HABITAT LOSS AND FRAGMENTATION IN DYNAMIC LANDSCAPES: AVIAN PERSPECTIVES FROM THE BOREAL FOREST

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Abstract. Although habitat loss and fragmentation are widely regarded as major factors contributing to the decline of many populations, the relative importance of each phenomenon is seldom evaluated. Some researchers have questioned the generality of responses to habitat fragmentation, given variation in life history characteristics, the natural dynamics of systems, and land use patterns. Furthermore, a fundamental mismatch may exist between ecological theory, with its emphasis on the spatial configuration of habitats, and empirical observations of population response. Nevertheless, the paucity of quantitative land management guidelines often leads to inappropriate generalizations of conservation paradigms to regional issues. We reviewed the empirical evidence for true fragmentation effects in boreal bird communities in Fennoscandia and Canada, and concluded that most responses may be attributed to pure habitat loss in landscapes where forest harvesting is the dominant land use practice. In these dynamic landscapes, total forest cover may not change, and predicting patterns of species decline requires identification of the habitats and species of concern. We constructed simple empirical models of benchmark communities in boreal forests of Finland and Canada based on species composition, species abundance distribution, and habitat requirements, in order to identify features of bird species sensitive to the loss of older forests. These models require a solid understanding of the underlying structure of the community of interest, and predict species loss based on a random-sample hypothesis. Our results were consistent with observed patterns of bird population decline and species loss in these regions. This approach provides null models for comparison with habitat remnants in order to test for fragmentation effects, and a basis for more detailed exploration of population dynamics and persistence in these systems. The results of our review and analyses indicated that system- and species-specific considerations are important when assessing the potential outcome of habitat loss and fragmentation on regional biota. Indiscriminate application of conservation paradigms may lead to misguided research efforts and poor management guidelines.

Key words: boreal birds; boreal forest; Canada; dynamic landscapes; Finland; forest harvesting; habitat fragmentation; habitat loss; random sample hypothesis.

INTRODUCTION

Habitat loss and fragmentation are widely regarded as major factors contributing to the decline of forest bird populations (e.g., Rappole 1996). Although research has focused for more than three decades on the ecological effects of fragmentation, recently there has been considerable debate as to the relative influence of habitat loss and changes in spatial configuration on population trajectories in disturbed landscapes (e.g., With 1999, Fahrig 2002). As well, the context in which habitat loss and fragmentation occur is being considered more carefully (e.g., Haila 1999). A recent review by Harrison and Bruna (1999) indicated a lack of congruence between ecological theory and results from empirical studies of fragmentation. Theory emphasizes the role of dispersal, landscape connectivity, and spatial configuration of landscape elements for population persistence, whereas existing empirical evidence highlights the importance of habitat degradation (e.g., through physical and biological edge effects).

Destruction of natural habitats involves three factors, often acting in concert: (1) habitat loss, (2) area and edge effects, and (3) habitat isolation. The last two factors are termed habitat fragmentation (Andrén 1994, Fahrig 1997). It is important to distinguish between pure habitat loss and true fragmentation effects when assessing population responses, because resultant land management recommendations may differ. When habitat is lost from the landscape, individuals are also lost, resulting in population declines. Habitat loss also implies a corresponding increase in other landscape elements (e.g., Rolstad 1991), which may affect the dynamics in the remaining, original habitat. Fragmenta-
tion effects (decreases in patch size and increases in the amount of edge and in patch isolation) can compound the effects of pure habitat loss, producing an even greater population decline (Bender et al. 1998), which may result in population extinction even if suitable habitat still exists.

In highly modified forest systems, where forest lands have been converted for agricultural production or urban expansion, the identification of remnant natural habitats and associated edges is often much clearer than in similar forest systems managed for timber production. Forest conversion results in near static landscape configurations; in contrast, forestry practices result in dynamic landscapes that remain primarily forested, while undergoing spatial and temporal changes in composition and age structure. In this context, the sharpness of edges varies with forest regeneration and succession. Therefore, it seems reasonable to expect that biotic and abiotic responses to these human disturbances might differ among forest systems with varying landscape contexts. There is also considerable variation in the rates and types of natural disturbances within forest systems, which might influence the response of biota to human-mediated habitat change. Despite increasing recognition that naive application of conservation paradigms to regional land management issues is misguided, a paucity of quantitative guidelines can result in inappropriate generalizations. We use the application of fragmentation concepts in boreal forest research and management as a case in point.

The circumpolar boreal forest is one of the earth’s most extensive terrestrial systems. Historically, large-scale natural disturbances, such as fire and insect outbreaks, resulted in forests that were both spatially and temporally dynamic. Fire still acts as a major agent of disturbance in Canada and Russia, whereas intensive suppression has largely removed it from boreal forests in the Nordic countries. Although some conversion of boreal forest for agricultural production has occurred along the southern periphery of its distribution, much of the boreal forest is actively managed for timber production. Because they have a relatively short history of exploitation, the boreal forests of Russia and Canada contain almost half of the world’s intact pristine forest (Bryant et al. 1997).

Our objective is to evaluate the application of fragmentation paradigms, based largely on studies of temperate forests in agricultural mosaics, to managed boreal forests. We begin with a brief overview of broad-scale population trends and bird community structure in Fennoscandia and Canada. We then review the empirical evidence for fragmentation effects on boreal bird communities in these regions. Secondly, we present a null model approach for rapid assessment of the outcome of habitat loss and the existence of fragmentation effects in these dynamic landscapes. We use data from Finland and Canada to generate predictive models for bird population decline and species loss in boreal forests of these regions, based on the identification of common features of sensitive species. We conclude with some general guidelines for research and management in dynamic forested systems.

**Broad-scale Trends in Boreal Bird Populations**

Birds are the richest vertebrate taxon in boreal forests, comprising >75% of all terrestrial vertebrate species (Smith 1993, Mönkkönen and Viro 1997). However, this diversity fluctuates seasonally, as many bird species that breed in the north migrate to winter farther south. In Canada, long-distance migrants (species that winter in the tropics) comprise 50% of the breeding species, followed by short-distance migrants (species wintering in temperate areas) at 30%, and permanent residents at 20% (Erskine 1977). In Fennoscandia, short-distance migrant species dominate (45%), followed by long-distance migrants (30%) and permanent residents (Niemi et al. 1998). In both regions, resident species are disproportionately rare; migrants comprise ~90% of all breeding individuals.

There is a long history of monitoring bird populations in Fennoscandia, particularly in Finland. The oldest population estimates for birds date back to the early 20th century, and broad-scale population data exist since the 1940s. Finnish data indicate that more species have increased in abundance than have decreased with the conversion of relatively natural forest landscapes to intensively managed landscapes (Järvinen et al. 1977). The general trend between the 1940s and 1990s has been for many of the common species to become more numerous, while many of the rarer species have declined. In northern Finland, where the changes in landscape structure have been the most dramatic during the 20th century, data suggest 16 significant population decreases and 16 increases among forest birds since the 1940s (Haila and Järvinen 1990).

Helle and Järvinen (1986) concluded that a substantial proportion of the population changes of bird species in northern Finland could be traced to a change in the availability of preferred habitats. Although species preferring edges or early successional habitats have increased, species requiring old forest and avoiding edges have decreased with the extensive harvesting of northern Finnish boreal forests. Among declining species, certain life history traits are particularly pronounced (Imbeau et al. 2001). These include habitat-related traits, such as large area requirements, association with old-growth forests, and dependence on decaying wood for foraging, as well as nesting-related traits—cavity nesting, in particular. These traits were especially common among resident species, which are prominent among species that have declined. However, patterns observed at the scale of individual forest remnants are not always consistent with regional population trends in northern Finland (Väisänen et al. 1986). For ex-
ample, Virkkala (1991) found that population declines of birds in managed forests of northern Finland were not observed in virgin forest remnants. Although populations of Capercaillie (Tetrao urogallus), Three-toed Woodpecker (Picoides tridactylus), Siberian Tit (Parus cinctus), Siberian Jay (Perisoreus infaustus), and Pine Grosbeak (Pinicola enucleator) have declined overall in northern Finland, they have remained relatively stable in large blocks of virgin forest.

Comparable data for bird populations in boreal Canada are lacking. Breeding bird atlases have been conducted in some regions (e.g., Cadman et al. 1987, Semenchuk 1992), but these are one-time snapshots of general distributions. Some North American Breeding Bird Surveys (BBS) have been conducted in boreal forests (USGS Patuxent Wildlife Research Center 2000), but visitation has been erratic and, because they are roadside counts, they do not sample forest species well (F. K. A. Schmiegelow, unpublished data). In general, existing broad-scale coverage is sparse and is concentrated at the southern edge of the boreal region. As well, most ecological studies are relatively recent, localized, and/or short in duration.

A summary of the 70 BBS routes that fall within the Canadian boreal forest found that over the past 30 yr (1966–1996), five bird species had experienced significant population declines, while two had increased (Niemi et al. 1998). None of the declining species exhibit strong affinities for older forests (perhaps due to sampling bias), but all are long-distance (neotropical) migrants. Trends from the Ontario Forest Bird Monitoring Program (Welsh 1995) for the 1987–1997 time period show five species increasing significantly and three declining (in Niemi et al. 1998). Two of the declining species are short-distance migrants associated with older forest. In a recent review, Imbeau et al. (2001) suggest that in conifer forests of Quebec, the boreal species most sensitive to forest change are residents, most of which are cavity nesters reliant on older forests.

Despite a recent increase in avian research in Canadian boreal forests, documentation of broad-scale patterns in bird population trends for this region is seriously hampered by a paucity of data and lack of standardized sampling techniques. Generalizations are further confounded by geographic variation in forest cover types, natural disturbance histories, and associated bird communities. This is of significant concern, given the recent acceleration of harvesting throughout these forests.

**Evidence for Fragmentation Effects in Boreal Forests**

Our goal is to assess the empirical evidence for fragmentation effects, but most studies we reviewed did not clearly distinguish between the effects of fragmentation (changes in habitat configuration) and those due to habitat loss, nor were they designed to. McGarigal and Cushman (2002) provide guidelines on experimental approaches to address this problem. We attempt to separate these effects by classifying studies into those examining potential edge effects (biological and physical), area effects, and isolation effects. Within each category, we critically evaluate the interpretation of results with respect to the strength of the evidence for fragmentation per se, vs. patterns that might also be explained by habitat loss. We briefly review the potential effects of additional changes in species interactions that could result from modified abundance relations, due to either habitat loss or fragmentation.

**Biological edge effects**

**Nest predation.**—Recent compilations of data from temperate forests show a general increase in nest predation rates with decreases in forest cover (Robinson et al. 1995, Hartley and Hunter 1998), which could be attributed to either habitat loss or fragmentation. However, many temperate-zone studies have demonstrated increased predation on bird nests at forest edges (e.g., Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988). In the boreal forest, this edge effect appears to be more variable. A general pattern in boreal forests seems to be that increased nest predation occurs at forest–agricultural land edges (Andrén et al. 1985, Kuutinen and Helle 1988, Andrén 1995, Bayne and Hobson 1997, Hannon and Cotterill 1998). At forest–clearcut edges, however, an increase in nest predation is not evident in most cases (Andrén 1995, Hanksi et al. 1996, Huhta et al. 1996, 1998, Bayne and Hobson 1997, Song and Hannon 1999; but see Mönnkönen et al. 2000).

Disturbance by forest harvesting and by forest clearcutting for agriculture differ in their consequences for nesting birds in boreal landscapes. This has been attributed to larger changes that take place in nest predator communities with habitat loss due to agriculture rather than to forest harvesting, due to the introduction of novel habitat. Andrén (1992) showed that corvid densities are higher in agricultural landscapes, resulting in increased predation rates close to forest–farmland edges and in small forest fragments surrounded by agricultural land. Likewise, in boreal Canada, Hannon and Cotterill (1998) showed increased predation rates by corvids, but not by small mammals, at forest–farmland edges. Bayne and Hobson (1997) attributed higher rates of predation in agricultural vs. managed forest landscapes to a greater diversity of predators at edges and to higher densities of red squirrels (Tamiasciurus hudsonicus) in remnant forest patches of the agricultural landscape.

It is widely appreciated that the effects of predation on the breeding success of birds are dependent, among other things, on the landscape context and the predator community (Martin 1993, Andrén 1995, Bayne et al. 1997, Tewksbury et al. 1998). Angelstam (1986) and
Andrén (1992) suggested that the steepness in the productivity gradient between forests and the adjacent matrix is the main determinant of predation rates at edges. The sharper the gradient, the more pronounced the edge-related predation. Accordingly, nests in forest patches in agricultural landscapes suffer from higher predation rates because the matrix supports a high density and diversity of nest predators.

Although increased nest predation is often implicated in the decline of temperate forest bird populations (Whitcomb et al. 1981, Terborgh 1989), direct evidence is scanty. In boreal birds, the most convincing support for the role of increased nest predation in relation to population declines concerns forest grouse in Finland. Habitat change in Fennoscandian forest landscapes has increased the abundance of generalist predators (Kurki et al. 1998) and reduced the breeding success of ground-nesting forest grouse (Kurki et al. 1997). Simultaneous decline of all forest grouse species in Finland since the 1960s (Lindeén and Rajala 1981, Tornberg et al. 1999), despite different habitat associations (Swenson and Angelstam 1993), suggests a common reason. Increased predation seems the most plausible factor contributing to declines in these ground-nesting birds; however, these effects are exacerbated by habitat fragmentation only where forests have been converted for agriculture (Kurki et al. 2000). Nevertheless, while Kurki et al. (2000) conclude that increased forest fragmentation results in reduced breeding success of forest grouse, and is a probable cause of population declines, most of the variation in breeding success could be attributed to increasing percentages of agricultural land in southern areas, and a decreasing percentage of older forests due to forest harvesting in northern areas.

The general pattern in boreal forests is that forest harvesting does not usually lead to elevated nest predation rates at edges (Andrén 1995), but may result in an overall increase in nest predation rates in harvested landscapes (Kurki et al. 1997). Most nest predators in boreal landscapes are habitat generalists, which only secondarily feed on bird eggs and nestlings. Their spatial distribution and abundance varies according to the distribution and abundance of their main food. Nest predation appears to be linked to vole cycles or seed crops and to overall increases in small-mammal densities in harvested landscapes. For example, Cotterill and Hannon (1999) found significant temporal variation in predation rates in boreal forests of western Canada that had been recently harvested. Similarly, a three-year study in northern Finland revealed high between-year variation, as well as significant spatial variation in predation rates (E. Huhta, J. Jokimäki, M. Mönkkönen, and M. Korhonen, unpublished data). In this study, predation pressure varied as predicted by the alternative prey hypothesis (Angelstam et al. 1984, 1985), with highest rates in clear-cut areas during a vole peak year, and in forest habitats in vole crash years (see also Huhta 1996). Although increased predation may contribute to long-term bird population declines in northern boreal forests, as suggested for forest grouse in Finland, this may be explained by changes in available habitat due to forest harvesting, rather than to fragmentation effects per se.

Brood parasitism.—The Brown-headed Cowbird (Molothrus ater) is a brood parasite of many species of North American passerines, and has been implicated in the decline of migratory forest songbirds in temperate forests of eastern and central North America (e.g., Böhning-Gaese et al. 1993). Although there is some evidence that parasitism rates increase with decreasing forest cover and increasing fragmentation (Robinson et al. 1995), Hahn and Hatfield (1995) suggest that the proximity of agricultural infrastructures (fields, cattle, farms) can result in high parasitism rates in large forested areas, even when forest cover is high.

In a recent review of edge effects in western North American forests, Kremsater and Bunnell (1999) conclude that, even in agricultural settings, patterns of cowbird parasitism are not consistent, and that there is no evidence for elevated parasitism rates in managed forests of northwestern North America. Cowbirds are, in fact, very rare in these systems (Schieck et al. 1995a). Similarly, Schmiegelow and Hannon (1999) report that cowbirds are rare and parasitism rates very low in recently harvested North American boreal forest. Cowbirds are recent colonists in the boreal forest, having been associated with shortgrass prairies historically, and potential host species may exhibit few behavioral defense mechanisms to avoid parasitism (e.g., Hobson and Villard 1998). However, unless clearing of forests is associated with conversion for agriculture, cowbirds seem unlikely to reach high abundances in North American boreal forests.

The Cuckoo (Cuculus canorus), also a brood parasite, is a relatively common species in Fennoscandian forests (Väisänen et al. 1998), but there is no indication that parasitism rates vary with habitat loss or fragmentation. Cuckoos have been present in these forests for a long time. Thus it is likely that host species have evolved avoidance behaviors to reduce parasitism rates (Davies 2000). In fact, Brooke and Davies (1987) suggest that the Cuckoo’s reproductive success is limited by its ability to find and deceive suitable hosts. For example, von Haartman (1981) suggested that Finnish Cuckoo populations are tracking the annual fluctuations in populations of the Redstart (Phoenicurus phoenicurus), its main host, rather than causing them.

Physical edge effects

Forest harvesting has resulted in an increased amount of edges in boreal forest landscapes (Angelstam 1992), causing an increase in physical edge effects in remnant forests (e.g., Esseen 1994). Physical edge effects include such factors as the increased amount of
sunlight, wind, temperature variation, and other changes to microclimatic conditions (Matlack 1993, 1994, Chen et al. 1995). Esseen (1994) showed that changes in microclimatic conditions could result in an increased mortality of trees, ground herbs, and epiphytic lichens at edges. Indirectly, physical edge effects may have important consequences for forest birds. Increased amounts of forest edges in harvested landscapes may affect food availability. For example, in central Swedish boreal forests, the density of arboreal insects (the main food of many forest birds) was reduced in managed, selectively logged forests in comparison with unmanaged stands (Pettersson 1996, Pettersson et al. 1995). The reduction in arthropod densities was related to reduced arboreal lichen abundance in the managed stands. These studies were conducted in late winter, when invertebrate abundance is lowest and small differences may be critical to foraging birds. Although results from selectively harvested stands cannot be directly compared to forest edges, Esseen (1994) notes that arboreal lichens are particularly sensitive to physical edge effects; therefore, food availability may also be reduced for insectivorous birds in winter in edge-dominated landscapes.

In contrast, some studies have reported increased arthropod densities at forest edges in summer. For example, Jokimäki et al. (1998) collected arthropods in northern Finnish boreal forests and concluded that arthropod abundance decreased from forest edge to forest interior; larger forest patches (>5 ha) had lower abundance than smaller patches. The total number of arthropods was positively correlated with the density of the shrub layer, which in turn was denser at forest edges than in forest interiors. Likewise, Helle and Muona (1985) and Halme and Niemelä (1993) have shown that Coleoptera species were more abundant at forest edges than in forest interior habitats. In boreal forests of western Canada, Song (1998) found no difference in the biomass of flying insects between clearcut edges and interior forest, but increases in the biomass of ground-dwelling arthropods at edges. The contrasting result for flying insects may be explained by differences in forest type. Although most Fennoscandian studies have been conducted in conifer-dominated forests, Song’s (1998) study focused on deciduous-dominated forest. In this latter forest system, creation of edges by clear-cutting resulted in decreases in shrub cover at edges, due to the prolific suckering of trembling aspen, *Populus tremuloides*, and balsam poplar, *P. balsamifera*, (Harper 1999). In summary, food availability (arthropod densities) at edges may be reduced in winter, but possibly enhanced in summer, as a result of forest harvesting. If winter conditions are regulating populations of birds (for a review, see Newton 1994), net effects of forest landscape changes are likely to be negative, at least for boreal forest residents. Such negative effects could be attributed to habitat loss, fragmentation, or an interaction of the two.

**Bird densities at edges**

A logical question arising from the patterns in biological and physical edge effects is whether or not they affect habitat selection by birds. Villard (1998) concluded that area-sensitive bird species do not avoid edges in most forested areas of North America. One could, in fact, hypothesize that in some boreal forest landscapes, bird densities at forest–clearcut edges should be elevated because of increased food availability, without concomitant increases in nest predation or parasitism. This pattern should be particularly clear among migrant insectivores in coniferous forests. Bird densities were ~40% higher at forest edges than in forest interior habitats in a northern Finnish study (Helle 1983). All species clearly preferring edges were, as expected, insectivorous. Very few species clearly avoided edges; among them were both insectivores (e.g., Song Thrush, *Turdus philomelos*, and Pied Flycatcher, *Ficedula hypoleuca*) and seed eaters (cross-bills, *Loxia* spp., and Siskin, *Carduelis spinus*). However, Helle and Järvinen (1986) suggest that sedentary species of old forests (titmice, *Parus* spp., Tree Creeper, *Certhia familiaris*, and Siberian Jay, *Perisoreus infaustus*), as a group, clearly avoid edges. Nevertheless, Sklepkovych (1997) showed that nesting success in the Siberian Jay was negatively correlated with distance to edge, and indicated that jays may, in fact, gain foraging benefits from forest edges. In western Canada, Song (1998) found no evidence for increased densities of boreal birds at deciduous forest–clearcut edges.

**Species interactions**

If habitat loss and degradation result in modified community structure, ecological interactions may also be altered. As in the earlier example of the relationship between overall landscape productivity, increased primary prey of generalist predators, and their effects on breeding productivity of alternative prey, altered abundance relations could also affect the outcome of competitive or mutualistic interactions. Evidence of such indirect effects is limited, but several studies suggest that colonization of new habitat patches can be dependent on the presence of other individuals (Reed and Dobson 1993). Among forest birds, migrants selecting breeding sites often prefer settling close to conspecific (Svärdson 1949) or heterospecific individuals; residents in particular (Mönkkönen et al. 1999). Time constraints associated with a short breeding season and large year-to-year variation in environmental conditions, both characteristics of northern environments, presumably render these habitat selection tactics profitable (Mönkkönen et al. 1997). Consequently, absence of resident birds from remnant boreal forests could reduce the rate of colonization of these patches by other
species, such as migrants, resulting in an increased extinction probability in degraded landscapes.

Area effects

Although the magnitude of biological and physical edge effects on bird populations is related to the area of remnant habitats, additional area-related phenomena, such as the effects of decreased patch size on the occurrence of species with large home ranges, or density-related patch size effects, may also be important. In general, migrant species have a smaller average body size than resident species (Mönkkönen 1992). Body size is also correlated with other life history attributes, such as home range size (Southwood 1976, Peters 1983). Because larger species will generally require larger home ranges, resident species should exhibit the greatest area effects. Furthermore, because resident species may adjust their winter territory sizes to reflect food availability (e.g., Enoksson and Nilsson 1983), and some residents form single- or mixed-species flocks in winter, resident boreal birds may also require larger forested areas during nonbreeding periods (see Schmiegelow 1997). Both habitat loss and fragmentation could contribute to population declines as a result of area effects.

Area effects could be exacerbated by fragmentation at an individual level if patches were smaller than the area requirement of an individual, or at the population scale if persistence of local populations is related to patch size and isolation (Andrén 1994). However, this assumes a binary landscape of suitable and unsuitable habitat, and that individuals use only one habitat patch. In boreal forests of Fennoscandia, Capercaille (Tetrao urogallus), Northern Goshawk (Accipiter gentilis), and Black Woodpecker (Dryocopus martius) can compensate for reductions in preferred habitat by including multiple patches of older forest within larger territories (Wegge and Rolstad 1986, Rolstad 1989, Widén 1989, Tjernberg et al. 1993). Similarly, Bonar (2001) demonstrated that the Pileated Woodpecker (Dryocopus pileatus), an ecological equivalent to the Black Woodpecker, also includes multiple patches of preferred habitat within territories in managed boreal forests in western Canada.

In Andrén’s (1994) compilation of studies, no patch size (area-related changes in density) or isolation effects were found in studies from boreal forest landscapes (see also Mönkkönen and Reuman 1999). In a more recent study from northern Sweden, Edénius and Sjöberg (1997) report that small patches of forest (<5 ha) supported fewer species and large patches supported more than expected by sample size. However, at the species level, no patch size effects were evident. Bender et al. (1998) analyzed data for a variety of species and systems and found no evidence that patch size effects were related to landscape characteristics, including amount of habitat, median patch size, or scale of investigation. However, they report greater mean patch size effects for resident than for migrant species.

The only boreal sites included in their analyses were from Finland and Sweden, and no such patterns were apparent among migrant and resident birds from these areas (data extracted from Bender et al. 1998: Appendix C). Moreover, although there was considerable variability within each group, the mean patch size effect was negative for both, i.e., density was higher in smaller patches. Similarly, Connor et al. (2000) concluded from their meta-analysis of patch size effects for a variety of taxa and systems that birds generally exhibited moderately large to large, positive effects, and that relationships were stronger in temperate and boreal environments than in tropical environments. However, the mean relationship for boreal birds was, again, negative (Connor et al. 2000: Table 2).

Nevertheless, the patch size effects reported here for boreal sites should be interpreted cautiously, as we did not undertake a formal reanalysis of the data reported in either Bender et al. (1998) or Connor et al. (2000), and mean effect sizes within taxa mask individual species variability. Further, the sample size from boreal systems was low, included only Fennoscandian sites, did not distinguish between naturally isolated (island and wetland) habitat patches and those isolated due to human activities, and failed to consider landscape context.

Isolation effects

Although most fragmentation-related theory emphasizes the role of habitat isolation and dispersal capabilities on population persistence in remnant habitats (e.g., MacArthur and Wilson 1967, Levins 1969), empirical tests of the importance of these attributes in real landscapes are few. Debate continues to rage over the efficacy of corridors as a conservation tool in alleviating the effects of habitat fragmentation (for a review, see Simberloff et al. 1992). However, corridor presence is often correlated with other habitat or landscape variables (e.g., patch size and landscape context), thereby confounding assessments (Beier and Noss 1998).

In an experimental study of recently harvested boreal forest in western Canada, Machtans et al. (1996) reported elevated use of riparian forest corridors by juvenile birds immediately following harvest of the adjacent forest stands. However, a longer term study of one of these corridors showed that use diminished rapidly over time, as adjacent harvested areas regenerated (Robichaud et al., in press). Several studies in boreal forests of eastern Canada have demonstrated that bird movements across forest gaps are significantly reduced relative to movement rates through forest, both in summer (Desrochers and Hannon 1997) and winter (St. Clair et al. 1998). Nevertheless, in a recent analysis of the persistence of bird species in remnant patches of older forest, Hannon and Schmiegelow (in press) found...
that habitat affinity was a better predictor of abundance response to fragmentation by forest harvesting than gap-crossing behavior (a surrogate of dispersal ability). Old-forest specialists were most sensitive to fragmentation resulting from habitat loss, and corridors did little to alleviate these effects. Similarly, Andrén (1994) found no evidence of isolation effects in studies from boreal forest landscapes.

Mönkkönen et al. (2000) found that species number and abundance of resident old-forest species in northern Finnish forest reserves declined with distance from continuous forests in Russian Karelia. This may indicate that isolation from the extensive source areas in the east has a negative impact on resident forest birds. However, the contribution of the landscape structure around the reserves was not properly accounted for: the observed patterns may also result from habitat loss, as there is a gradient from east to west in northern Finland along which the proportion of old forest in the landscape decreases.

Habitat Loss in Dynamic Landscapes

In boreal landscapes where forest harvesting is the dominant land use, population trajectories of birds appear to be more strongly related to habitat loss and degradation, and their affects on species abundances and interactions, than to fragmentation sensu strictu. Here, we aim to derive null expectations about the relative effects of habitat loss and fragmentation, based largely on the structure of the underlying community. In the absence of fragmentation effects, our hypothesis is that species loss, due to overall habitat loss, should be predicted by the regional species abundance distribution (after Preston 1948). Reduction of particular habitat types, in conjunction with habitat specialization, results in the loss of rarer species by chance alone. If additional factors compound habitat loss, then species loss should be more rapid than predicted. This model is consistent with the random-sample hypothesis (Connor and McCoy 1979, Haila 1983). We use this approach to establish benchmark communities and identify common features of boreal bird species sensitive to loss of a specific habitat type.

In managed forest landscapes, quantification of habitat loss and degradation requires more explicit consideration of habitats of concern. In many cases, total forest cover may remain constant, while the age structure and relative proportions of different habitat types change dramatically, resulting in habitat degradation for some species. In boreal forests, two habitat types are becoming increasingly scarce: old forest, particularly in large tracts (e.g., Niemelä 1999), and early-successional, post-burn stands (e.g., Murphy and Lehnhäusen 1998, Kouki et al. 2001). Here, we focus on the potential implications of loss of older, pristine forest (>80 yr old) for boreal birds. We use 80 yr as our threshold, as most commercial forest types are merchantable at this age, and are harvested, unless provisions for protection exist.

Methods

We generated bird species abundance models for older forests using long-term census data from reference areas in Oulanka National Park, Finland (1977–1997) and Alberta, Canada (1993–1999). Oulanka National Park (267 km²) is located in northern Finland at the Finnish–Russian border (66° N, 29° E). Oulanka is a forested peninsula in a harvested landscape, stretching west from the continuous forests in Russia (Russian green belt). It is one of the few remaining reference areas of pristine forest bird assemblages in Finland, due to extensive harvesting elsewhere during the past 50 yr. The dominant tree species are Scotch pine (Pinus sylvestris) and Norway spruce (Picea abies), with birch (Betula spp.), aspen (Populus tremula), and goat willow (Salix caprea) present in mixed stands. The Canadian site is located in northeastern Alberta, in boreal mixed-wood forest near Calling Lake (55° N, 113° W). Boreal forests in western Canada have only recently been allocated for timber harvest, and thus exist in a relatively pristine state. The Calling Lake reference area remains contiguous with adjacent tracts of older forest; a portion acts as a control for an experimental fragmentation study (Schmiegelow and Hannon 1993, Schmiegelow et al. 1997). This forest is dominated by trembling aspen (Populus tremuloides), white spruce (Picea glauca), and balsam poplar (Populus balsamifera), with lesser amounts of white birch (Betula papyrifera) and balsam fir (Abies balsamea).

Finnish bird data were derived from line-transect surveys, whereas point counts were used in the Canadian surveys. We included all forest passerine, woodpecker, and grouse species known to breed in these areas in our community descriptions. We used aggregated data from all years to represent the regional species pool and to construct cumulative species abundance distributions. We used detection frequencies of species in different habitat types (from additional, unpublished data sets) to identify species clearly favoring forests >80 yr old (after Raivio and Haila 1990). Where possible, we validated our classifications against published accounts (Helle 1985, Raivio and Haila 1990, Schieck et al. 1995b, Jokimäki and Huhta 1996, Kirk et al. 1996). Species identified as mature-forest specialists were found primarily in older forest, and were detected at very low frequencies in silvicultural mosaics, whereas old-forest specialists were never observed in the mosaics. These are consistent with two of the five groups identified by Raivio and Haila (1990), but are combined in all analyses that we report.

We created rank abundance plots (e.g., May 1975) from repeated, random subsamples (n = 10 and n = 100) to assess the distribution of mature- and old-forest specialists in the resultant communities. Species-spe-
Resident species, such as the Boreal Chickadee and the Three-toed Woodpecker, are threatened by the loss of older boreal forests, due to habitat specialization and rarity. Photographs by Chris Fisher, Curtis Stambaugh, and Fiona Schmiegelow.

Specific probabilities of absence were then compared between old-forest specialist and generalist species, and between resident and migrant species, using Mann-Whitney \( U \) tests. Finally, we used rarefaction (e.g., Hurlbert 1971, James and Rathbun 1981) to estimate the expected number of species (all and mature-old forest specialists only) in samples of varying size (see Plate 1). The resultant species accumulation curves represent null models to which species lists from remnant habitats can be compared.

**RESULTS**

**Bird communities of older boreal forest**

The bird species abundance models for old forests in Finland and Canada fit a lognormal distribution (\( P = 0.200 \) for both areas). There was no evidence of truncation of the curve for either system, indicating that our data provide good representations of the true distributions. Bird species richness and mean annual abundance were higher in the Canadian reference area than in Finland (Table 1), and the percentage of species identified as old-forest specialists differed markedly between the systems.

Rank abundance plots (Fig. 1) illustrate distributions of the old-forest specialists within the larger bird communities. A notable pattern in the Finnish data is the extreme dominance of two species: the Brambling, *Fringilla montifringilla*, and Willow Warbler, *Phylloscopus trochilus* (for a discussion, see Greenberg et al. 1999). Most of the Finnish old-forest specialists are moderately rare to rare, whereas the Canadian specialists are relatively evenly distributed among abundance ranks. However, despite the very different richness and distribution of this group in the two systems, their density relative to the larger community was remarkably consistent (Finland 31%, Canada 30%). Resident species in Finland, although a richer component of the community than in Canada, tend to be rarer. Nevertheless, in both systems, resident species are overrepresented among old-forest specialists, relative to their richness in the larger community (Table 1).

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Finland</th>
<th>Canada</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species</td>
<td>48</td>
<td>61</td>
</tr>
<tr>
<td>Mean annual breeding density (no. pairs/km²)</td>
<td>100–120</td>
<td>400–550</td>
</tr>
<tr>
<td>Number (and %) of old-forest specialist species</td>
<td>27 (56)</td>
<td>19 (31)</td>
</tr>
<tr>
<td>Density of old-forest specialists (no. pairs/km²)</td>
<td>30–40</td>
<td>120–170</td>
</tr>
<tr>
<td>Number (and %) of resident species</td>
<td>17 (35)</td>
<td>14 (23)</td>
</tr>
<tr>
<td>Number (and %) resident of old-forest specialist species</td>
<td>14 (52)</td>
<td>8 (42)</td>
</tr>
</tbody>
</table>
Fig. 1. Rank abundance plots for boreal birds in forests more than 80 yr of age in (a) Finland and (b) Canada. Species are ranked from most to least common. The top curve in each panel represents the full data set from each reference area. The number of pairs is an aggregate count over multiple sample years for all species in the total sample ($N$). Triangles represent old/mature forest specialists, and circles represent other species. Open symbols indicate resident species, and solid symbols indicate migrants.
Species loss from random samples

We expected subsamples from the larger distribution to exhibit ve line (e.g., Preston 1948), inferred from the shape and truncation of the lower curves in each rank plot (Fig. 1). Moderately rare to rare species are better represented with increasing sample size. Old-forest specialists were missing more often than non-specialists in sample sizes of 10 and 100 from Finland ($P = 0.019$ and $0.009$, respectively), but not from equivalent-sized samples from Canada ($P = 0.54$ and 0.71, respectively). Resident species in both boreal areas generally had a higher probability than migrants of being absent in random samples of 10 and 100 individuals drawn from a pool representing the larger community ($P = 0.017$ and 0.021, Finland; $P = 0.045$ and 0.014, Canada).

Asymptotic values for inclusion of old-forest specialists are reached at different sample sizes in Finland and Canada (Fig. 2) because of differing abundance distributions and ranks of old-forest species. The 90th percentiles for old-forest specialists occur at total sample sizes (i.e., samples including all species in the regional pool) of ~2000 pairs in Finland and 1100 pairs in Canada. These represent null models for species loss, in the absence of significant fragmentation effects. Below these asymptotic values, species loss in conjunction with habitat loss is predicted to occur due to sampling effects alone.

Discussion

In forested landscapes where timber harvesting is the dominant land use practice, forest cover cannot be considered equivalent to habitat amount for specialist species (i.e., a binary classification of landscapes is not appropriate). Predicting the outcome of habitat deg-

radation requires identification of habitat types and species of concern. Using long-term bird census data from boreal forests in Finland and Canada, we demonstrated how simple species abundance models can be used to identify vulnerable species and test hypotheses about habitat loss and fragmentation.

Predicting species loss from older boreal forests

Old-forest specialists account for almost one-third of all birds breeding in older boreal forests in both Finland and Canada. Although the richness and ranked abundances of members of this group varied between regions, we were able to identify some common features of sensitive species. Among the boreal bird species that specialize on older forests, residents should exhibit the greatest sensitivity to habitat loss, due to their lower abundance. This rarity falls in one of the 12 categories in the three-way classification scheme of Rabinowitz et al. (1986): boreal residents generally have a broad geographic distribution (several are circumpolar), demonstrate habitat specificity, and are supported as relatively small populations wherever they are found. Populations of resident species in the northern boreal forest are regulated by winter conditions (e.g., Lahti et al. 1998). Although this may also be true for residents in other systems (e.g., Newton 1994), low food availability and severe winter weather result in lower population sizes in the northern boreal zone than elsewhere (Forsman 2000). For example, in the United States and Britain, resident species are typically more than twice as abundant as migrants (O’Connor 1981, 1992). Residents in other systems also have broader taxonomic representation and evolutionary histories than do boreal residents, many of which have behavioral, morphological, and physiological adaptations for winter conditions (e.g., food-caching, specialized plumage, and regulated hypothermia). Additionally, many boreal residents are reliant on older forests because of nesting (availability of suitable trees for cavities) and foraging (dead or decaying wood) requirements (Imbeau et al. 2001).

The migrant old-forest specialists in both Finland and Canada are not so easily compartmentalized. Some species are relatively abundant, whereas others exhibit characteristics of several of the rarity categories of Rabinowitz et al. (1986). As a group, they are not consistent in either their nesting or foraging requirements on the breeding grounds (e.g., Schieck et al. 1995b, Kirk et al. 1996, Väisänen et al. 1998). However, many of the migrant species specializing on older, boreal forests have similar breeding and wintering habitats (i.e., they depend on forested habitats year-round), which may make them particularly vulnerable to habitat loss and fragmentation, due to a lack of behavioral plasticity.

A null model for assessing species loss

In both Finnish and Canadian boreal forests, our analyses indicate that species gain over small areas will
be rapid because of the relatively even species distributions represented in small samples. This is a general characteristic of communities characterized by log-series or lognormal distributions: the slope of the species–area relationship will be steepest when calculated over small areas. Very steep slopes for species–area curves have been reported from boreal forests in Sweden (Boström and Nilsson 1983) and Canada (Schmiegelow et al. 1997). However, apparent increases in diversity with area were spurious, resulting simply from larger sample sizes (Rosenzweig 1995, Schmiegelow et al. 1997). Such results highlight the danger of drawing erroneous conclusions about fragmentation. Although steep species–area slopes have been associated with insular systems (e.g., MacArthur and Wilson 1967), the shape of the species–area curve is a function of the underlying species abundance distribution, and thus is sensitive to sample size. This suggests a scale dependency that may also apply to density-related patch-size effects. In either case, patterns from habitat remnants must be compared to equivalent-sized areas from contiguous reference areas before any conclusions about fragmentation can be drawn.

We generated bird species accumulation curves for older boreal forests using rarefaction, in order to construct null models to which species lists from remnant habitats can be compared. Similar to approaches aimed at identifying thresholds in the population persistence of individual species (e.g., Wither and Crist 1995, Fahrig 1998), identifying the inflection point in species accumulation curves for communities of concern could provide useful conservation guidelines. For example, given known densities of breeding birds in reference areas, one could extrapolate from sample sizes required for representation of old-forest species to estimate the habitat threshold below which species loss is predicted to occur due to sampling effects alone. Such threshold estimates do not represent the minimum area required for regional population persistence; reserve sizes necessary to support self-sustaining populations would undoubtedly be several magnitudes larger (e.g., Preston 1962). However, they do provide a benchmark against which to assess the effects of habitat fragmentation on species occurrence. This approach provides for more efficient allocation of research efforts and management actions through identification of the conditions under which the spatial configuration of habitats really matters (sensu Fahrig 1998). Where potential fragmentation effects are identified, mechanistic studies may be required to assess the cause of population declines. Otherwise, conservation and management interests would be better served by greater intellectual investment in determining the area requirements of communities of concern.

CONCLUSIONS

In the research–management interface, ecologists are often challenged to provide guidelines in the absence of complete understanding. We demonstrated that, for boreal birds, application of conservation paradigms from other systems do not provide a very useful framework for projecting the outcome of habitat loss and fragmentation in forested boreal landscapes managed primarily for timber production. Natural dynamics, land use patterns, and management issues differ between systems, and so too will responses (see also Haila 2002). Further, there is likely to be both inter- and intrataxal variation in response within systems, due to differing life history characteristics (e.g., Schmiegelow and Nudds 1987, Hansen and Urban 1992, Mönkkönen et al. 1992, Mönkkönen 1994, Mönkkönen and Welsh 1994).

In dynamic landscapes, such as those managed for forestry, habitat loss is specific to habitat types and fragmentation effects may not be readily apparent because of the transient nature of the matrix. Forest lands are not permanently converted for other land uses; rather, they undergo continuous state changes from harvest through succession. The vulnerable components of the forest are those with high initial conversion value, such as pristine older forests, or those with diminishing commercial return, or lost opportunity costs; again, these are older forests and habitats created by large, natural disturbances, such as postfire, early-successional forests. In these cases, a random-sample hypothesis (e.g., Connor and McCoy 1979, Haila 1983) may adequately predict the outcome of selective habitat loss, but identification of the elements of concern is crucial. Sample effects alone may be sufficient to cause regional population declines and a loss of sensitive species, highlighting the importance of quantifying the effects of habitat loss (e.g., Fahrig 1997).

We focused on boreal bird communities in Finland and Canada and constructed simple empirical models for projecting patterns of species loss with reductions in the area of older forest. Our predictions were generally consistent with observed patterns of population decline and species loss from these areas. These null models provide a basis for comparison with habitat remnants, and for more detailed exploration of population dynamics and species persistence in these systems. Nevertheless, we do not advocate widespread application of the particular null models presented here: that would contradict the very premise of our arguments. Whereas Harrison and Bruna (1999) highlight the mismatch between ecological theory and empirical studies of fragmentation, we lament the indiscriminate generalization of empirical observations. However, we do encourage a revival of one of the fundamental concepts of insular ecology and foundations of sampling design, namely, a firm understanding of the underlying structure of the community of interest. In some cases, exploration of species abundance distributions may provide the most parsimonious explanation for the effects of habitat loss and a useful conduit for communicating potential ecological responses to land man-
agers. Detailing the composition and structure of benchmark communities in reference sites is therefore critical to facilitate the rapid assessment of assemblages from comparative sites (e.g., Colwell and Codding-ton 1994). In this manner, the relative influence of habitat loss and fragmentation on species occurrence may be discriminated and research and management priorities may be established.

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LITERATURE CITED


