Conserving biodiversity in managed forest landscapes: The use of critical thresholds for habitat

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ABSTRACT

In Canada, as in other large forested countries of the world, managers and scientists alike question what can happen to forest biodiversity under long-term industrial forest management. Recent studies may help us understand how species react when habitat is lost past a certain threshold in the landscape. In the case of population, a "critical threshold for habitat" does exist in forested habitat, which is defined by the minimal proportion of habitat needed to be preserved to avoid drastic population declines or massive species loss. In this paper, two types of thresholds are described, the first refers to population, and the second refers to the community of species. Many ecologists agree with the assumption that the specialist, sensitive species are the first to disappear (local extirpation for specialist species). For most species with large home range (such as birds), the threshold may generally be located between 30% and 40% of the habitat still remaining, compared to the proportion observed under a natural disturbance regime. We suggest, in order to protect the most sensitive species and to deal with uncertainty associated with thresholds, to maintain at least 40% of residual habitats. Although there is still much to understand concerning these thresholds, we nevertheless recommend their use for the diagnostic analysis that must be performed in the context of forest management planning and biodiversity conservation, as these thresholds could represent the minimal proportion of habitat to preserve integrity of the forest ecosystem. However, to be effective, the application of thresholds should be based on detailed knowledge of ecosystem characteristics and dynamics.

Key words: ecological threshold, forest management, forest ecosystem, habitat loss, older or late-seral forests, population, community, biodiversity, conservation

RÉSUMÉ

Au Canada, comme dans les autres grandes régions forestières mondiales, les gestionnaires et le public interrogent les scientifiques sur les effets à long terme du régime d'aménagement au regard du maintien de la biodiversité. Des études récentes ont montré que les risques d'extinction locale d'espèces peuvent s'accroître fortement lorsque la proportion d'habitat franchit un certain seuil, nommé « seuil critique d'habitat ». La notion de seuil critique d'habitat peut s'appliquer soit à une population d'une espèce donnée, soit à une communauté formée de plusieurs espèces. Dans le cas d'une population, ce seuil est défini comme la proportion minimale d'habitat qu'il faut conserver dans un paysage pour maintenir une population viable. Dans le cas des communautés, le seuil critique d'habitat correspond à la proportion minimale d'habitat en deçà de laquelle on assiste à une diminution importante du nombre d'espèces au sein de la communauté d'origine. La plupart des experts sont d'avis que les espèces spécialistes et sensibles sont les premières à disparaître. Bien que des efforts doivent encore être consentis pour l'identification des seuils au sein des différents écosystèmes forestiers, les résultats de plusieurs études convergent et permettent de conclure à la pertinence de leur utilisation dans un cadre de planification forestière et de maintien de la biodiversité. Les études montrent que le seuil critique d'habitat pour des espèces à grand domaine vital (tels que les oiseaux) peut se situer entre 30 % à 40 % de la proportion de l'habitat considéré (ex : vieilles forêts) observé sous un régime de perturbations naturelles. Nous suggérons, afin de protéger les espèces sensibles et d'embrasser l'incertitude associée aux seuils, de maintenir au moins 40 % des habitats résiduels. D'après le principe de précaution, nous suggérons de considérer ces seuils comme étant le minimum acceptable en deçà duquel il deviendrait difficile d'assurer la conservation de la biodiversité. Toutefois, pour être efficace, leur utilisation doit être combinée à de bonnes connaissances du fonctionnement des écosystèmes naturels.

Mots clés : seuil écologique, aménagement écosystémique, perte d'habitat, écosystème forestier, aménagement forestier, population, communauté, biodiversité, conservation.

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Introduction

Background

In Canada, as elsewhere in the world, managers and citizens look to scientists for answers regarding how forest management impacts biological diversity. According to the principles of ecosystem management, a prudent approach to conserve biodiversity is to maintain or restore the key ecological characteristics of a region so that they lie within their limits of natural variability using preindustrial forest conditions as the main reference (Landres *et al.* 1999, Gauthier *et al.* 2008). The term "preindustrial" refers to forests that evolved under natural disturbance dynamics before the influence of industrial logging (Boucher *et al.* 2009a). Historical ecology methods (e.g., historical maps and inventories, fire histories) allow the principal characteristics of past ecosystems to be reconstructed. The basis of ecosystem management is the premise that floral and faunal communities are adapted to a region's natural disturbance regime and will therefore be relatively tolerant to the effects of forest management if the forest management techniques reduce the differences between characteristics of the preindustrial forests and those that currently exist (Seymour and Hunter 1999, Gauthier *et al.* 2008).

The operational capacity to employ these strategies is not always obvious. For example, the forests of eastern Canada were once characterized by abundant old-growth forests that were the basis for the development of the logging industry for over a century (Etheridge *et al.* 2005; Bergeron *et al.* 2007; Boucher *et al.* 2009b,c). In contrast, in certain regions of New England, it is the reduction in areas containing the first stages of succession that is a concern for some animal species (DeGraaf and Yamasaki 2003, Lorimer and White 2003).

In these circumstances, the management challenge is to identify the thresholds over which the risk of species loss becomes unacceptable within the framework of sustainable forest management. Consequently, an important question asked by forest ecosystem managers is: what is the minimum proportion of different forest habitats that must be preserved at the landscape scale in order to avoid species loss? This leads to another question concerning management targets: should the targets correspond with the level of the threshold or should they be placed above in order to better prevent endangering the populations? Recently, several studies have addressed these questions and have attempted to evaluate the responses of animal species in ecosystems subjected to forest management. The conclusions of these studies suggest keeping a minimal proportion of diverse habitats in order to reduce the risk of local species extinction. This minimum proportion can be referred to as the extinction threshold, the landscape threshold, the population threshold, or the ecological threshold (Lande 1987; With and King 1999; Fahrig 2001, 2003; Flather and Bevers 2002; Betts *et al.* 2007; Betts and Villard 2009; Drapeau *et al.* 2009). However, we suggest the term "critical habitat threshold" to represent the minimum habitat required to be preserved. This critical level, which should be defined in terms of preindustrial forest characteristics (age structure and composition) (see Boucher *et al.* 2009c), and represents one of the key parameters that ought to be considered in the context of an ecosystem management approach that aims to maintain biological diversity. This article aims to better understand these thresholds that are applicable to all types of forest ecosystems despite variances in the processes that alter their habitats. However, we will focus on boreal and temperate forest ecosystems, as they represent the current debate concerning the management of forest resources in Canada.

The goal of this article is to review the concept of the critical habitat threshold for species with large home ranges (such as songbirds) and to consider the pertinence of its integration into forest management plans aiming to maintain biodiversity. Songbirds were used as an example in this study, as they represent a good indicator of animal population dynamics responding to forested ecosystem modifications (Carignan and Villard 2002, Drapeau *et al.* 2003). We also believe that songbirds could be efficiently used to monitor forest management objectives (CEF 2008, Betts and Villard 2009, Drapeau *et al.* 2009). With the help of several recent publications, we review the scientific basis of the threshold concept and its importance to conservation biology. The hypotheses and results of these research studies, observed from a practical standpoint, will illustrate the concept and allow suggestions to be formulated for its pragmatic use in helping to preserve biological diversity. This article does not aim to give an exhaustive review of thresholds, but instead to give the reader an understanding of their basis and application. Currently, there is still an important forest management debate concerning what is an "acceptable" level of harvest for the environment.

The solution to this debate should not be found in this article. Instead, with the information provided in this article in mind, thresholds should be regarded as a tool to determine the minimum proportion of habitat required at the landscape level to preserve the integrity of forest ecosystems.

Definitions

Habitat loss is recognized as the primary factor affecting the world's loss of biodiversity (Pimm *et al.* 1995). A reduction in habitat area leads to the irretrievable loss of individuals of one or several species restricted to these habitats (Fahrig 2003). Several types of responses exist for species affected by habitat loss. Some species gradually disappear following the loss of their habitat, while others disappear more abruptly. The latter, which are more sensitive to changes in their habitat, may have their population sizes drastically reduced or even disappear before the habitat is completely gone. The critical habitat threshold can therefore be defined as the minimum proportion of habitat at the landscape scale that must be preserved in order to maintain a viable population of these sensitive species (Fahrig 2003, Betts and Villard 2009). Once a threshold is crossed, there is a sharp and pronounced reduction in the population or in the case of communities, the number of species, which can go as far as extinctions on the local scale (Radford *et al.* 2005). It is important to note that the viability of the population is not based uniquely on presence–absence data. Data concerning the demographics of the species is required to determine if the population is viable. There are several factors underlying habitat loss that affect demographics including mortality rates (predation), birth rates (reproductive success) and recruitment (decreasing immigration or connectivity to a source population). These are the mechanisms that are altered once a threshold is passed and that explain the short- or long-term decline of the population. Several recent studies (Betts *et al.* 2006, 2007, Rompré *et al.* 2009) have shown that thresholds do indeed exist for species with large home ranges, which confirms predictions made using models (Lande 1987; Andrén 1994; Andrén *et al.* 1997; With and King 1999; Fahrig 2001, 2003). In forest environments, regardless of the type of forest, habitat loss is defined as a decrease in the area occupied by the forest type. This loss of habitat usually occurs over long periods and is generally accompanied by the isolation of residual patches (e.g., residual patches of older forest surrounded by regenerating stands). This isolation in vegetation type or aged stands can be considered as a form of fragmentation and is usually defined as forest fragmentation (Franklin *et al.* 2002). However, when forest patches are completely isolated from each other with non-habitat (such as agricultural land or water), this isolation is defined as habitat fragmentation (see Franklin *et al.* 2002). In this article we use the term "forest fragmentation" to define the isolation of residual patches (such as forest type), and the term "habitat fragmentation" to define changes in the land use type (e.g., the loss of forest habitat to agricultural development). In both cases, we believe that the changes will have long-term effects that may also affect species considered sensitive (Betts and Villard 2009). Finally, the area of residual habitat is defined as the proportion of habitat, fragmented or not, that is currently present in the landscape in comparison with its preindustrial extent.

The Foundations of the Critical Habitat Threshold Concept

The scientific literature describes two types of thresholds, the first refers to one or more species populations affected by habitat loss (Andrén 1994, With and King 1999, Fahrig 2003), while the second, more recently described, concerns the number of species (species richness) affected by a loss in habitat (Radford *et al.* 2005, Rompré *et al.* 2009).

The critical habitat threshold of populations

In the early 1990s, Andrén and collaborators (Andrén 1994, Andrén *et al.* 1997) were among the first to describe the threshold effect using an empirical data model (meta analysis of already published studies) describing the reaction of generalist and specialist species populations to changes brought to the landscape structure. The results suggested that the severe decline of certain species might be indicative of a threshold effect that compromises the viability of the populations in question. According to their model, the threshold was located between 20% and 40% of residual habitat. The authors suggested that species populations react differently to habitat loss depending on their degree of specialization to the habitat (Fig. 1). For example, a specialist species of a particular forest habitat will have a tendency to have its numbers decline more severely than a generalist species that is normally capable of adapting to the multiple conditions generated by habitat modification. Thus, species that are more sensitive to anthropogenic changes should have a higher critical habitat threshold (around 40%) than more generalist species (around 10%) (Betts *et al.* 2007, Betts and Villard 2009). It appears, however, that these models, established at the landscape scale, are more suitable for species with relatively large home ranges (in the order of several hectares), while those with smaller home ranges might obtain more complex responses (Homan *et al.* 2004).

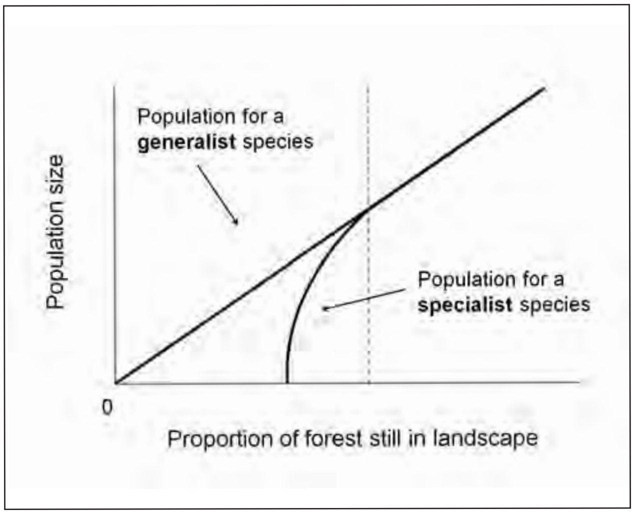

Fig. 1. Relationship between abundance of two populations and decrease in amount of forested habitat available, according to their ecological niche. The dotted vertical line represents the proportion of habitat at which the critical threshold occurs. Adapted with kind permission from Fig. 8 (Fahrig 2003) and Fig. 4 (Ranius and Fahrig 2006).

Over the last decade, Fahrig (2001, 2003), in a manner similar to Andrén *et al.* (1997), has documented the existence of thresholds. These authors (see also Andrén 1994), state that in addition to habitat loss, the degree of fragmentation can also affect species populations. Furthermore, other authors (Jansson and Angelstam 1999; Betts *et al.* 2006, 2007; Poulin *et al.* 2008) have empirically demonstrated that, beyond habitat loss alone, there appears to be a related phenomenon: the fragmentation of the residual habitat. The effect of forest fragmentation becomes important in regards to the extirpation of a population once a habitat occupies less than 30% of the landscape (Flather and Bevers 2002; see also Betts *et al.* 2007). The fragmentation of the residual habitat acts as a catalyst for the extirpation of populations; thus, below a certain threshold, both isolation and fragmentation add to the effects of net habitat loss and contribute to the rate of species loss. The degree of habitat fragmentation can be more important than simple net habitat loss in tropical areas that are rich with specialist and endemic species (Rompré *et al.* 2007). The specific needs in terms of ecological niches, the lack of connectivity between fragments (weak recruitment and increased predation), and the impossibility for certain species to adapt to a new environment are all reasons that have been cited to explain species loss (Stratford and Robinson 2005, Moore *et al.* 2008).

Threshold effects can be observed at various levels of habitat loss depending on the species and its capacity to adapt to changes in its habitat (Guénette and Villard 2005, Betts and Villard 2009). In this sense, the results published by Betts *et al.* (2007) concerning the abundance of certain bird species in managed forest areas in New Brunswick are revealing. For example, a species recently recognized as sensitive to forest fragmentation, the Ovenbird (*Seiurus aurocapilla*), possesses a threshold of around 33% residual habitat, while the Black-throated Blue Warbler (*Dendroica caerulescens*), a more common species and one that is considered less sensitive, possesses a threshold of around 10% (Betts *et al.* 2007). Similar results as those obtained for the Ovenbird were found for Bicknell's Thrush (*Catharus bicknelli*), a very sensitive species that nests only in the dense high-altitude balsam fir forests (>600 m ASL) of eastern North America. This species will be affected if the areas of dense balsam fir decrease and become more isolated following forest harvesting or other anthropogenic activities (Rimmer *et al.* 2001, Frey 2008). In the forests of western Québec, Drapeau *et al.* (2009) showed that Swainson's Thrush (*Catharus ustulatus*) critical habitat threshold was reached when the proportion of older forests (late-seral stages) dropped below 40%. Furthermore, this proportion of older forests corresponds approximately to the minimum abundance of older forest that previously occurred within the natural variability of the study area, which was estimated by an anthracological study (Cyr *et al.* 2009). As presented by Andrén *et al.* (1997), the critical habitat threshold corresponds to the increased risk of extinction that occurs with a certain level of habitat loss due to the cumulative effects of the fragmentation of the residual habitat. A species associated with native habitat, which forms a significant portion of the landscape and that subsequently becomes fragmented, can continue to exist within the new environment, but at lower population levels than had previously existed in the unfragmented environment. However, if the proportion of habitat decreases below the critical habitat threshold, there is an increased risk of population extinctions at the local level. This indicates that a species would have a greater chance of surviving in large areas of continuous habitat, but will become more at risk for extinction if there is a loss of habitat or if the habitat becomes fragmented. Thus, the proportion of habitat below which a population cannot maintain itself varies with (1) the species in question (Mönkkönen and Reunanen 1999, Guénette and Villard 2004, Saint-Laurent *et al.* 2009), (2) the degree of fragmentation of the original habitat (Rompré *et al.* 2007, 2009), and (3) the spatial configuration of the residual habitat (Drapeau *et al.* 2000; Fahrig 2003, Betts and Villard 2009).

Some studies have taken a deeper look at the intrinsic factors that lead to the critical habitat threshold. Indeed, a recent study (Poulin *et al.* 2008), describes the threshold from the habitat structure characteristics and the ecological requirements of a species, which go beyond the simple principles of habitat loss and fragmentation. Based on past research, the Brown Creeper (*Certhia americana*) is considered to be a species sensitive to the loss of old coniferous forests (see Drapeau *et al.* 2003). However, we know very little about the intrinsic factors, i.e., the Brown Creeper's ecological requirements, which cause this sensitivity. These authors showed that the decline of Brown Creepers at the landscape scale may be caused by a reduction in large-tree density (≥ 30 cm DBH) and of snags (≥ 10 cm DBH) following logging. Elsewhere, Ranius and Fahrig (2006) reached the same conclusion concerning the low abundance of deadwood on saprophytic species (species dependent on deadwood) in managed forests and the presence of threshold for these species. These studies, which focus on the attributes favourable for the persistence of sensitive-species populations, are important for understanding the critical-habitat threshold because they not only confirm, through empirical data, previously developed theoretical models, but also identify causal factors. In addition, these works can help identify sensitive species that can act as indicators of the proportion of older forest present at the landscape scale.

The critical habitat threshold for ecological communities

The approach based on ecological communities (species richness) may also prove to be relevant given the challenges presented by threshold variability as a function of the species being considered. According to this approach, the critical habitat threshold can be found not only at the level of a population, but also for the species richness found within an ecological community (Rompré 2007; Rompré *et al.* 2007, 2009). Few studies have been conducted in this area of ecology with most of the results coming from tropical environments where the loss of habitat and fragmentation are typically synonymous with species extinction (Pimm *et al.* 1995, Brooks *et al.* 1999). The complete habitat fragmentation (and not only forest fragmentation) of forests has an important effect, independent of a simple reduction of their area, on the distribution of forest bird species. Indeed, given the same quantity of habitat, the degree to which it is fragmented will influence the species richness. This phenomenon has not only been observed in the tropical forests of Panama (Rompré *et al.* 2007), and Australia (Radford *et al.* 2005), but also in the mixed boreal forest (Drapeau *et al.* 2000), and within urban

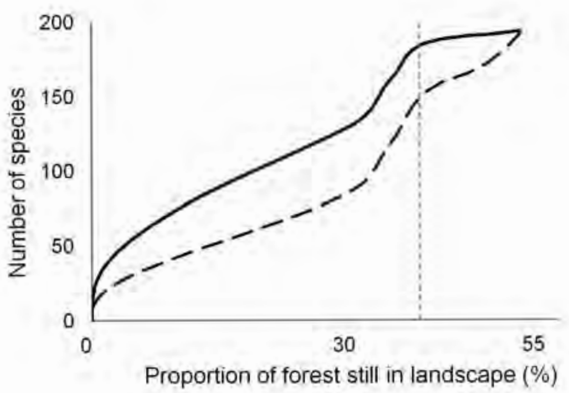

Fig. 2. Effect of forest habitat loss on forest bird species richness in Central Panama. Both curves represent two habitat loss scenarios, one is gradual (solid line curve; predictions calculated form environmental factors) while the other is accelerated (dotted line curve, predictions calculated from socio-economic factors) (see text for more details). In both cases we observe a drastic decline in forest bird species at around 40% of the historical forest cover of the Canal region of Central Panama. The dotted vertical line represents the proportion of habitat at which the critical threshold occurs. Modified from Rompré *et al.* (2009).

forests (Marzluff 2005). By using the species–area relationship (Rosenzweig 1995, Seabloom *et al.* 2002) to compare bird species communities within forest fragments in Panama, Rompré and collaborators recently published predictions calculated from empirical data representing the reduction in the number of species following a decrease in habitat area (Rompré *et al.* 2009). They predicted a massive loss of species following the loss of habitat to a level of residual habitats between 30% and 40% of their original area (Fig. 2; Rompré *et al.* 2009). These results were obtained from habitat loss scenarios derived from environmental and socioeconomic data in the study area (i.e., factors affecting the distribution of species as well as factors that caused habitat loss; see Rompré *et al.* 2007, 2008 for more details). A deep understanding of these factors and their actual effects on the current uses and conversions of forests in Panama allows these scenarios to be considered as "realistic" levels of habitat loss.

Implications of the Critical Habitat Threshold and Suggestions for Its Use within an Ecosystem Management Framework

Two types of thresholds have been described so far. Although each was measured using different methods, both thresholds were found to be between 10% and 40% residual habitat. Furthermore specialist species possess a threshold of between 30% and 40% of residual habitat. Because the threshold is a function of the degree of specialization for a given species and its consequent ability to tolerate habitat change, it is necessary to provide specific conservation measures taking into account specialist species (Huggett 2005). By setting a threshold above the 30% residual habitat level, based on the response of the majority of specialist species, both the specialist species and those in the same habitat that are less sensitive will be protected. However, we suggest a more cautious approach in conservation strategy to maintain at least 40% of the habitat in order to protect even more sensitive species. Furthermore, certain extremely sensitive species, possessing a very high threshold, may not be protected at these levels and therefore require special conservation measures using a fine-filter approach (Seymour and Hunter 1999, Huggett 2005). This may be the case for endangered or at risk species, such as Bicknell's Thrush (Rimmer *et al.* 2001).

Case Study: An Ecosystem Management Pilot Project in the Réserve Faunique Des Laurentides (RFL)

The discussion so far presented in this article was initiated within the framework of a pilot project implementing ecosystem management over the vast area (8 000 km^2) of the Réserve Faunique des Laurentides (RFL), and was conducted under the guidance of the Ministère des Ressources naturelles et de la Faune du Québec (Thiffault *et al.* 2007, see Fig. 3). The identification of the threshold associated with the proportion of older forests represents a particularly important question for the partners involved in the management of the area (Comité scientifique sur les enjeux de biodiversité 2007). An analysis of forest inventory maps from the start of the 20th century indicated that older forests comprised around 60% of the preindustrial forest matrix (Leblanc and Bélanger 2000). Following the scientific advisory report of Rompré and Bélanger (2008), the region's management targets were calculated using a critical habitat threshold of 33%, which corresponds to a third of the mean proportion of older forests present in the preindustrial landscape. The 33% threshold was selected by the land managers after considering both our study, the economic difficulties that would arise with a threshold of 40%, and the 2008 report filed by the Center for Forest Research (Centre d'Étude de la Forêt [CEF]) which proposed a minimum threshold of 30% (CEF 2008). The identification of the late-seral forest threshold allowed us to establish performance indicators for each of the land planning units within the RFL. Three levels of performance units were defined: (1) the "problematic" level with 0% to 20 % of the region occupied by older forests (one-third of 60 %), (2) the "acceptable" level with >30% older forests (one-half of 60%) and finally, (3) an intermediate "reasonable" level containing 20% to 30% of older forests. The entire management plan development process was validated by a scientific committee and endorsed by project partners (Table des partenaires 2009). Currently, there exists, on average, 25% of late-seral forests in the RFL. Research is currently underway to identify land planning units below the threshold and the appropriate restoration methods that should be applied to get them up to a more acceptable level.

Time Lapse between Crossing the Threshold and Species Disappearance

Once a threshold is crossed, the changes to the habitat may provoke a change in the state of equilibrium that makes these changes permanent (regime shift; Zhang *et al.* 2003, Folke *et al.* 2004, Radford *et al.* 2005). It is important to note that the phenomenon of local species extinctions is not observed immediately after crossing the threshold. Studies indicate that a delay of between 30 to 50 years may elapse before the

Fig. 3. Geographical location of the Réserve faunique des Laurentides (RFL) pilot project, positioned in the balsam fir–white birch bioclimatic domain of the boreal forest (Grondin and Leduc 2003), province of Québec, Canada.

disappearance of a species (Pimm *et al.* 1995, Brooks *et al.* 1999). In Québec, a forest may take between 70 to 250 years before reaching a late-seral stage (Kneeshaw and Gauthier 2003), which means that the process of species loss has already started before the forests begins to recover. A situation illustrating this mechanism is given by the vascular plants situated within the old balsam fir forests of the boreal zone (Desponts *et al.* 2002, 2004). In these forests, once the critical habitat threshold is passed, there is a high risk for a massive loss of species in the medium term, which may eventually lead to an alteration of the underlying ecological processes over the long term.

Conclusion

Although ecological thresholds are an interesting avenue for the management of forest ecosystems, we recognize that they can be difficult to determine due to the variable responses of species and communities to changes in their habitat and because these responses can occur over different spatial and temporal scales (Groffman *et al.* 2006). A management approach that combines thresholds to maintain managed landscapes within their limits of natural variability (Landres *et al.* 1999, Gauthier *et al.* 2008, Drapeau *et al.* 2009) would greatly help avoid the risk of creating environments too different from those in which populations and species are suited to prosper, which could compromise their survival within these landscapes. Based on the studies reviewed in this document, we suggest using a minimum critical habitat threshold of between 30% and 40%. The critical habitat threshold should not be considered to be the ultimate target of the forest manager. Managers should rather be cautious and try to avoid reaching this point and aim to maintain the proportions of habitat within their region's limits of natural variability over the long term (Landres *et al.* 1999, Lindenmayer and Luck 2005, Boucher *et al.* 2009a, Drapeau *et al.* 2009). To do this, we suggest maintaining at least 40% residual habitat in order to protect the most sensitive species and compensate for the uncertainties associated with thresholds. The current state of residual habitat will allow the identification of the areas that will likely be the most susceptible to problems and allow us to establish priorities concerning the restoration of forest ecosystems.

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