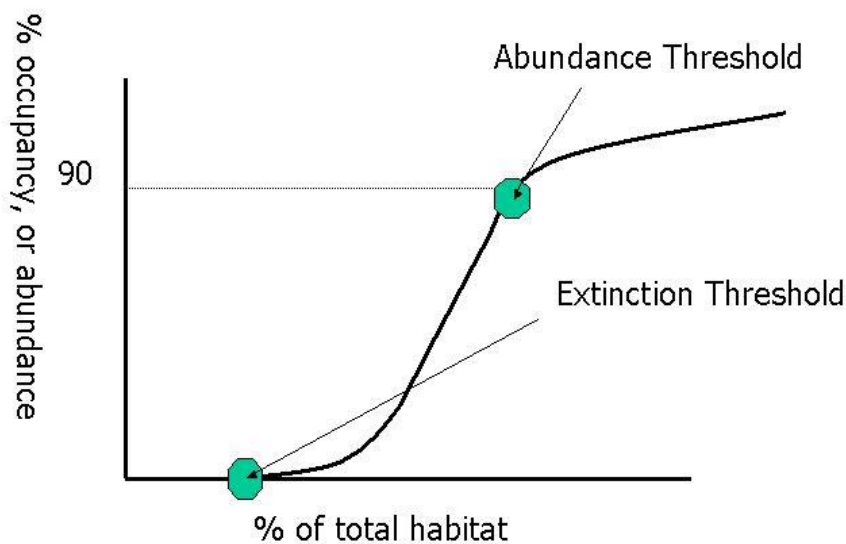


Figure 2. Two types of 'threshold' from the literature. The Abundance Threshold is one where the abundance or occupancy of the species in a landscape rapidly declined. The Extinction Threshold was associated with the level of total habitat where the species was no longer present in suitable habitat within the landscape.

Empirical vs. modeling studies: We focused on empirical studies because they examine real landscapes and communities, capturing complexities that may be missing from models. We included empirical tests of models, but excluded model-based predictions, even when the models were based on empirical data (by far the largest section of the published literature on thresholds). Models, either percolation models on black-and-

white landscapes, or based on real organisms and habitats, provide additional lines of evidence for the existence of thresholds that we discuss in section 2.3.

Landscape Scale: 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. Although it is sometimes possible to extrapolate these latter studies to provide data on habitat amount this extrapolation involves high uncertainty (i.e., given patch size and isolation on a binary landscape, it is mathematically possible to calculate landscape amount, but the strength of the function is unknown on real landscapes). Because species response varies with scale and life history (Holland et al. 2005), we considered landscapes at the scale relevant to each organism. Hence landscapes varied in size from hundreds of square metres for beetles to hundreds of square kilometres for birds. This ecological definition of “landscape” differs from the definition based on human perception that is used in operational forestry.

Suitable Habitat: Comparisons of habitat elements at local and landscape scales suggest that landscape-level patterns are apparent only when local habitat is favourable (Hagan and Meehan 2002, Lichstein et al. 2002). Hence, we excluded studies without clear definitions of “suitable” habitat, or that did not discriminate between suitable and unsuitable habitat in their analyses. We did not, however, require that studies performed detailed multivariate analyses of habitat structure and composition.

Internal Inconsistencies: Finally, we excluded studies with apparent internal inconsistencies. Unfortunately, potentially useful papers summarising surveys across decades included inconsistencies that reduced our confidence in the patterns presented (e.g. Virkkala 1991, Väisänen et al. 1986).

Defining Threshold Location: 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 analyses, 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 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 to allow re-analysis. 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.

When analysing binary data (e.g. presence/absence), most people use logistic regression (e.g. Angelstam 2004, Reunanen et al. 2004, Villard et al. 1999). This technique is well-accepted and has been compared favourably to other modeling methods (Manel et al. 1999). However, logistic regression models a probability of occurrence for each habitat amount, but does not pinpoint the threshold, necessitating subjective choice of a particularly 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 (Figure 1). This point is essentially equivalent to a Type II threshold, where an organism is always present above a threshold and sometimes absent below (Guénette and Villard 2004). In many cases, this point is also very close to the maximum change in the rate of decline.

Thresholds in continuous data (e.g. species richness, abundance, reproductive parameters) can be detected using split regression (e.g. Bascompte and Rodriguez 2001, Homan et al. 2004, Radford et al. 2005). 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 have 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 have used the 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 (e.g. Carlson 2000, Drolet et al. 1999, Summerville et al. 2001). 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 provide complete sigmoidal curves, from maximum occupancy to absence; most are able to examine only a portion of the relationship.

More recently, studies with binary data have employed statistical techniques that optimise threshold location (analogous to split regression) to maximise the correct assignment of zeros and ones, including non-parametric binomial change point (Homan et al. 2004) and ROC (receiver-operator characteristic) analysis (Guénette and Villard 2004). Future reviews will likely be able to compare optimised thresholds for all types of data.

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 species, finding thresholds for some and linear declines for others. We listed each species with a detected threshold separately, and did not include those species apparently declining linearly. When thresholds were presented as ranges, we selected the most ecologically-relevant value if possible (e.g. for the largest landscape) or else used mean values, assuming that a range more often implied uncertainty around a mean than a well-defined range.

Matrix hostility: We collected additional information on habitat for each study. We noted suitable habitat type and matrix habitat for each study, to allow comparison of thresholds in hostile and less hostile matrices. We included studies of old forest patches within a harvested forest matrix, and studies of unmown grass in mown grass in a “non-hostile” category. “Hostile” matrices included agricultural fields or sub-urban matrices around patches of forest, and bare soil or rock around vegetation.

Benchmark: We also looked for information on the range of natural variability in that habitat type, to allow calculation of threshold as a percent of natural habitat benchmark rather than as a total amount. Unfortunately, many studies are unclear as to their context in relation to a ‘natural benchmark’ (i.e. how much habitat remains today in comparison with the amount that naturally occurred). From most studies we were required to extract information on the total amount of habitat, without any reference to natural habitat amounts (see discussion).

2.1.3. Results

Twenty papers (out of hundreds of primarily theoretical papers which discuss thresholds) met our criteria (details of selected studies listed in Appendix 1). 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, 11 birds and three mammals, as well as communities of woody plants, mites and birds.

We were unable to perform a traditional meta-analysis, plotting response strength against an indicator variable (in this case % of habitat) because we expect that different species will respond differently; i.e., we have no a priori reason to assume that 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.

Studies began to detect species-level thresholds when habitat declined below about 70% of total amount (Figure 3). **Four species crossed thresholds above 60% total habitat. Below 60% of total habitat, the number of species or communities crossing thresholds increased linearly for both abundance and extinction thresholds. More than one-third of species or communities crossed thresholds above 50% of total habitat; nearly two-thirds reached thresholds before their habitat dropped to 30%.**

Variation among species was considerable. Out of 15 species or communities exhibiting extinction thresholds, six crossed their threshold at or below 20% of total habitat; six species or communities crossed some type of threshold between 51 and 60% of total habitat.

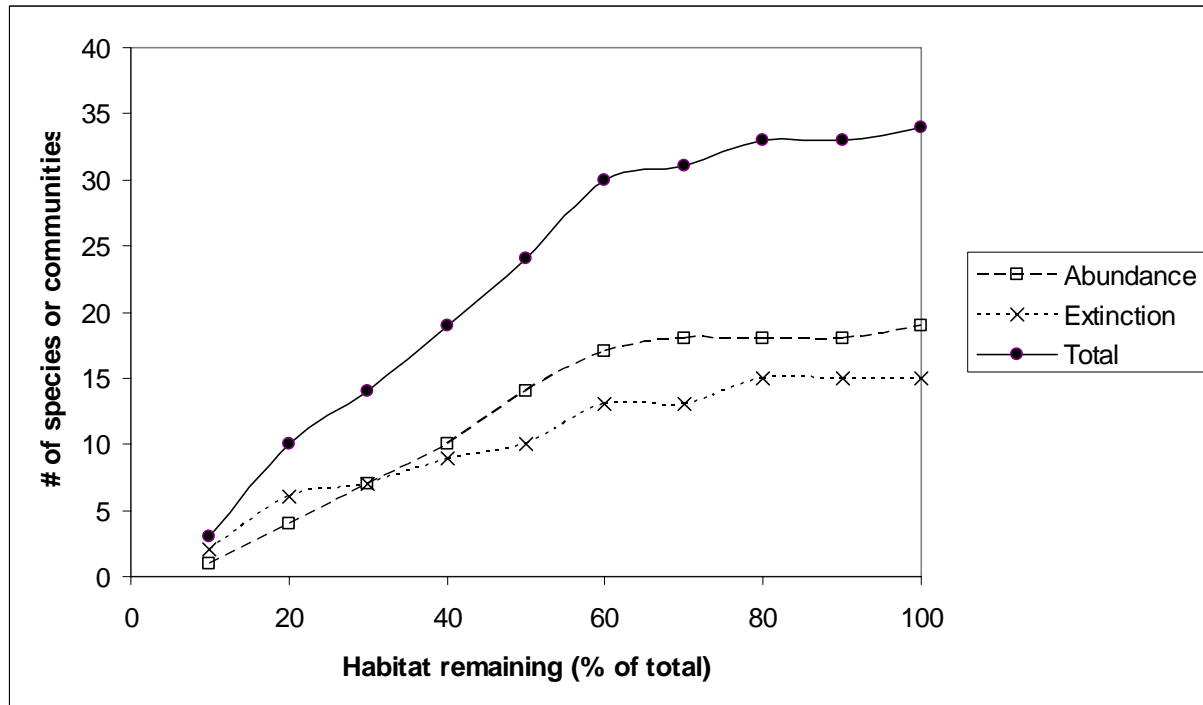


Figure 3. Cumulative frequency distribution of published Abundance and Extinction thresholds for species and communities as a function of the percent of total habitat remaining (10% classes; points joined to improve clarity of figure).

Community thresholds: community thresholds identify the place where the community as a whole demonstrates a change in rate of species loss, and are particularly important to consider because they examine potential community disassembly as the rate of extinction increases. **The three studies that detected community thresholds found a wide range of thresholds (10%, 35% and 53% of total habitat;** Bascompte and Rodriguez 2001, Gonzalez and Chaneton 2002, Radford et al. 2005).

Taxonomic variation: Thresholds varied significantly among taxonomic groups, but not statistically detectably by matrix hostility or threshold type (taxon: $F_{4,27} = 2.5$, $p = 0.07$; matrix hostility: $F_{1,27} = 1.4$, $p = 0.2$; threshold type: $F_{1,27} = 1.4$, $p = 0.2$; analysis of variance, main effects model, no significant interactions).

Birds crossed thresholds at significantly lower levels of remaining habitat than other groups, accounting for the variation among taxa ($F_{1,27} = 7.4$, $p = 0.01$; orthogonal contrasts; Figure 4). Analysis for other taxonomic groups is hindered by the low number of studies for some of the groups.

Threshold type: Although not detectable statistically, abundance thresholds tended to occur at higher habitat levels than extinction thresholds (note the higher proportion of species or communities with extinction thresholds at or below 20% habitat on Figure 3). These lines, however, are not strictly comparable because most points come from different studies.

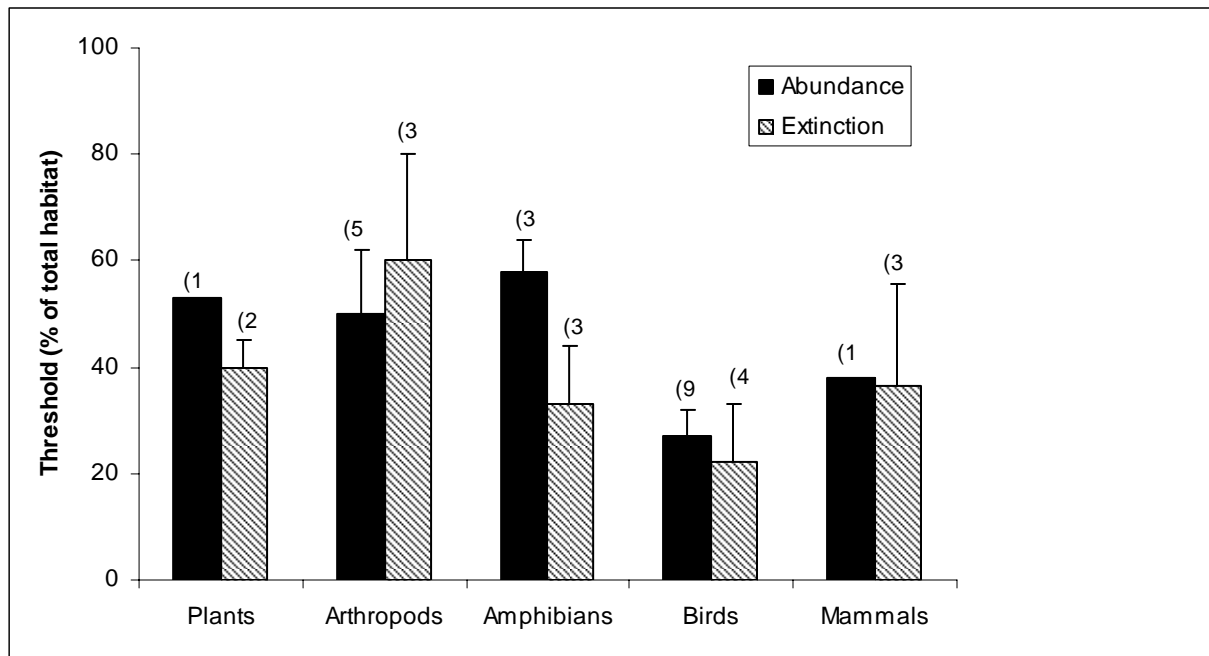


Figure 4. Mean (\pm se) abundance and extinction thresholds (as a percent of total habitat) by taxonomic group from published literature. Sample size is given in brackets..

Matrix Hostility: We had expected that matrix hostility would affect the relationship between habitat loss and population abundance, assuming that the effects of loss in a truly hostile matrix would be more definitive. However, within the available sample of studies, **matrix hostility had no detectable effect on threshold value** (Figure 5). These findings were not limited by the number of studies finding thresholds in non-hostile matrices, but were limited by the lack of studies within our review comparing matrices. Note that the single paper that compared hostile and non-hostile matrices (Radford and Bennett 2004) did find a strong effect of matrix hostility on an isolation threshold (consistent with other studies that have compared matrices). The large variation among species and necessarily unbalanced design may have overwhelmed matrix effects.



Figure 5. Mean (\pm se) abundance and extinction threshold values (as a percent of total habitat) in hostile and non-hostile matrices from published literature. Sample size is given in brackets.

Spatial Scale: 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 (crossing a threshold at 88% forested habitat when analysed within 30m of their pond versus at 44% analysed at within 1km), while spotted salamanders were more sensitive to the amount over larger landscapes (crossing a threshold at 32% within 30m versus 51% within 1km of their pond; Homan et al. 2004). Similarly, gentian population extinction thresholds varied with the size of the field containing habitat patches (35 – 55% threshold in 15 ha fields versus 55 – 70% threshold in 2.5 ha fields; Lennartsson 2002). In smaller fields, bees did not visit (and pollinate) gentians unless the habitat patches were easily accessible (Lennartsson 2002).

Benchmark habitat amount: Very few studies included data to allow calculation of habitat thresholds as a function of the natural amount of habitat. Where feasible (reliable only for two papers), we used information in the papers to identify the natural amounts of a particular habitat type, and used that to examine how thresholds change as a percent of 'natural' rather than as a percent of total. **Abundance thresholds for the two papers with information increased from 13 of total habitat to 50% of 'natural' and from 14% of total to 47% of natural, and from 10% to 33% for an extinction threshold in one of the papers.** The species in these two papers use an ecosystem that is naturally uncommon (old deciduous stands within boreal forest; Carlson 2000, Jansson and Angelstam 1999). For white-backed woodpeckers in Finland, Carlson (2000) estimated population change as a function of the percent of natural habitat lost, allowing direct calculation of a threshold as a function of the natural level. For long-tailed tits, information that natural deciduous forest in Sweden was naturally about 30% (Carlson 2000) allowed us to convert 10 and 14% of total habitat to 33 and 47% of natural. At least one other study in the review notes that natural habitat for its study species is naturally rare (Radford and Bennett 2004); hence for this species, conversion to a percent of natural would also change the threshold considerably. Insufficient data are provided to make this calculation for other studies.

Marten as an example in Coastal Ecosystems:

Of the studies we reviewed, only the one on marten concerned a species native to the West Coast and the threshold reported was among the highest documented. Because of both reasons and because Huggard

(2007) just completed a review of effects of habitat loss on marten, we looked more closely at this example. Other studies support the likelihood of a high threshold. Huggard combined the results of Hargis et al. (1999) (that we used in our analyses) with his own work⁴ and those of Potvin et al. (2000⁵). Huggard's analyses showed that in combination the studies predict that marten would not be found in landscapes with 54% open area, and that declines in marten density begin quickly with reduction of forest cover. Chapin et al. (1998) also measured habitat use relative to amount of open area in Maine and found compatible responses (65-ha cells used by marten averaged 25% open area, while unused cells averaged 69% open). These additional studies (which we were not able to use to look at thresholds specifically) support the finding of high habitat loss thresholds for marten.

In each of these studies the openings recorded were generally unsuitable marten habitat (i.e., clearcutting or natural openings). Marten are known to persist in broad landscapes that have had a higher percentage of the area harvested than the threshold identified suggests when harvested areas provide more suitable habitat. In those cases, harvesting has occurred over a number of decades, allowing some cutblocks to start becoming suitable habitat again, or partial cutting or natural disturbances retained structure on the cutblocks (Soutiere 1979, Buskirk and Ruggiero 1994, Paragi et al. 1996, Chapin et al. 1997, Payer and Harrison 2003, Poole et al. 2004). Some authors have also suggested that openings may be more tolerated, or even beneficial, if they are small (Brainerd 1990, Thompson and Harestad 1994), but the evidence for this is unclear. Marten responses to forest cover are likely the product of a variety of variables including structure, prey abundance and trapping pressure. This discussion suggests that landscape-level amounts of habitat interact with stand-level features and reflects the realworld complexities of examining habitat requirements for individual species – habitat can sometimes be made useful, or not, by relatively subtle changes in attributes or configuration.

Because species at higher trophic levels (e.g. predators like marten) tend to be particularly sensitive to habitat changes, and also tend to be functionally important within the ecosystem, changes in population or distribution can have a disproportionately large impact on ecosystem functioning (Srivastava and Vellend 2005). Marten, then, as a potentially sensitive and functional species in coastal forests would be a candidate for a regionally-occurring indicator species most sensitive to habitat loss. Several authors have suggested that such species should be used to set management targets (Jansson and Angelstam 1999, Monkkonen and Reunanen 1999, With and King 1999, Fahrig 2001).

2.1.4. Discussion

From the broad literature, it is clear that as total habitat declines, both population size and number of species decline. Our review focused on studies where a 'threshold' or 'rate change' was detected, which we believe suggests a significant ecological change is occurring.

Our detailed review of thresholds identified the following pattern: few species crossed abundance or extinction thresholds above 60% total habitat (at 70 and 75%); below 60%, the number of species or communities crossing a threshold increased; this number increased linearly as habitat continued to decline. About two-thirds of species reached thresholds before their habitat dropped to 30% total habitat. Community composition changed significantly at a range of habitat from 10 to over 50%.

Linking thresholds to risk levels within the CIT framework: Our review of studies of (largely) individual species shows how individual populations change with habitat availability. In relation to landscape management however, we are really interested in the much broader question of how ecosystem function will be affected. Looking at the composite pattern of species' responses sheds some light on this question.

The existence of thresholds indicates levels of habitat abundance where organisms may pass through a functional shift and are likely moving into higher risk of extirpation or have reduced probability of recovery.

⁴ Huggard (1999) measured use by marten of 40-ha study units with 33% removal in uniform arrays of 0.1-ha and 1-ha openings, at the Sicamous Creek study area in southern B.C.

⁵ who measured home range size of 20 radio-collared marten occupying areas with 0-40% open regenerating cutblocks, in western Quebec

Maintaining habitat amounts below a threshold likely poses a high risk of species loss, with unknown ecosystem consequences. Based on currently available, published, landscape-level, empirical studies, we conclude that certainty is high that maintaining representative habitats at 60% or more of total habitat will maintain ecological integrity because only a few studies found abundance thresholds at habitat levels above 60%. The science suggests that:

- **Maintaining habitat at greater than 60% of total habitat therefore equates to low risk (i.e. a high probability that ecological integrity will be maintained).**

More than a third of organisms and communities which reported thresholds, responded at habitat amounts above 50% of total habitat, and nearly two-thirds reached thresholds before the total habitat dropped to 30%. Hence, the chance of crossing a threshold increases rapidly as habitat amount decreases below 60%. The science suggests that:

- **Maintaining habitat at equal or less than 30% of total habitat equates to high risk (i.e. a high probability that ecological integrity will not be maintained).**

Within these patterns it is also clear that the literature shows **high variability among species**. This finding is unsurprising. Species perceive landscapes at different scales, have different dispersal and reproductive strategies and different levels of habitat specificity (review in Dykstra 2004). In general, responses at higher habitat amounts are likely for poor dispersers, habitat specialists and rare species (e.g. Gibbs 1998, Summerville and Crist 2001, Gonzalez and Chaneton 2002, With et al. 2002). Dispersal tendency and habitat specificity may interact. Species with high habitat specificity and low dispersal tendency (e.g. some amphibians; Gibbs 1998) may be unaffected by changes to the surrounding landscape provided that their habitat patch remains suitable. Habitat generalists, whether good dispersers or not, may be similarly unaffected. Species with high habitat specificity and high dispersal tendency will be those most predisposed to sensitivity to habitat over the broader landscape (Gibbs 1998). Early successional species can show relatively little response to the amount of habitat compared with late successional species (Lichstein et al. 2002), perhaps again because of an interaction between habitat specificity and dispersal ability.

Because of the variability among species, and because of the impossibility of examining all species, a number of authors have suggested using the habitat threshold for the regionally-occurring species most sensitive to habitat loss to set management targets (Jansson and Angelstam 1999, Monkkonen and Reunanen 1999, With and King 1999, Fahrig 2001).

In our review, 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 studied most frequently, their lack of sensitivity as a group generally make them poor indicators of landscape-level thresholds.**

Rare species: Low population density appears to exacerbate sensitivity to habitat amount. In the two studies looking at a range of invertebrate species, rare species were most likely to show thresholds (Gonzalez and Chaneton 2002, Summerville and Crist 2002). However, in most studies, rare species were not found frequently enough to meet the statistical requirements to detect thresholds, and were often eliminated from analyses. This difficulty poses challenges for any species-based management: frequently, the most sensitive species may be hardest to detect, study and monitor. In addition, rare species are least likely to be distributionally congruent with umbrella species or biological hotspots (Grenyer et al. 2006). **Rare species, often among the most sensitive species, are least likely to be included in any science studies.**

Habitat abundance versus pattern: By reviewing a full range of threshold studies, we were able to test the generality of theoretical predictions about habitat thresholds. Very few species had thresholds above the fragmentation thresholds described initially by percolation theory (reviewed in Dykstra 2004) and subsequently refined to be more appropriate to real ecosystems (Boswell et al. 1998, Flather and Bevers 2002). Theoretical studies have found that physical connectivity is easily maintained with habitat amounts above 60%, but that below this threshold, connectivity depends upon a variety of other factors. Empirical exceptions from our review include several species of butterfly in a grassland experiment, the red-spotted newt in ponds along a rural-urban gradient, and the American marten. Three independent studies of marten provided data

suggesting very similar thresholds in forest habitat within regenerating clearcuts (Hargis et al. 1999, Chapin et al. 1998, Potvin et al. 2000). **The overall message from the literature is that habitat abundance is more important than habitat pattern, until low levels of habitat are reached.**

Matrix quality: Contrary to expectations, we found **no evidence from the landscape papers that the surrounding habitat matrix quality affected thresholds.** Although studies have found easier movement through less hostile matrices, (see Section 2.2), where detected, effects of matrix quality have been found to be secondary to amount of habitat and species attributes (review in Dykstra 2004). It is relatively unsurprising that our review did not support the importance of the matrix because we are included a wide variety of species in different landscapes. It can be difficult to specify whether a matrix is hostile or not because different species view similar matrices as having different degrees of hostility depending upon their movement scale, habitat specificity and dispersal tendency (e.g. With et al. 2002). Our classification was, by necessity, too general to discriminate these fine points.

2.1.5. Uncertainties

As with any meta-analysis, integrating the results from disparate studies is complex. 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 (review in Dykstra 2004; details in Appendix 1). The following factors all create some uncertainty in interpretation, and some suggest a directional influence on the interpretation of observed thresholds. Under each header, we suggest the potential direction (if any) on the threshold levels and associated risks identified above.

Benchmark identification: Almost all studies reviewed considered the absolute amount of habitat available, rather than calculating the amount of habitat relative to that expected under a natural disturbance regime. Because organisms are adapted to habitats with different disturbance regimes, data on thresholds as a percent of total habitat can be difficult to compare. For example, consider two 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. It is difficult to compare a threshold of 30% for the first species and 12% for the second species: the second species cannot experience a threshold at any amount above 15%, simply because the amount of natural habitat is constraining. Rather than comparing thresholds of 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). However, we were unable to calculate sufficient thresholds related to natural amounts for analysis, beyond noting that mathematically, thresholds described as a percent of natural are considerably higher than thresholds described as a percent of total habitat. **Direction on thresholds identified: Upwards pressure.**

Summing species into community response: Detecting thresholds in community response (e.g. an increase in the rate of loss of all species) is particularly challenging. Because suitable habitat is a species-specific concept, groups of species are unlikely to respond in the same way to changes in habitat amount. Loss of species at various habitat amounts may smooth out any threshold in community measure such as species richness (Lindenmayer et al. 2005, Monkkonen and Ruenanen 1999). Compensation among species can also hide effects measured by abundance (Gonzalez and Chaneton 2002). As habitat amount decreases, and fragmentation increases, "generalist" species may decrease in direct proportion to habitat amount, "interior" species may decrease more than predicted from habitat loss alone (due to fragmentation), and "edge" species might decline less than expected, or increase (Bender et al. 1998). When community thresholds are detected, they will be at lower habitat levels than thresholds for individual species as they represent the end-point of multiple extinctions. **Direction on thresholds identified: Unknown, or complex.**

Detecting functional responses: Applying the concept of thresholds to process and function rapidly becomes even more complex. Not all species exhibit thresholds at the same amount of habitat and this variation can exacerbate intra-habitat changes to communities as some organisms decline at a low rate, while others, past their threshold, decline precipitously, changing relative abundance. Even if all species decline

linearly with habitat loss, rates may vary, and hence relative proportion and therefore community function could still change. These changes may be revealed in community-level thresholds, but will be harder to detect than single-species responses. In a study of many generations of micro-arthropods, community biomass decreased in fragments beyond the level predicted based on loss of species, an effect primarily attributable to reduced dispersal (Gonzalez and Chaneton 2002). **Direction on thresholds identified: Unknown, or complex.**

Time lags and extinction debt: Published studies are mostly short-term and typically unable to look for effects over more than one generation for their species. A time lag in response to habitat alteration therefore makes it increasingly difficult to detect consequences of habitat loss (Cooper and Walters 2002). Immediately following habitat loss, abundance of motile organisms can increase as they pack into a smaller area (e.g. Darveau et al. 1995). For relatively long-lived organisms, changes in abundance can take many years (Carlson 2000). Studies on extinction debt suggest that longer-term studies might detect severe impacts when no change can be detected initially. In an experiment on microarthropods in fragmented habitat, the effects of isolation on community biomass and abundance of each species only emerged after several generations (Gonzalez and Chaneton 2002). This community disassembly occurred long after initial losses of rare species, providing evidence that effects on ecosystem function may take even longer to detect. A study of brown treecreepers found that landscape effects became clearer over time, even though habitat had been lost decades before the study (Cooper and Walters 2002). **Direction on thresholds identified: Upwards pressure.**

Response variable - occupancy versus fitness: Most published studies examine species occurrence within suitable habitat. However, the presence of a particular species does not reveal demographic status or guarantee their persistence (Guénette and Villard 2004). Reproductive traits influence persistence most (review in Dykstra 2004). Although empirical studies are rare, thresholds for reproductive parameters have been found at higher habitat amounts than occurrence thresholds (Angelstam 2004, Guénette and Villard unpublished data cited in Guénette and Villard 2004, Swift and Hannon 2002). Many acknowledge that occurrence is a crude measure, and that studies of reproductive processes would provide a better gauge of habitat sufficiency, again suggesting that long-term impacts may be missed by short-term studies. **Direction on thresholds identified: Upwards pressure.**

In addition, uncertainty about the risk to ecological integrity always exists when decisions are based on reductionist studies of particular organisms. Knowledge of all organisms and their interactions will never be sufficient to micro-manage for all needs. This uncertainty is well recognised, and is the reason for the design of coarse and fine filter approaches.

2.2. Stand Level: Considering stand/landscape trade-offs

After retention levels have been determined for an ecosystem, a number of factors can be considered to determine how the retention should be laid out in the landscape. Most studies agree that total amount of habitat is more important than pattern, except at low habitat levels (McGarigal and McComb 1995, Fahrig 2002, Schmiegelow and Monkkonen 2002). The importance of considering habitat for the full diversity of organisms that live at a variety of scales, however, has led to considerable debate about the merits of dividing retention among large reserves, small reserves and within-stand retention (E.g. Murphy 1989; Tschardt et al. 2002). Silvicultural systems that retain some of the original forest structure in the cut area have a number of benefits for biological diversity compared to clearcutting, including maintaining some forest-dwelling species in recently harvested areas, and creating structural diversity in regenerating stands (Franklin et al. 1997). In this section, we consider the scientific information relating to trade-off between retention at the landscape and stand scale. Specific questions of interest are:

- Are stand-level reserves effective enough to promote landscape level reserve trade-offs?
- If so, is there an optimum, or minimum, level of stand-level reserve that should be applied in order to promote maintaining biodiversity at the landscape level?

Unfortunately, most studies evaluating effects of stand-level retention do not describe the characteristics of the surrounding landscape. Conversely, studies of landscapes rarely describe the type of retention in managed stands surrounding suitable habitat patches. Consequently we do not know how species' responses to stand-level retention might change in different landscapes, neither do we know how responses to amount of habitat might change depending on characteristics of the surrounding landscape.

Very few studies attempt to shed some light on the trade-offs or complementary roles of stand and landscape retention of old forest. These studies are almost entirely limited to birds. Rather than attempt our own review (as for the landscape section above), we summarise a recent review of birds by Huggard (2006).

2.2.1. Methods

Huggard (2006) examined the literature for studies of bird abundance within stands with different levels of retention. He presents a likelihood-based meta-analysis of 51 North American studies treating 69 different bird species that occur in uncut forests. He focused on western North American sources for the research projects and government documents, but included published studies from all areas of North America and used studies if they met all the following conditions:

- 1) Presented information on the abundance or relative abundance of individual bird species in treatment units.
- 2) Included at least one treatment with a partial retention harvest system.
- 3) Included an uncut control treatment or pre-harvest measurements.
- 4) Provided information on the percent retention in the partially harvested blocks.

Studies used generally were conducted shortly after harvest; there were too few studies with older retention harvest treatments to include time-since-harvest as a factor in the analysis. He didn't include studies that simply compared clearcuts and uncut forest or studies of silvicultural treatments of young stands. He required the actual number of birds of each species counted in each treatment so when this information was not presented in a paper, he examined the reported methods to back-calculate the actual count from reported abundance indices.

Huggard's analysis is based on the assumption that, even without knowing landscape context, knowing the shape of the relationship between species abundance and within-stand retention can help decisions about whether to retain trees within stands or in landscape reserves. For example, if this relationship is more than proportional (e.g. retaining 20% of trees in a cutblock maintains a species at 40% of its abundance in uncut forest, Figure 6, green) then within-stand retention influences abundance more than landscape retention. In a sense, the stand-level retention is 'buying' extra organisms in each stand, supporting retention in cutblocks. For these species, a partially-cut stand remains "suitable" habitat. Conversely, if the abundance is below proportional (e.g. 20% retention maintaining the species at only 5% of its abundance in uncut forest, Figure 6, red) then retention is less useful in cutblocks and it would be better for that species to allocate the given retention level to larger reserves. These specialists have a narrower range of "suitable" habitat. If the abundance of a forest-dwelling species is directly proportional to the retention level (Figure 6, black), the total abundance of the species in a landscape depends only on the total retention level, whether this is retained within stands or in landscape reserves, or in a combination of the two. A sigmoidal curve means that abundance changes from more to less rapidly increasing as retention levels increase.

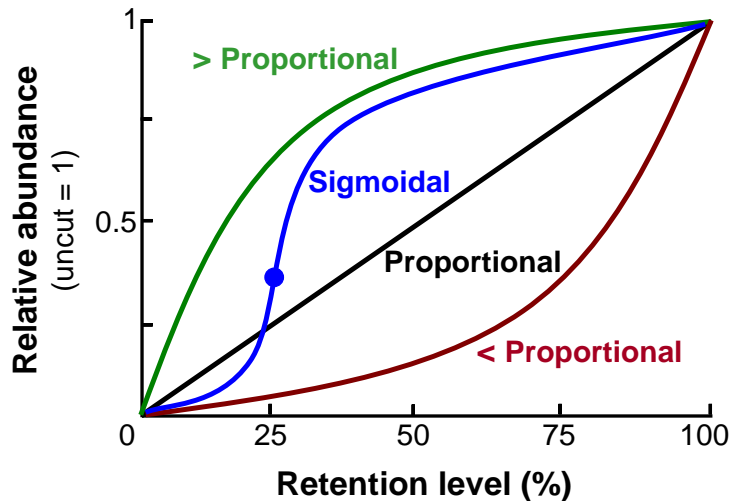


Figure 6. Examples of response curves with abundances greater than proportional, less than proportional, proportional to retention levels, or showing a sigmoidal relationship with retention levels.

2.2.2. Results

As expected, birds showed a variety of responses to retention levels. Approximately 1/3 of the birds using forests were generalists. Partial cutting did not represent habitat loss for these species. Of the 2/3 that dropped in abundance with harvesting, **most would benefit from retaining trees within stands and only a few would be better off if retention was instead allocated to landscape reserves.** Ten species showed sigmoidal relationships and four had abundances less than proportional across the range of retention levels (details in Appendix 2). These latter species are most sensitive to harvesting, declining substantially in stands with even low levels of disturbance and high levels of retention.

Two retention levels stand out from Huggard's review. **Sensitive species showed declines below about 35-40% retention. Many less-sensitive species decreased below 15-20% retention.** Figure 7 shows examples of abundance relationships.

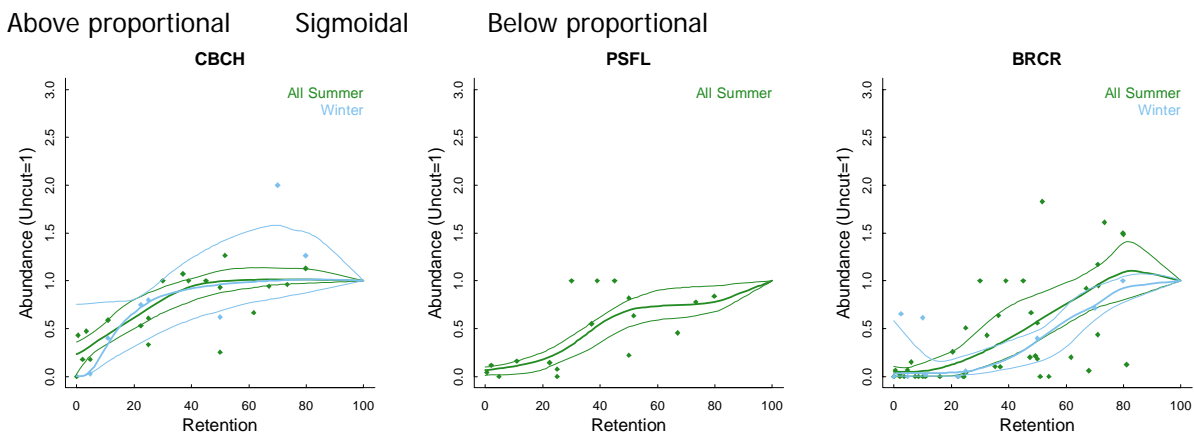


Figure 7. Examples of species that declined above and below proportionally and sigmoidally (Huggard 2006). Thin lines are 5% and 95% quantiles. CBCH = chestnut-backed chickadee; PSFL = Pacific slope flycatcher; BRCR = brown creeper

When Huggard examined all species together in an artificial “community”, he found **an immediate change in community similarity with even small amounts of harvesting** (Figure 8). Beyond this initial drop, similarity then declined gently until retention levels dropped below about 12%.

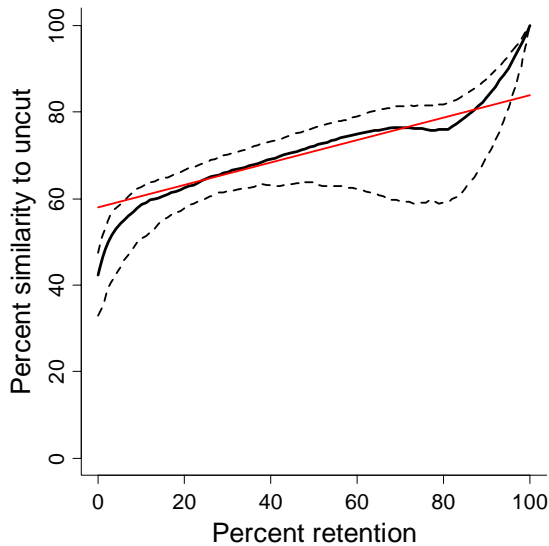


Figure 8. Percent similarity with uncut forest, across the range of retention levels. Dotted lines are 5% and 95% quantiles from bootstrap resamples. Red line is linear fit to middle 75% of the retention range.

For all bird species, **retention system (uniform versus aggregated) had little substantial effect on the relationship:** retention level was a much more important variable.

Beyond Huggard’s study, several types of studies can inform consideration of the interaction between stand and landscape retention. Some studies have examined response to matrices of differing hostility. For example, several studies have found that hazel grouse cross larger gaps between patches of suitable habitat in a managed forest matrix than in an agricultural matrix (Aberg 1995, Saari et al. 1998, Jansson et al. 2004). These and similar studies show that the character of the matrix affects the amount of forests needed to maintain populations by increasing the ability of individuals to move between suitable habitat patches, disperse, and maintain gene flow. A study of mammalian communities in riparian corridors found that old-growth corridors contained fewer forest-dependent species when the matrix had less old growth (Perault and Lomolino 2000). In this case, the young and mature forest surrounding the corridors was apparently hostile to some species. Similarly, in small old-growth reserves surrounded by managed forest in Scandinavia, bird communities were more similar to those in young forest than to those in ecologically similar large reserves, again emphasizing the importance of the landscape on stands (Vaisanen et al. 1986, Virkkala 1991).

Beyond vertebrates, studies of epiphytic lichens have demonstrated the importance of within-stand retention (Esseen et al. 1996, Neitlich and McCune 1997, Price et al. 1998). In coastal forest, although old-growth lichens can persist in small patches of trees (Neitlich and McCune 1997), retention of 25% was not sufficient to maintain communities similar to those in old growth, even in 120-year-old stands (Price and Hochachka 2001).

2.2.3. Discussion

Huggard’s study found that the most sensitive bird species would benefit from landscape-level reserves, that somewhat sensitive birds benefit from 40% within-stand retention and that retention of 15-20% should maintain abundances of many forest-dwelling birds that are less sensitive to harvesting. He found that

community composition of forest-dwelling birds changed with even small amounts of harvesting, and found a sharp drop in community similarity with uncut forest at about 12% retention.

Without knowing landscape context, however, these studies remain difficult to fully interpret. For example, a stand with 15-20% retention surrounded by old growth may be perceived by some organisms as quite different from a stand with similar retention levels surrounded by clearcuts. Even when inhabited by a given species, these stands may act as population sinks, requiring dispersal from elsewhere to maintain abundance (*sensu* Pulliam and Danielson 1995). Other caveats include the lack of studies examining fitness parameters, the limited time since harvest (studies were all within a few years of harvest, yet populations of long-lived organisms may take longer to respond), the emphasis on birds and the lack of studies of the broad functional roles provided by intact ecosystems. Our analysis of landscape-level thresholds in Section 2.2 suggests that birds may be the least sensitive indicator of suitability of landscape-level retention; there is no reason to assume that they should be a better indicator of stand-level retention. We conclude that the area of stand-landscape trade-offs is ripe for further research.

2.3. Summary of science at landscape and stand scales

Several lines of evidence confirm that thresholds exist

The evidence for habitat thresholds at the landscape scale arises from several approaches: theoretical modeling, empirical models, and studies in a variety of landscapes that detect thresholds in habitat amount. The thresholds relate to the life history traits, behaviour and habitat requirements of individual species and the characteristics of the habitats they are found in. From these different approaches we can find a continuum of predicted and observed thresholds. More details on the evidence for thresholds can be found in Dykstra's (2004) extensive review.

The highest values and most easily detected thresholds come from theoretical modeling usually involving percolation models. These models generally consider habitat to be black and white – either completely good or completely hostile, and usually assume that habitat use and dispersal is severely limited or non-existent through hostile habitat. As 'cells' of habitat in the theoretical grid are changed from good to bad habitat, suitable habitat becomes disconnected and sudden population declines (thresholds) of modeled species start to appear at 60 to 70% remaining habitat. As early percolation models were adjusted to allow more complex movement, or combined with empirical information, thresholds generally became lower and more variable (29 – 50% depending on habitat arrangement; With et al. 1997, Hill and Caswell 1999, Fahrig 2002).

Similarly, in real world situations, thresholds are easiest to detect and are generally higher where habitat changes have been "good" to "bad" (black and white) for the species of concern. When habitat changes introduce shades of grey, that is habitats change from good to something less preferred but not totally hostile, detecting thresholds becomes more difficult and those thresholds detected tend to be lower. For example, empirical research in forest/agricultural settings demonstrates clearer thresholds than studies in forest/forest settings (e.g. Andr n 1994). Although the studies we were able to use to in our analysis of thresholds did not allow us to detect effects of the matrix, other studies make it clear that matrix and landscape context have large influences. It is very unlikely that thresholds in forested landscapes where forests are converted to younger forests would be any higher than for areas where forests are converted to other land uses. Probably they will be lower, but specific effects will likely vary with the life-history traits of individual species, natural patterns of disturbance in any given ecosystem, and by rates of recovery of habitat attributes.

One of the key generalizations to emerge from the thresholds literature links species traits to thresholds in habitat amount. Studies in experimental model systems show that rare species are disproportionately affected by landscape thresholds (Summerville & Crist 2001), as are dispersal-limited species (With and Crist 1995) In an empirical study in the Canadian boreal forest, Schmiegelow & M nkk nen (2002) also show that rare species are particularly sensitive to loss of habitat. Modeling shows that reproductive traits have the primary influence on the threshold response of species to landscape change (Fahrig 1998, 2001; Venier & Fahrig 1996; With & King 1999b, 2001).

Summary of results

At the landscape level, it is well-established that as total habitat declines, both population size and number of species decline (Section 1). Our detailed review of empirical, landscape-level thresholds (Section 2.1) provides guidance on the amount of habitat leading to potential significant ecological changes.

Our detailed review of thresholds identified the following patterns:

- A few studies detect abundance and extinction thresholds above 60% total habitat (at 75 and 70%),
- Below 60% of total habitat an increasing number of species cross an abundance or extinction threshold,
- The number of species crossing a threshold increases linearly as habitat continues to decline from 60%,
- Approximately 2/3rds of the species reported on reached thresholds before their habitat dropped to 30% total habitat,
- Of the studies of communities, community composition changed significantly at a wide range of remaining habitat (53%, 35%, 10%)

What have we learned that is relevant to management?

Our review of threshold science supports the following statements in relation to management:

Maintaining habitat at greater than 60% of total habitat equates to low risk to ecological function.

Maintaining habitat at equal or less than 30% of total habitat equates to high risk to ecological function.

We stress that these risk assessments are based on total habitat rather than on a percent of natural. We also note that the uncertainties outlined in Section 2.1.5 suggest that more precautionary, rather than less precautionary numbers may be appropriate. Difficulties of detection, time-lags, effects on communities, and climate change (which we do not attempt to address) suggest that more rather than less habitat will be needed to avoid crossing species' response thresholds.

At the stand level, it is well-established in forests that retaining some elements of old forest in cut forest benefits a variety of organisms. Huggard's study sheds some light on how stand-level retention benefits forest-dwelling bird species, and offers suggestions about how to allocate total retention across scales.

Huggard's stand level study suggests that:

- landscape-level reserves are necessary to maintain intact forest bird communities (as communities change with even small amounts of harvesting)
- the most sensitive bird species would benefit from landscape-level reserves
- somewhat sensitive birds benefit from 40% within-stand retention
- retention of at least 15-20% should maintain abundances of many forest-dwelling birds that are less sensitive to harvesting; this level of retention also avoids the sharp drop in community similarity with uncut forest that occurs below about 12% retention.

The review of forest-dwelling birds supports the following:

Irrespective of stand-level retention, sufficient landscape-level reserves are necessary to maintain low risk for old-growth forest-dwelling bird communities.

Landscape reserves are necessary to maintain low risk to the most sensitive bird species.

Within-stand retention of more than 40% equates to low risk for most forest-dwelling bird species.

Within-stand retention of less than 15% equates to high risk for many forest-dwelling bird species.

Other studies also show the importance of matrix in allowing movement and habitat through the landscape, but trade-offs between stand and landscape level retention are almost completely unaddressed by the literature.

The landscape review suggests that birds may be the least sensitive indicators of habitat loss; hence these numbers should not be considered conservative.

At both scales, there is general agreement in the published literature (confirmed by the reviews) that amount of habitat is more important than pattern, until habitat declines considerably. Maintaining sufficient habitat to pose low risk means that issues related to pattern should be minor.

It is important to note that some species will benefit and others lose from any change to habitat amount or pattern. The question of habitat quality for individual species, however, is largely irrelevant, because the stated goal of EBM is to maintain overall ecological functioning and this requires assessment at the coarse-filter level of landscape abundance.

3. The CIT approach to coastal management – progress to date.

This section provides a history of how current targets were recommended for the coast by the Coast Information Team (CIT), and then assesses how refinements have been used to date.

3.1. What is 'habitat' on the coast?

As already outlined, 'habitat' of course differs for the specific species under consideration, and habitat discussions are typically presented from a reductionist, single species approach. When thinking about habitat at the stand level it is relatively easy to assess whether the specific attributes of an area are adequate to allow a single species' occupation in that specific area. However, the more relevant scale is that of the landscape – are there adequate habitats distributed adequately to maintain sufficient populations in distribution and abundance to maintain biodiversity and all the associated functions. When considering multiple species then the composite matrix of habitat distribution and abundance through space and time must be considered. This complexity is the reason why a coarse filter approach is used, and why natural disturbance regimes are used to contemplate habitat abundances and distributions.

Habitat loss impacts have been most clearly demonstrated when one habitat type is being replaced by a significantly different one (e.g., forest being replaced by agriculture or urban development; Bunnell 1999). In coastal forested systems where old growth is replaced by earlier seral conditions rather than rural or suburban conditions, the effects of losing old forest habitat are more complex. However, that said, given that species composition and physical structures differ so drastically, and for such significant lengths of time, it is appropriate to consider seral stage as part of the definition of a habitat type. We know that many species can use seral stages other than old growth, but some are restricted to old growth and many are more abundant in old forests. Certainly communities in old forests differ from those in younger forests. Since different species or communities exist in different structural stages, and different processes occur forests of different ages or structures we are also concerned with habitat loss as old forest is converted to younger forests.

Two important factors are how stand level practices maintain natural distribution of structures in the landscape, and secondly how the extent and rate of change occurs at the landscape level. The extent to which a harvested area maintains habitat for an individual species will depend on that species' specific

requirements, on the surrounding landscape and on the rate of recovery of attributes through time. A second important timescale is to consider whether the same habitat will be maintained after a second rotation (e.g. are their sufficient large trees or snags to be maintained through time).

In summary: while there are many species on the coast of BC that are associated with other habitats (young forest, non-forest, wetlands etc), we are chiefly concerned with forest dwelling species, and because most coastal forests across a landscape are old under natural conditions, we are primarily concerned with old forest habitat. The whole philosophy of the coastal EBM planning is that species are adapted to the historic distribution of ecosystems and seral stages (Bunnell 1995).

Temporal variability and the idea of recovery of old growth does give an added dimension to the question – and in attempting to answer these questions it is relevant to consider how younger forest recovers for different elements of biodiversity over time. Alternatively, it is also necessary to consider how multiple rotations will affect structures retained over time.

3.2. The original CIT approach to sustaining ecological integrity

The Coast Information Team examined the question of habitat targets in relation to species' responses, and decided to use a risk framework for setting targets. The risk framework automatically includes the idea of *chance* or *probability* that something will happen, which embodies the idea that forest management is a large experiment with uncertain outcomes. In the CIT work, high risk was defined as a high probability that significant negative ecological responses would occur, and low risk that there was a high probability that significant negative ecological responses would not occur. Operationally, risk is defined as the probability that a particular objective will not be met. Failing to meet the objective is assumed to be a severe consequence; hence high risk equates to a high probability of a severe consequence. The notion of probability is used because there is uncertainty (sometimes considerable) around actual risk level. Hence, ensuring low risk means that there must be high certainty that risk is low.

The CIT also focused on the coarse filter approach to maintaining ecological integrity on the BC coast and focused specifically on planning to maintain a certain abundance of old forest ecosystems over watersheds, landscapes and regions (CIT 2004 EBM Planning Handbook). Recommendations on amounts and patterns of forest to protect are based on the principle that the further away an ecosystem is from 'natural' amounts and patterns, the higher the chance of losing species and ecological function. Under this paradigm, the lowest risk to ecological systems would be to leave the areas unmanaged. However, direction from the CIT recognizes that human activity and viability of local communities and economies are also important goals for the region. Thus, the problem becomes defining how much and what type of human activity can occur while continuing to maintain a high probability that populations or species are not lost, or ecological function changed as a function of forest management activities.

From initial investigation of available science, it was agreed that there appeared to be 'thresholds' around 70% of habitat and around 30% of habitat. However, because there was a focus on old forest as the coarse filter habitat, and because in BC it had already been recognised that natural disturbances profoundly influence natural levels of old forest, the targets were suggested as a percent of the natural level of old forest⁶. This use of targets 'as a percent of natural' should be considered the first 'refinement' of the targets based on ecosystem variability (see Section 4.2).

In addition, the CIT recognized that in each of those subject areas there is considerable uncertainty in scientific knowledge, particularly about how knowledge can be applied to the forests of coastal BC. For example, the targets known to maintain species, or the combination of reserves and stand level retention that

⁶ Recognising that there is a 'range' of natural variability for individual ecosystems but that in general our state of knowledge around this variability is low, it is typically considered as a mean of the known range that is used to describe the 'natural' level of old forest.

poses low risk to species persistence or ecological function on the coast are unknown. To acknowledge these uncertainties, the CIT adopted a philosophy incorporating precaution and adaptive management⁷.

In summary: The original CIT work suggested that a low risk target could be met by retaining, for each ecosystem, 70% of the natural levels of old forest at the regional level, with lower levels possible at landscape and watershed levels. They also identified '30% of natural' as a high risk minimum target that should only be applied locally (at the watershed level) under the assumption that at the regional level the low risk target of 70% of natural was being maintained. This effectively allowed a zoning approach while maintaining the overall level of habitat at a low risk level.

3.3. Targets “as a percent of natural”

The CIT recommendations (2004) therefore suggested targets to be applied at the level of site series which would result in a low risk approach to coarse filter management. At the regional level the targets were to meet a 70% of the natural levels of old forest in each ecosystem. We have noticed that this wording often gets forgotten, and turns into a '70%' old growth target. This is unfortunate because in reality, a '70% of natural old forest' target is intended to result in a quite wide range of actual old forest targets. For example, a hemlock/balsam-leading moderate productivity unit in the CWHms2 is estimated to naturally have approximately 73% old growth forest under the natural disturbance regime, which results in the 70% of natural target asking for an actual target of 51% of the landscape in old-growth. For this same type, the high risk target (30% of 73%) results in 22% of the landscape as old growth in that type. Alternatively, fir-leading moderate productivity stands in the CWHdm are estimated to have 48% old growth under natural disturbance regimes, and the low risk 70% target results in 34% of the landscape in old growth, and the high risk target as 14% of the ecosystem in old growth (Figure 9).

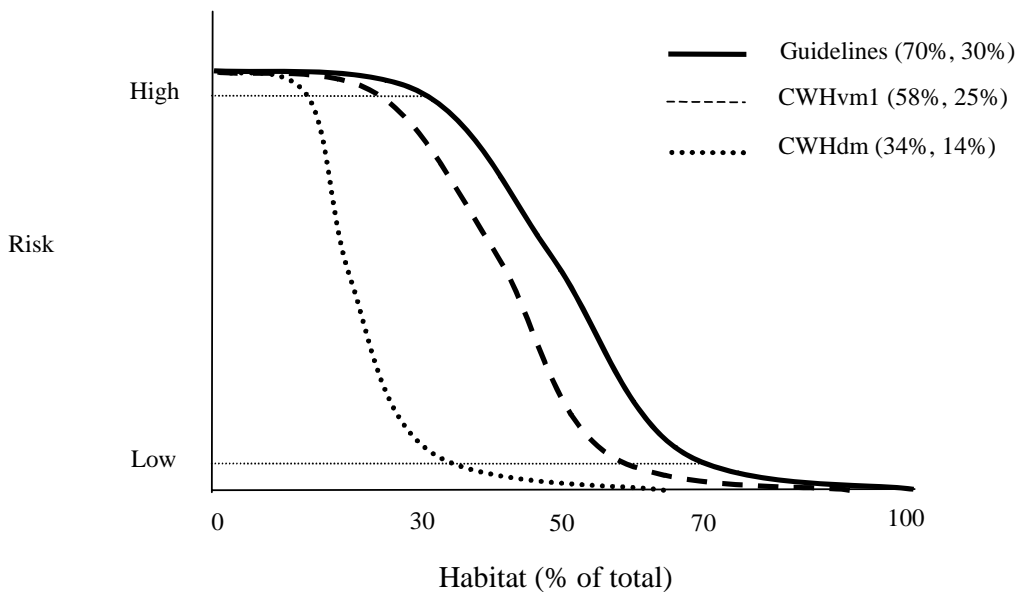


Figure 9. Risk associated with the amount of old forest retained as a *percent of total forest* for two example ecosystems, given current guidelines. Note that retaining 70% of natural means retaining a considerably lower amount of total old forest.

Other examples are provided in Table 1.

⁷ Both of these concepts are proving difficult to implement.

Table 1. Examples of actual targets for different AU x BEC combinations. Where AU's are variable, two examples are provided.

Analysis Unit	BECv	Area	Percent OG	Actual target at 70% of natural	Actual target at 30% of natural
Cedar_Good	CWHMS2	800	73	51	22
Cedar_Good	CWHVH1	3,566	90	63	27
Cedar_Low	CWHVM1	140,484	93	65	28
Cedar_Moderate	CWHDS2	1,794	68	48	20
Cedar_Moderate	CWHVH2	45,166	97	68	29
Fir_Good	CWHDS2	754	50	35	15
Fir_Good	CWHXM2	2,438	73	51	22
Fir_low	CWHDS2	6,943	68	48	20
Fir_Moderate	CWHDM	1,859	48	34	14
HemBal_Good	CWHMS2	7,395	73	51	22
HemBal_Low	CWHMS2	12,184	73	51	22
HemBal_Low	CWHVH2	24,515	97	68	29
HemBal_Moderate	CWHMS2	59,367	73	51	22
HemBal_Moderate	CWHVH2	38,402	97	68	29
Sp_Good	CWHVM1	6,291	83	58	25
Sp_Moderate	CWHVM1	6,526	83	58	25
Sp_P_Low	CWHDS2	5,882	99	69	30

3.4. Refinement of original CIT landscape targets

The intention of the CIT to allow further examination and refinement of targets and approaches to habitat retention was formalized in an agreement between CFCI (Coastal Forest Conservation Initiative) and RSP (Rainforest Solutions Project). They agreed that “a more refined approach to establishing representational thresholds at the sub-regional/territorial level needs to be developed. They presented several suggestions which are considered in detail in Section 4.2 below.

As a result of that agreement and on-going negotiations between stakeholders, an ‘interim’ set of EBM targets are being applied to the coastal landbase (Schedule B). These targets were based on the original work, but modified based on the idea (we assume) that it is reasonable to reduce the ‘low risk’ target for the most common ecosystems. As a result, a working group (through CFCI and RSP December 2003) proposed that targets be applied to ecosystems based on their frequency distribution on the landscape: that group determined to separate ecosystems based on simply taking the full suite of potential ecosystems (AU x BEC combinations) and separating these into 5 equal groups which they then defined as ‘very common to rare’ (Table 2). A problem with these definitions is that the scale of the units does not appear to be relevant to the scale of ecosystems in coastal BC (Table 2).

Table 2. The approach to defining common ecosystems for coastal BC, as used in the current guidelines (Schedule B; as modelled in Cortex 2005)

Term	Cut-off Target	Cut-off Area	Number of ecosystems	Total Area Classified
Very common	>0.3% area	>5110 ha	35	1,668,652 (98%)
Common	>0.09 – 0.3%	>1533 ha	39	
Modal	>0.02 – 0.09%	>340 ha	40	34,880 (2%)
Uncommon	>0.004 – 0.02%	>68 ha	39	
Rare	<0.004	< 68 ha	45	
Total Area				1,703,532

These categories (Table 2) were then used to apply revised targets: the two groups of ‘common ecosystems’ (98% of the landbase) received a 30% of natural target and the least common ecosystems (2% of the landbase) receive a 70% of natural target.

3.5. Risk level associated with interim scenario

The interim scenario results in landscapes with reserve levels considerably different from those outlined under the low-risk guidelines of 70% of natural as outlined in the CIT Planning Handbook (2004). For example, in a landscape with an average of 90% old forest under natural disturbance, the interim scenario leads to 28% old forest ($[90\% \times 0.3 \times 0.98] + [90\% \times 0.7 \times 0.02] = 27.7\%$). Similarly, a more southerly landscape with an average of 60% old forest naturally, would be left with 18% old under the interim scenario. With exceptions for rare ecosystems, the interim scenario subjects all landscapes to management that from the literature review likely poses high risk to ecological function.

The logic for changing the targets seems to stem from an interpretation of the conservation rule that suggests it is good strategy to over-represent rare ecosystems in a conservation plan. This idea is based on the idea that if the intention is to protect, say 50% of something, but you have an ecosystem that is rare, and only 2ha exist, then protecting 50% of it results in 1ha protected which is clearly not a functional conservation strategy. However this idea seems to have been turned around and used as the rationale that over-representation of rare actually is equivalent to under-representation of common ecosystems.

4. Applying the science

In this section we use the science reviewed in Section 2 to examine whether the current approaches outlined in Section 3 can be refined based on new knowledge. We attempt to be clear where our knowledge is strong and also to identify where uncertainties remain large.

4.1. Refining the Targets

In a discussion of the application of threshold science to management, Lindenmayer and Luck (2005) offer three cautions to consider:

1. there is no convincing evidence pointing to a single threshold value,
2. concentrating on thresholds ignores the population declines and species loss that occur above a particular habitat amount threshold, 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.

They suggest that the focus should be “on 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” (Lindenmayer and Luck 2005). We suggest that **this would equate to 60% as a minimum level of total habitat** as outlined in Section 2.1.

Our analyses demonstrate the first consideration—variability among thresholds—clearly. One potential solution is to use the threshold for the most sensitive species in a region (Mönkkönen and Reunanen 1999), provided that this species uses habitat similar to that of less sensitive species (i.e. acts as an umbrella species; Fleishman et al. 2001, Carignan and Villard 2002). Because the data will never be available to examine thresholds for all species in a particular region, analyses of thresholds detected elsewhere can be used, with caution and consideration, to inform management. This solution **suggests considering a minimum of 70 – 75% of total habitat**. Although not all these studies were based in coastal ecosystems, there is no reason to assume that coastal forest organisms need less habitat than organisms elsewhere. The forests of coastal BC experience a lower natural disturbance rate than most of the ecosystems studied (Daniels and Gray 2005). Hence coastal forest dwellers may be more sensitive to changes in habitat amount than organisms living in more changeable regions. In particular, there may be more dispersal-limited species occupying old forests.

The second consideration is important. Providing a single number as a target, while easy to manage, enforce and monitor, is not the goal of ecosystem-based management. While data from threshold studies can provide useful evidence about where risk level increases, linear declines above thresholds may also be cause for concern. This caution suggests that thresholds are no panacea, that **different targets should be applied in different areas, and that monitoring and adaptive management are critical to improving knowledge**.

The 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. Lindenmayer and Luck (2005) suggest that attention should be paid to habitat quality, not merely area covered. The solution to this caution suggests that **ecosystems should be monitored by type (e.g. site series) to ensure that all ecosystems are represented**.

Studies in the review were based on absolute amount of habitat, not amounts relative to natural levels. When viewed as absolute habitat, the current guidelines of 70% of natural translate into 40 to 60% (or less, see Table 2 and Figure 9) of total habitat. Hence **the current guidelines about low risk (70% of natural; CIT Handbook) are supported by our literature review**. There is uncertainty about whether risk to ecological integrity increases below 70% of natural. However, our analysis suggests that risk to ecological integrity is no longer *known* to be low below that point.

The review suggests that retaining less than 30% of total habitat poses high risk. The regional targets outlined by the CIT Handbook do not allow this absolute value to be reached over the region.

The high risk levels outlined by the CIT Handbook at the watershed scale (30% of natural) allow the total habitat within a watershed to go below 30% total habitat (15-25%). This (as stated in the handbook) likely represents high risk at the watershed level, but the landscape is maintained overall at low risk because of the regional target. Note that the interim guidelines (i.e. Schedule B) allows the vast majority of ecosystems to move into this high risk realm without a regional target in place.

Potential consideration should be given to providing absolute minima as well as guidelines based on percent of natural forest.

A complicating factor in applying threshold research to coastal ecosystems is that habitat around old forest patches becomes less hostile to most organisms if it contains more attributes of intact forests (i.e. stand level retention), and, as it grows older, softening the effects of habitat loss, reducing edge effects, and allowing easier dispersal. Although our review did not find a significant effect of matrix quality on abundance and extinction thresholds, individual studies have demonstrated easier dispersal when patches are embedded in less hostile matrices. **Our analysis of stand level work suggests that higher levels of stand level**

retention, which reduces matrix hostility, could be used to offset to some degree, landscape level requirements.

4.2. Other Criteria that Could Refine the Targets

As outlined in Section 3.4, there remains interest in examining how targets could be refined. Suggestions for refinements from the CFCI and RSP agreement include

- “grouping ecosystems according to specified ecological criteria (e.g. the habitat value of individual ecosystems, connectivity value of the ecosystems, sensitivity of ecosystem function to reductions in old seral stage conditions, the portion of ecosystem reserved in protected areas, relative frequency/rarity of ecosystems, and the potential ecological impacts of excess levels of mid and early seral habitats),
- developing group specific risk curves and thresholds,
- establishing a range of precautionary targets for each ecosystem grouping based on the ecological criteria as well as the estimated reliability of data (where surrogates are used) and
- specifying spatial deployment strategies.”

We assess each of the ideas raised, in terms of their applicability in this setting. We used available science information where feasible, however we note that science is not readily applicable to some of these questions. In these cases, we use our combined expert opinion, or simply apply logic, to provide guidance. Note also that we are assessing whether it is feasible to refine the targets outlined for Full EBM implementation, which in cases is complicated or made irrelevant by the current Interim Schedule B information.

4.2.1. Natural disturbance rate and pattern

Can it be used to refine? YES. The CIT Planning Handbook already revised a total habitat target to one based on a percent of the natural old-growth in each ecosystem.

Direction of pressure? Downwards (because it is not possible to have more than 100% of old).

Rationale: The risk associated with an absolute level of habitat loss is hypothesised to vary among these ecosystems because these systems have evolved with different levels of disturbance. It makes no sense to reserve 70% old forest if naturally only 40% is old. The fundamental issue is to ensure adequate levels of any habitat, not just enough old forest. The targets, however, focus on old forest because it dominates the natural landscape and is also the most at-risk habitat type on the coast. For old forest, the amount found naturally is determined by disturbance frequency. Within coastal BC, disturbance frequency and severity increases from north to south, from hypermaritime to sub-maritime and within certain landforms (e.g. fluvial ecosystems, steep slopes, wind-exposed areas; Dorner and Wong 2003; Price and Daust 2004).

What’s needed? We have estimates of natural disturbance for the coast, at the level of biogeoclimatic variants, and further ecological refinements are possible: For example, Price and Daust 2004 clustered ecosystems statistically to have the most consistent within-group and most different among-group disturbance rates. This system, or some other ecologically relevant grouping of ecosystems, should be used to apply the disturbance information.

Current guidelines in Schedule B are based on AU/BEC classification, however, and these are weak ecological units. **Efforts should be stepped up to ensure coast-wide implementation occurs using ecologically appropriate ecosystem classification and disturbance units.**

4.2.2. Ecosystem type

Use to refine? YES

Direction of pressure? No pressure on overall amount, rather more about checking the 70% is evenly distributed—so upwards in some ecosystems and downwards in others.

Rationale: Conservation science calls for representation of all habitat types, not just old forest in general. Hence, we should ensure that we have representation of each type of ecosystem. Calculating representation for each ecosystem type ensures that all types are represented, including productive ecosystems that are subject to the most pressure from timber harvesting.

What's needed? We have an operationally useful ecological classification system (BEC site series), however efforts should be stepped up to ensure this becomes useful for strategic planning (i.e. coast-wide mapping). We may need to place these site series into carefully-thought-out groupings, trying to minimise overlap among ecosystem type. If groupings are used for planning, site series themselves can be used for monitoring to make sure none are missed.

Site series or even site series groups are theoretically and practically, the wrong scale for estimating natural disturbance, so that must be done at a broader scale.

4.2.3. Grouping ecosystems / Spatial deployment

Use to refine? POSSIBLY

Direction of pressure? Downwards as in 4.2.1.

Rationale: The notion of grouping ecosystems is to make planning practical, reduce numbers of small units to address, and presumably reduce the problems associated with GIS slivers. It may be that we need to group site series in order to meet some of these planning efficiencies, but we suggest reviewing actual scenarios to see if planning can be practical using site series. If site series are demonstrated to be impractical they could be grouped cautiously into ecologically defensible units. In theory site series groups should consider a) the ecological variability inherent in that type (i.e. 17 site series may require 6 groups, whereas 9 site series may be appropriately grouped into 3 types), b) should ensure groups do not include high and low productivity types, c) must retain the biogeoclimatic variant differential (i.e. don't lump across variants or subzones), d) must not include rare site series.

Irrespective of how planning is undertaken, complete complex TEM polygons should be used to 'check' the representation of all site series (based on area weightings), and reserves should be rearranged as appropriate if under-represented types are observed.

Regardless of ecosystem unit used, locating reserves (spatial deployment) will still need to be thoughtful and include flexibility to shift and combine small areas into ecologically relevant areas. The actual pattern of reserves will not affect the amount required to be maintained.

What's needed? Actual examples (maps or computer scenarios) that show problems of site series and problems/benefits of grouping in various ways.

4.2.4. Habitat value

Use to refine? NO

Direction of pressure? None

Rationale: There is no ecological rationale, given current knowledge, for treating different ecosystems/habitats differently with respect to how much is required to be reserved. For example, a rich ecosystem (e.g. a floodplain) and a much less rich ecosystem that supports unique species (e.g. a bog) both have high habitat value. Provided that we can divide ecosystem types (as in #2 above) into non-overlapping groups, such that one "ecosystem type" is not a subset of another, there is no evidence for assigning more value to particular habitats. We acknowledge that perhaps there are ecosystems and species of higher social value than others, but that is beyond the scope of science.

What's needed? Nothing.

4.2.5. Frequency/rarity

Use to refine? YES, for truly rare ecosystems; NO, for common ecosystems

Direction of pressure? Upwards for truly rare ecosystems.

Rationale: The rationale for conserving more of truly rare ecosystems is a practical one. Conservation theory has posited that rarer ecosystems should have higher levels of protection than common ecosystems, because **they are more likely to be lost due to rare disturbance events, and because assuming their spatial extent is small, retaining some percentage of that area may fail to retain a functional ecosystem.** As well, rare ecosystems may provide habitat for rare species (at a coarse filter level as well as fine filter).

There is no ecological theory that suggests common ecosystems should have less protection than the average. Perhaps practically they are in less danger of being lost to unusual disturbances, but the literature we present on habitat loss effects has mostly come from common ecosystems (grasslands, forests), so the numbers we present are for common ecosystems. We know of no rationale for decreasing these.

What's needed? The challenge is to define truly rare ecosystems. Red- and blue-listed ecosystems are already defined. We are not sure all rare ecosystems are captured by that classification, nor are we sure that all red and blue ecosystems are truly rare. The inventory of truly rare ecosystems needs to be updated, for example, including those ecosystems listed in Pojar's North Coast report. We need to ensure that we don't consider GIS "slivers" as rare ecosystems—these are artifacts of GIS analyses and non-ecological boundaries. We should look at each potentially rare ecosystem and assess 1) whether it's a true ecosystem and 2) whether it is truly rare. The scale for consideration of rarity should be regional/territorial—certainly not within watersheds, and not within landscapes unless they are very large.

4.2.6. Connectivity value

Use to refine? YES (already included for hydroriparian ecosystems)

Direction of pressure? Upwards for connecting hydroriparian ecosystems

Rationale: For connectivity to be helpful in distinguishing among groups of ecosystems, some ecosystems should have a higher value for connectivity than others. Hydroriparian ecosystems connect headwaters, valley bottoms and estuaries, and have a high connectivity value (see Hydroriparian Planning Guide and background documents). These ecosystems have already been separated from others in the Hydroriparian Planning Guide.

Connectivity is also important between valley bottoms and ridges. Apart from hydroriparian ecosystems, however, there is no readily identifiable group of ecosystems that has a higher value in linking valleys to ridges than any other group of ecosystems, so connectivity value does not affect representation targets as such.

Note that the science is clear that with adequate levels of protection, landscape pattern, or connectivity is less important. However, we note that the current targets being used (in Schedule B) pose high risk, and at this level of broad representation, connectivity issues would become extremely important.

What's needed? Connectivity has already been included somewhat by including hydroriparian guidelines. The guidelines of the Hydroriparian Planning Guide, specifically calling for connectivity, however, are not included in the current set of guidelines. Following the currently included hydroriparian guidelines does not guarantee connectivity; the removed connectivity guidelines from the HPG be revisited for this function.

4.2.7. Proportion of ecosystem in protected areas

Use to refine? POSSIBLY (already affects requirements on rest of landbase)

Direction of pressure? Inverse to amount protected

Rationale: The current representation targets focus on one aspect of ecosystems – old forest. Where old forest occurs in Protected Areas this area is intended to count towards the regional targets⁸. However, within Protected Areas there may exist significant area of natural younger forest which has significant value as part of a large Protected Area. Where this area is not a result of previous harvest, and is unroaded and part of a natural landscape context, it would be reasonable for it to contribute towards the total regional target.

Where significant area that has been previously harvested is now captured within Protected Areas, it would be reasonable to allow it to contribute to the target as it ages. One proposal is that mature forest (e.g. 80 years) could begin to count towards the old-growth target, acknowledging the recovery of values in that stand over that time period. Again, an assessment of ecological functioning of the area would still be required, and should include whether there is, or is likely to be, development, roads, disturbance etc in that area.

What's needed? When a regional low-risk target, as outlined in the CIT Planning Handbook is in place, allow old forest ecosystems, and some portion of unmanaged younger forest in parks to count towards this target. If targets are reduced below the level suggested by the literature review, more emphasis on the amount of old forest will be necessary. In this case, currently young or mature forest in Protected Areas will count less towards old forest targets.

Undertake an assessment of ecosystem representation in Protected Areas to determine whether any particular ecosystems have high levels of representation that is not old growth, nor harvested. If this is a large issue, develop a sliding-scale of age to area in order to contribute towards the target. Lack of ecosystem mapping within older Protected Areas remains a knowledge gap.

4.2.8. Sensitivity to decrease in old seral

Use to refine? YES (already included through RONV)

Direction of pressure? Downwards (as in #1—i.e. most sensitive are close to 70%; others are less)

Rationale: The assumption is that if an ecosystem naturally has more area in an old seral stage, the overall sensitivity of the ecosystem will be higher, so the absolute amount of old should be higher assuming that organisms have adapted to a particular disturbance regime. **This concept is already addressed** in section 4.2.1. We know of no additional information that would suggest any additional refinement based on inherent ecosystem sensitivity.

There may be secondary effects of decreasing the amount of old seral. For example, on fans, steep slopes or karst ecosystems, harvesting old seral ecosystems can change hydrology as well as changing seral stage. However, these secondary effects are already included within the curves for groups of hydriparian ecosystems (see Hydriparian Planning Guide).

What's needed? As in #4.2.1 and 4.2.2, the basics that are needed are estimates of natural disturbance frequency by ecosystem type or groups.

4.2.9. Sensitivity to excess mid and early seral

Use to refine? NO (partially already included through RONV)

Direction of pressure? None

Rationale: This is simply the corollary of 4.2.7 above.

Alternatively, if this issue was included because individual species (in particular grizzly bears) respond to excessive amounts of early and mid seral on the landscape 'at a particular time' then these **temporal/spatial bottlenecks for species should be dealt with directly through modeling of species needs and habitat supply.**

⁸ With the current Schedule B there is no regional target set, so this causes a major implementation question of how large set aside areas (Protected Areas, Cultural areas etc) are used to offset local requirements. In this current framework this question therefore becomes moot because no Protected Areas are used against regional targets.

What's needed? Nothing.

4.2.10. Achieving targets while natural disturbance continues

Use to refine? NO (doesn't change the targets, does change management options)

Direction of pressure? None necessary to targets; downwards to amount logged

Rationale: The targets apply to how much old forest is desired to keep all species and ecological function. What type of disturbance reduced the old forest to these levels is not really the issue. **It may be that to meet the targets harvesting will have to adjust for natural disturbance so that together they keep targeted amounts.** The papers we reviewed do not address this issue.

What's needed? Nothing, but recognize if a natural disturbance dramatically reduces old on the landscape, harvesting should be adjusted downward.

4.2.11. Old growth and recovery of attributes

Use to refine? YES.

Direction of pressure? Upwards and Downwards

Rationale: The functional attributes of **old forests are not captured well by FC inventory definitions.** Currently forests that are classified as Age Class 8, 9 and even maybe 7 contain very old trees, usually much older than indicated by the age class categories. Consequently, **today there is more old forest than indicated by age class 9. The same will not be true many years in the future when second growth forests become 200 and 250 years old etc. Forests that regenerate after harvesting and become 251 years old will be different from the 'old-growth' forests of today.** We have no way of assessing just how different these forests will be as managed coastal forests are barely mature. We know that even with structural retention (at least with the selection cutting as practiced previously in Scandinavia), managed forests differ from natural.

Soft reserves that allow old forest to be cut as young forests grow to 250 years old, are inappropriate as a main strategy because 250 years since stand-replacing disturbance is different from 10,000 years since stand-replacing disturbance. We do not know how different; there will be gradation of functioning at different ages and structural compositions that will vary with the particular value under consideration. For example some hydrologic processes recover with 'green-up' of the stand, while others can have continued impacts over centuries (Church and Eaton 2001). Poor dispersers and slow growers such as epiphytic lichen communities and canopy arthropod communities may also have long recovery periods (Price and Hochachka 2001, Pettersson et al. 1995). Data on recovery times for different elements are weak.

What's needed? Nothing immediately. This issue will not arise for many years, during which our management ideas will have changed several times. On-going work into development of old growth attributes over time (before 250 years and after 250 years) will help refine this approach to managing coastal forests at the landscape scale.

4.2.12. Stand retention/landscape reserve tradeoffs

Use to refine? YES

Direction of pressure? Downwards

Rationale: The issue is when and how to count stand level retention towards landscape level targets. Stand level retention accomplishes different things than landscape reserves, and provides two main functions – including a) maintaining the habitat suitability of a patch of ground when it is harvested for species and b) increasing the rate at which that area of ground attains old forest functioning.

The literature review informs two issues: First, bird community studies show changes in community as soon as harvesting occurs and certainly below 80% retention. Thus for a stand to be counted fully as old growth, it

ought to be more than 80% intact. Second, the literature suggests that 40% retention is required to benefit more sensitive bird species. Harvested areas with levels of retention of 40% and higher should therefore be allowed to count towards landscape level targets provided:

- a) adequate inventory to ensure that the retention is representative of the stand⁹,
- b) if there is mapping of retention to ensure that it is in fact maintained as adjacent areas are harvested (i.e. it is withinblock, or mapped as long-term retention if adjacent to the block)

The literature suggests at both the stand and landscape level, that **retention amount is more important than retention pattern**. We therefore suggest that patch size is not the issue, which contradicts original direction by the CIT which allowed only blocks greater than 2 ha to count. Alternatively, we suggest that the science supports the idea that above 40% retention should count towards landscape targets regardless of pattern. Exactly how to credit them towards landscape targets is not informed by science but we suggest that, perhaps at 50% for 40% retention and higher as retention increased to full credit at 80% retention.

The literature also suggests large changes in community and rapid reductions in even low sensitivity species below 12% retention. This supports the minimum standard for stand level retention at 15%. However, we note that consistently locating this retention on the edges of blocks, fails to meet the objective of this 'stand level' retention since the intention is to increase the habitat values of the area that has been harvested.

What's needed? More work on non-birds and stand-level retention. More work on the links between stand and landscape (i.e. use of stand-level retention in a sea of immature forest).

4.2.13. Adaptive Management

Use to refine? Potentially

Direction of pressure? Upwards or Downwards

Rationale: Adaptive management is intended to be the corner stone of the new approach management, and is widely touted as a central piece of implementing EBM. However, we note that to our knowledge, no adaptive management studies have ever addressed the biggest and most important questions in a powerful and effective way – we lack the ability to test broad landscape issues such as 'how much is enough' to retain within coastal BC.

We stress that adaptive management has better potential to refine targets and approaches at lower scales (e.g. within watersheds – testing the effectiveness of different approaches to conservation design, or refining stand level targets and layout).

4.3. Conclusions

How much is enough

- A few studies detect abundance and extinction thresholds above 60% total habitat (75, 70%).
- Below 60% an increasing number of species cross an abundance or extinction threshold.
- The number of species crossing a threshold increases linearly as habitat continues to decline.
- Approximately 2/3rds of the species reached thresholds before their habitat dropped to 30% total habitat.
- Of the studies of communities, community composition changed significantly at a wide range of remaining habitat (53%, 35%, 10%).

⁹ We are concerned that high-grading of cedar or spruce from stands resulting in high levels of retention may be argued to maintain fully functioning old-growth. This is a concern not only from a habitat perspective, but perhaps more so from an economic perspective.

- The risk associated with habitat loss is hypothesised to vary among ecosystems because these systems have evolved with different levels of disturbance. **We propose that using a 70% of natural old-growth target aligns with the science which suggests a 60% of total habitat target as a low risk approach.**
- There remains uncertainty about the rate at which risk increases below 70% of natural, however the meta-analysis of studies suggests that it does increase, and at 30% total habitat 2/3rds of species reported on show a threshold. **This suggests that using a 30% of natural old growth target does equate to a high risk approach, at the landscape scale.**
- There should be consideration for setting a **minimum total habitat level**, even in areas where natural disturbance levels are high (i.e. in areas where 70% of natural results in a target less than 30% of total habitat).

Natural Disturbance and grouping ecosystems:

- We have estimates of natural disturbance for the coast for broad ecosystem groups. It may be that to meet the targets, harvesting will have to adjust for natural disturbance so that together they keep targeted amounts.
- Because different ecosystems provide different habitats and functions, we want to ensure that we have representation of each type of ecosystem. The definition or level of ecosystem that is considered for representation is undecided and somewhat flexible. We may need to place ecosystem site series into carefully-thought-out groupings, trying to minimise overlap among ecosystem type. The notion of grouping ecosystems is to make planning practical, reduce numbers of small units to address and reduce effects of non-ecological slivers. Regardless of ecosystem unit used, locating reserves (spatial deployment) will still need to be thoughtful and include flexibility to shift and add slivers to larger areas. There is no ecological rationale, given current knowledge, for treating different ecosystems/habitats differently with respect to how much is represented in reserves.
- Connectivity may be one aspect that should be considered in representation targets, but it has already been included somewhat by including hydriparian guidelines. Once the regional level target is implemented, include Protected Area ecosystems in calculations of area that meets representation targets.
- The rationale for conserving more of truly rare ecosystems is a practical one more than an ecological one. Conservation theory has posited that rarer ecosystems should have higher levels of protection than common ecosystems, because they are more likely to be lost due to rare disturbance events, and because assuming their spatial extent is small, retaining some percentage of that area may fail to retain a functional ecosystem. The challenge is to define truly rare ecosystems.
- No science evidence exists for turning around this assumption and reducing the target for common ecosystems.
- Temporal/spatial bottlenecks of habitat for species should be dealt with directly through modeling of species needs and habitat supply, not through adjusting representation targets.
- What is considered to be old forest may need adjusting over time. Old forests are not always captured well by inventory definitions. Today there is more old forest than indicated by age class 9. The same will not be true many years in the future when second growth forests become 200 and 250 years old etc. Forests that regenerate after harvesting and become 251 years old will be different from the 'old-growth' forests of today. Adaptive Management can help to understand how recovery of attributes maintains different ecological values through time.

Stand level retention

- The literature suggests changes in bird communities occur quickly in response to amount of harvesting. For a stand to be counted fully as old growth, it ought to be more than 80% intact. The literature also

suggests that 40% retention is required to benefit more sensitive bird species. Harvested areas with levels of retention of 40% and higher should therefore be allowed to count towards landscape level targets provided:

- adequate inventory ensure that retention is representative of the stand,
- mapping of retention ensures that retention is maintained as adjacent areas are harvested (i.e. it is withinblock, or mapped as long-term retention if adjacent to the block)

Science Summary:

- The science review provides no evidence to significantly alter the original CIT landscape level representation targets. A 70% of natural old forest target aligns well with the area of low risk shown by the literature.
- The most obvious refinement was undertaken at the outset by the CIT, by including variability by ecosystem. From the CIT guidance absolute coastal retention targets range from 34 – 69% by ecosystem.
- Other smaller refinements are possible while maintaining low risk, but are unlikely to have large implications to the overall regional level target.
- There remain large uncertainties – and this uncertainty should be used to guide how practical problems are addressed, and watershed scale adaptive management. However, the types of refinements suggested by current interim guidance are outside the scope of the scientific uncertainty.

Comments on the Future

The purpose of our literature review was to review the science behind the low- and high-risk targets (70% and 30% of natural respectively) listed in the CIT EBM Handbook, and consider ways to refine these targets. We realise, however, that the current Schedule B has changed many other aspects of management beyond representation targets, many of which affect our consideration and recommendations.

- Currently, there are a number of interim measures in place that do not meet the low risk approach suggested by the CIT and supported here. In particular, the refinement of the target to apply a 30% of natural target to 98% of the landscape (Schedule B 2007) is very likely to result in high risk
- Interim measures base representation on commonality of ecosystems (high-risk target for all but the rarest 2% of ecosystems). While the science does not support any division based on commonality, if policy-driven rationale is used to do so, the commonality of ecosystems should be determined using ecologically appropriate groupings and at an ecologically appropriate scale to apply to the coast of BC. In addition, the loss of regional-level targets (Schedule B 2007) results in the loss of flexibility at the landscape and watershed level. The lack of regional targets also reduces the ability to reasonably 'count' the ecological gains from Protected Areas across the entire region.
- We note that many of these current interim goals work contrary to full implementation of EBM which we understand is intended to be achieved by 2009 (AIP – RSP and CFCI). For example, any planning based solely on landscapes negates options for broader-scale planning efforts. We are unsure how these two contrary paths can be meshed without losing long-term conservation options in the interim.
- If the intention is to meet a full implementation of EBM, a useful approach would be to identify appropriate transition strategies, and identify barriers to this transition, as soon as possible. We caution that implementing the current Schedule B may hinder transition to EBM.

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Appendix 1. Summary of papers included in landscape-level threshold analysis.

List of papers for use in threshold summary. These papers describe empirical (or mix of model and empirical) landscape-level thresholds (occurrence, extinction, reproduction etc) in proportion of suitable habitat. Hence, they do not include stand-level studies, modelling studies or studies that define thresholds in patch size or isolation (extrapolating the latter studies to habitat amount involves high uncertainty). Updated January 22, 2007.

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
Angelstam 2004	Capercaillie	34% Fig 5 logistic regression	90% occupancy (reproductive; lekking males)	Forest in forest Sweden; mature boreal forest in younger forest	No	16 km ² landscapes (n = 10); new census data	Clear threshold and reliable study	
Angelstam 2004	Black grouse	22% Fig 4 logistic regression	90% occupancy (reproductive; lekking males)	Forest in forest Sweden: young boreal forest in mature forest	No	As above	As above	<ul style="list-style-type: none"> Black grouse uses young forest while capercaillie uses old
Bascompte and Rodriguez 2001	Woody plants	35% Fig 1 split-line regression	Community (start of decline)	Woody vegetation in prairie Konza tallgrass prairie	No	6400m ² (n = 164—a bit unclear); census data	Threshold is clear. Study documents natural patches of woody vegetation in grass rather than habitat loss, but results seem applicable.	
Carlson 1999	White-backed woodpecker	13% (mean of 9 – 17%) for extinction Lande's model + data 50% of RONV (Table 1)	0% (extinction) in regions Abundance over entire area	Deciduous in coniferous forest Finland; boreal mixed forest	No	Southern Finland; existing census data—change over time	Clear threshold and reliable study	<ul style="list-style-type: none"> Evidence for time lag (extinction debt) Gives RONV
Drolet et al.	Bay breasted	55%	0% occupancy	Forest in regenerating	No	100-ha landscapes;	Clear threshold and	<ul style="list-style-type: none"> Shows can be thresholds even for

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
1999	warbler	Figure 2	in patches	forest Canadian boreal forest		new census data	reliable study	<p>common species, even within forest context</p> <ul style="list-style-type: none"> Also relationship for solitary vireo and robin, but data not given
Gibbs 1998	Wood frog	24 and 55% Fig 3—mid-points based on Fig 2 I re-plotted data by landscape area and fitted a curve—matches	0% occupancy and 90% occupancy	Forest in rural and urban Connecticut US oak forest	Yes	2 x 10km strip; new census data	Not a sophisticated study, but fairly convincing (particularly in diffs among species)—could analyse data better I think	<ul style="list-style-type: none"> Poor dispersers OK (stay in patch), generalists OK (matrix not hostile), good dispersers do poorly—naturally disperse to pools in continuous forest, but with fragmentation, risk desiccation etc.
Gibbs 1998	Red-spotted newt	55 and 70% Fig 3 and 2	0% occupancy and 90% occupancy of suitable habitat	As above	Yes	As above	As above	
Gibbs 1998	Spotted salamander	24 and 55% Fig 3 and 2	0% occupancy and 90% occupancy	As above	Yes	As above	As above	
Gonzalez and Chaneton 2002	mites—community	53%	Community disassembly when not connected Multiple extinctions	Moss on rock Experimental model system	Yes	Moss on boulders (n = 8); experimental data	Interesting experiment. Only single landscape amount—but community disassembly at that point suggests thresholds at least that high	<ul style="list-style-type: none"> Extinction biased towards rare spp Evidence for time lag—no initial change in biomass or abundance Corridors mitigated effects

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
Hargis et al. 1999	American marten	75% Fig 5—capture rate	0% occupancy	Forest in forest mature-old forest in clearcuts (> 5 years) Utah US; Engelmann spruce/lodgepole pine/subalpine fir forest	No	9 km ² sites (n = 18); trap data	Reliable study and threshold	<ul style="list-style-type: none"> No structure in clearcuts (although plenty of food), so more hostile than areas with structure
Homan et al. 1999	Wood frog	15% and 44% (44 – 88%; largest scale) Fig 2—broken regression for 0%; non-parametric changepoint for 90%	0% occupancy and 90% occupancy	Forest in agriculture and suburban Massachusetts US; small ponds in woodland	Yes	1km radius around 168 ponds (n = 168); census data	Reliable study. Thresholds vary with analysis technique—exploratory. Thresholds lower than Gibbs.	<ul style="list-style-type: none"> Varies by scale; chose largest landscape for 90%
Homan et al. 1999	Spotted salamander	25% and 51% (25-51%; largest scale) Fig 1—as above	0% occupancy and 90% occupancy	As above	Yes	As above	Thresholds vary with analysis technique, but match those in Gibbs well.	<ul style="list-style-type: none"> As above
Jansson and Angelstam 1999	Long-tailed tit	10% and 14% Figure 1 and my plot 50 and 53% of RONV (based on Carlson)	0% and 90% occupancy	Deciduous forest in coniferous forest Sweden; boreal forest	No	1 km ² around deciduous stands (n = 28)	Reliable study and threshold	<ul style="list-style-type: none"> Inter-patch distance seems more important than landscape Stand variable not related
Lennartsson 2002	Gentians	45% (35 – 70%; mean of largest field) 53% (mean of 45 – 60%)	Extinction (selected largest field) 90% seed set	Grasslands fragmented by shrubs Sweden; natural grasslands	Yes	2.5 – 15 ha grasslands (n = 6); extinction prediction based on census data	Clear thresholds and reliable study	<ul style="list-style-type: none"> Varies by scale (smaller fields need more habitat within)

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
		Fig 3 and 4						
Radford and Bennett 2004	White-browed treecreeper	23% (11 – 23%; all suitable habitat) Fig 5—model of probability of occupancy	90% occupancy	Forest in forest and agriculture Australia; semi-arid woodland (buloke and belah)	Yes/no	100 km ² landscape around >50ha patches (n = 56)	Reliable study and clear threshold	<ul style="list-style-type: none"> Note that density was low—populations may not be viable Varies with habitat quality
Radford et al. 2005	Woodland-dependent birds—community	10% Figs 5 and 8	Community—collapse of woodland-dependent birds	Forest in agriculture Australia; Eucalyptus forest	Yes	100 km ² (n = 24)	Reliable study; variety of threshold detection techniques; sample biased to low cover.	<ul style="list-style-type: none"> Evidence for time lag
Reunanen et al. 2004	Siberian flying squirrel	14 and 38% Figure 4—model; discussion in text	0% occupancy and 90% occupancy	Mature forest in young forest and bog Finland; boreal mixed	Mostly no	300 – 1260 km ² landscapes (n = 4); field surveys (also regional scale)	Threshold based on model, but backed up by empirical data	<ul style="list-style-type: none"> Matrix important— young forest better than recent clearcuts
Rolstad and Wegge 1987	Capercaillie	50 % Fig 4 and text	Reproductive (lekking)	Mature forest in young forest Norway; boreal coniferous	No	1 km ² (n=14 leks); census data	Threshold in response to graininess of habitat. Not fully clear how to interpret, but study seems reliable.	<ul style="list-style-type: none"> Interaction between habitat amount and graininess
Saari et al. 1998	Hazel grouse	32%	Fragmentation	Forest in forest and agriculture Finland; boreal mixed	Yes	Patches of habitat from < 1 – >100ha; census data	Patch size study that finds threshold at given landscape	
Summerville and Crist 2001	Butterflies (6 rare species)	80 and 100%	0% and 100% occupancy	Unmowed in mowed grass (analogous to harvested forest) US; old field; experimental model system	No	15 x 15 m plots (n = 25); experimental model system	Reliable study, thresholds clear for rare species; note that landscape is small relative to organism	<ul style="list-style-type: none"> Thresholds in rare species; common species show linear response

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
Summerville and Crist 2001	Butterflies (10 rare species)	40 and 60%	0% and 100% occupancy	As above	No	As above	As above	
Tscharntke et al. 2002	Parasitoids on pollen beetles	20% Fig 4	edge effect below 20%	Grass in crops Germany; orchard meadows	No	1.5 km around patches (n = 33)	Reliable study, threshold not entirely clear (data not presented across range studied; just < and > 20%)	<ul style="list-style-type: none"> • Discussion of SLOSS; need to include all ecosystem types
Villard et al. 1999	Chestnut-sided warbler	50% Fig. 3—90% of fitted logistic regression; I re-plotted proportions by decile	90% occupancy	Forest in fields Ontario Canada; maple forest	Yes	2.5 x 2.5 km landscapes (n = 16); census data	Reliable study and clear thresholds	<ul style="list-style-type: none"> • Some linear changes in other species • Variety of patterns among species
Villard et al. 1999	White-throated sparrow	42% As above	90% occupancy	As above	Yes	As above	As above	
Villard et al. 1999	Ovenbird	14% As above	90% occupancy	As above	Yes	As above	As above	
Villard et al. 1999	Black and white warbler	8% As above	90% occupancy	As above	Yes	As above	As above	
Virgos 2001	Badger	20% Table 2; I plotted data	Abundance of setts	Forest in agriculture Spain; oak forest	Yes	100 km ² landscapes (n =12 in each of 3 cover categories); census	Clear threshold in one area, not in the other; otherwise seems reliable	<ul style="list-style-type: none"> • Habitat quality explains variation above 20%; isolation explains below 20%
Wikars 2004	Log beetle	25% Fig 3	Abundance	Forest in forest Sweden; boreal coniferous forest	Yes	1 km ² (n=20) in 25 km ² landscapes (n=4); census	Not very convincing threshold (especially for larger landscapes)	
With et al. 2002	Ladybird beetles	40% for native species	90% occupancy	Clover in bare soil	Yes	16 x 16 m plots (n=36);	Reliable paper. Threshold fairly clear.	<ul style="list-style-type: none"> • Thresholds in clover isolation matched by

Paper	Organism	Threshold amount	Threshold type	Habitat type	Matrix hostile	Scale and data	Assessment	Comments/useful info
		Fig 2 Lacunarity index		Experimental model system		experimental model system		aphids—introduced ladybird matched aphids; native species didn't, due to differences in movement.

Appendix 2: Details from Huggard's study

Individual species

Eleven "species" (including species in particular forest types) responded positively to harvesting at all levels (Table 5 "Positive"). Many other species undoubtedly also respond positively, but this analysis is restricted to species that occur regularly in uncut forest. Ten other species responded positively except for reduced abundance at the lowest retention levels (Table 5 "Positive except at low levels"). These species were often at low abundance in clearcuts or near-clearcut conditions, but at or above uncut abundances at other retention levels. However, widely scattered data points made the precise form of the relationship uncertain for several of these species. An additional 13 species were unaffected by retention level (Table 5 "Neutral").

Thirteen species were not affected by harvesting until low retention levels (<20%, Table 5 "Neutral except at low levels"). Some of these species did, however, decline substantially at these lower retention levels. Three species had abundances above uncut levels in harvested stands with higher levels of retention, but substantially reduced abundances below 30-45% retention (Table 5, "Positive high, negative low"). A large group of 16 species declined with decreasing retention levels, but with relative abundances that remained greater than the retention level (Table 5 "Above proportional"). For example, at 30% retention, these species would occur at greater than 30% of their uncut abundance.

Twelve species were maintained in harvested stands at abundances that were proportional to the percent retention (Table 5 "Proportional"). For example, a stand with 30% retention would be expected to retain these species at 30% of their abundances in uncut forest. Ten species showed sigmoidal relationships. Although the sharpness of the sigmoidal function differed among these species, they all showed abundances that were lower than proportional at low retention, and higher than proportional at higher retention levels, with a relatively steep gradient in between. Four species showed the most severe effects of harvesting, with abundances less than proportional across the range of retention levels, but only in some ecosystems. All four showed this relationship in deciduous or mixed deciduous stands, while only the brown creeper showed a less-than-proportional relationships in a conifer ecosystem (Interior dry conifers and conifers in winter).

Table 5. Summary of responses to reduced retention levels.

<p><u>Positive</u> AMRO BHCO CEWX CHSP DEJU – All exc. eastern HAWO – Conifer MacWA OCWA PISI – Interior conifer PUF1 RBGR</p>	<p><u>Positive except at low levels¹</u> [AMRE – Eastern (5%)]² BCCH (10%) CAWR (2%) [DOWO (15%)] [EVGR (5%)] [HAFL (10%)] [TOSO (20%)] [VEER (5%)] WETA (10%) WTSP (5%)</p>	<p><u>Neutral</u> BLJA DEJU – Eastern EWPE GCFL GRJA – Deciduous NOFL RBNU – Eastern [RECR – Interior+Boreal] RNSA STJA – Coast SWTH – Eastern WAVI – Conifer WIWR – Winter, Deciduous</p>
<p><u>Neutral except at low levels³</u> BTBW (20%) [CAVI (5%)] HAWO – Deciduous (15%) MOWA (10%) RBNU – Interior wet (15%) RCKI (5%) SCTA (20%) STJA – Interior+Boreal (10%) SWTH – Coast (10%) WBNU – Deciduous (20%) WIWA (10%) WWCR (5%) YBSA (10%)</p>	<p><u>Positive high, negative low³</u> MOCH (45%) NOPA (35%) TUTI (30%)</p>	<p><u>Above proportional</u> BLWA BRRCR – Interior wet BTNW – Eastern BTYW CBCH GCKI – Winter GRJA – Conifer HETH [LEFL] RBNU – Interior dry REVI TEWA VATH – Interior+Boreal WIWR – Conifer [WOTH] YRWA</p>
<p><u>Proportional</u> BOCH BRRCR – Coast [CAWA] GCKI – Conifer OVEN – Eastern PISI – Coast, Deciduous PIWO RBGR – Mixedwood RBNU – Mixedwood RECR – Coast SWTH – Int+Boreal, Mixed WAVI – Deciduous</p>	<p><u>Sigmoidal⁴</u> [BHVI (40,50%)] BTNW – Mixedwood (30,75%) [HEWA (20,50%)] [MagWA (20,45%)] PSFL (25,50%) RBNU – Winter (5,20%) [RBNU – Coast (20,40%)] TOWA (5,15%) VATH (5,10%) WBNU – Conifer (20,45%)</p>	<p><u>Below proportional</u> AMRE – Mixedwood BRRCR – Interior dry, Deciduous, Winter GCKI – Deciduous OVEN – Mixedwood</p>

¹ Value is percent retention below which species' abundance is less than in uncut forest.

² Species in brackets have wide confidence intervals – other forms of the relationship are also plausible.

³ Value is percent retention below which species' abundance drops substantially below abundances in uncut forest.

⁴ Values are percent retention below which and above which species' abundance is near the lower and upper asymptotes, respectively, of the sigmoidal curve.

Examples of each of these types of relationships are provided in Figure 4.

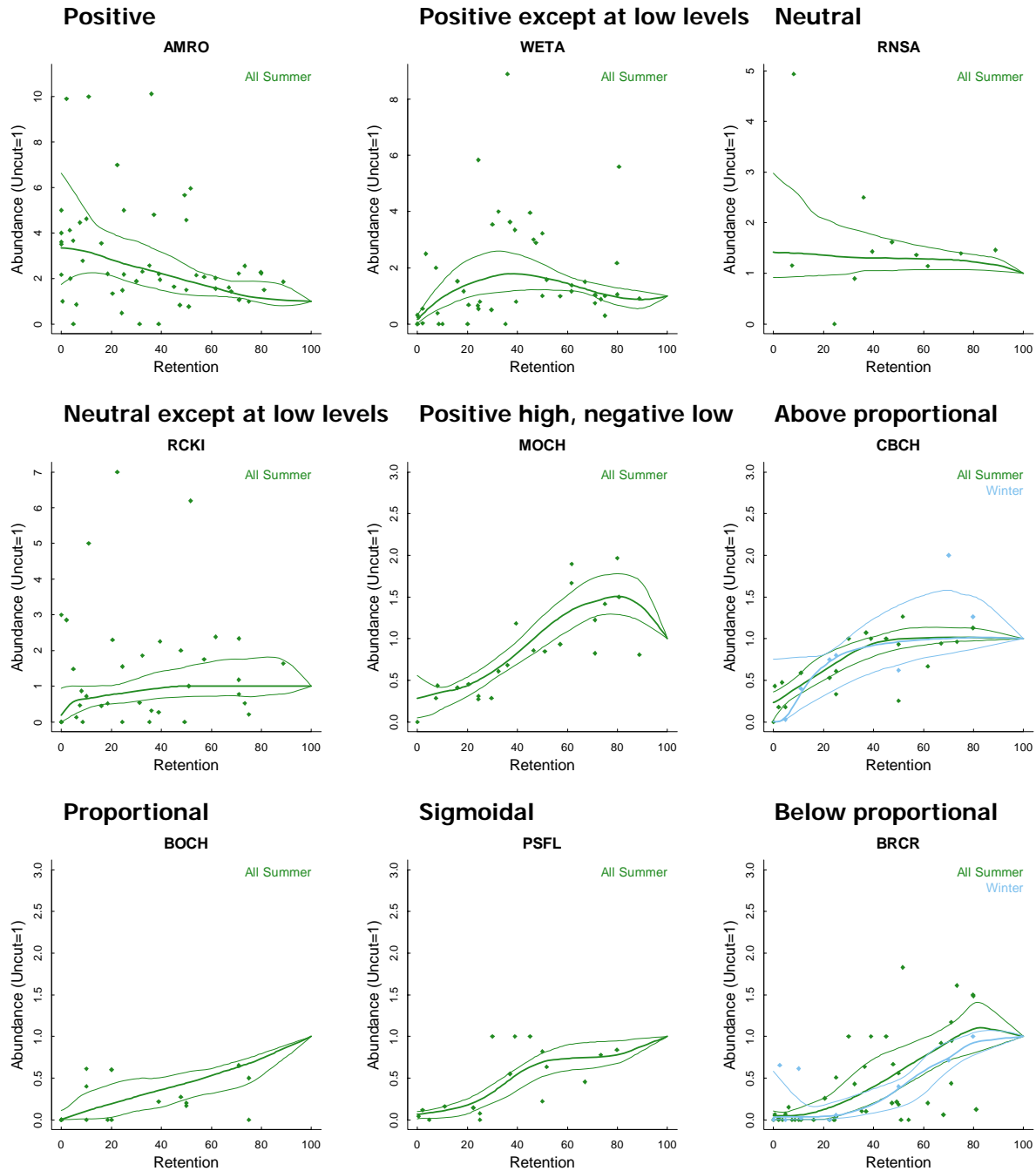


Figure 4. Examples of each form of relationship used in Table 4. Thin lines are 5% and 95% quantiles.

Composite species response

When the response curves from all 69 species are compiled, each standardized to an abundance of 1 in uncut forest, the total abundance of forest-dwelling birds reaches a maximum at approximately 50% retention (Figure 5a). This reflects the increases in a number of species that are more abundant at

low retention, and only modest decreases at higher retention levels for species sensitive to forest removal. Similarity with the “community” in uncut forest declines gently until retention levels drop below 12% (red line in Figure 5b), and then declines more rapidly at lower retention levels. Similarity also shows an initial rapid drop, as any harvesting modifies the community composition. [Note that the “community” here is a composite of all analyzed species, each standardized to the same abundance in uncut forest – a community that clearly would not exist in any actual location.] The wide confidence intervals on both graphs near 80% retention reflect the sparse data points at this retention level, and consequently the ability of flexible response curves to predict a wider range of abundance for any species.

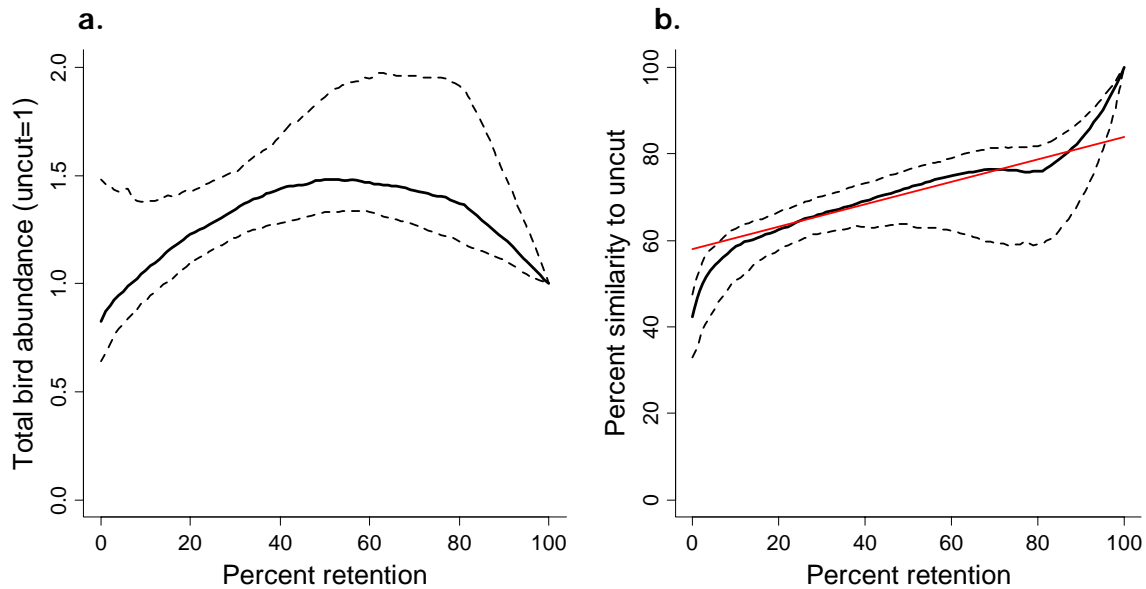


Figure 5. a) Total abundance of all 69 species, standardized to 1 in uncut forest, and b) percent similarity with uncut forest, across the range of retention levels. Dotted lines are 5% and 95% quantiles from bootstrap resamples. Red line in b) is linear fit to middle 75% of the retention range.

Interpretations of results

There are, of course, several issues to consider when interpreting his results. The studies reviewed here reported results from within about 10 years of harvesting. Longer-term responses of birds to retention levels should differ from these initial post-harvest results for several reasons. Since most reviewed studies included data from >1 year after harvest, abundances are not likely to be overly influenced by persistence of pre-harvest birds simply staying after their habitat was cut. More substantial changes in responses of forest-dwelling species should occur as harvested forests respond through growth of retained trees, regeneration of understory trees and eventual disease, death and decay of trees to produce old-forest structures that are often reduced in partially-harvested stands (Lindenmayer and Franklin 2002, Thompson et al. 2003). The rate of recovery of species in regenerating forests, and how this is affected by retention levels, are poorly documented but crucial for predicting the long-term abundances of species in partially-harvested stands. With little direct information, this question may have to be addressed through more difficult synthesis. Changes in birds’ abilities to use partially-harvested stands when there is less uncut forest in the landscape (Norton et al. 2000, Brotons et al. 2003). (Most studies he reviewed examined partial-cut stands in a context of stands of different ages and harvest histories, including uncut stands. We wouldn’t expect all species that are not negatively affected by harvesting to show the same response if all stands in a landscape were recently harvested to low

retention levels. However, that situation would also not be expected to occur in normal managed forests.) Other broad-scale effects like negative interactions with species that benefit from extensive harvesting could also change the landscape-level abundances.