

Bird Responses to Forest Fragmentation

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INTRODUCTION

In the 1970s, studies in the agriculturally-dominated landscapes of the eastern United States documented a surprising trend. Seemingly suitable forest stands that were small in area were devoid of several species of birds that typically occur in such habitats (Lynch and Whitcomb 1978, Whitcomb et al. 1981). Similar trends were soon discovered in Europe, Australia, and elsewhere (Terborgh 1989, Saunders et al. 1991). The ecological changes associated with habitat fragmentation are now well known and many conservation plans are designed to minimize fragmentation (Thomas et al. 1990, Suring et al. 1993). However, it is important to ask how well the lessons learned about forest fragmentation in heavily forested biomes apply to the Rocky Mountains, where relatively open forests are naturally interspersed with grasslands and shrublands. We address this question for birds in the Southern Rocky Mountains.

In contrast to the Eastern Deciduous Forest, habitats of the Rockies have been patchy and variable throughout pre-European settlement times due to interactions of abiotic gradients and disturbance (D. H. Knight, *this volume*; Veblen, *this volume*). Interactions among climate, soils, topography, and disturbance cause grasslands, coniferous forests, and deciduous forests to interdigitate to extents that vary dramatically with local topographic setting and disturbance history. This "natural fragmentation" may have selected for species that are relatively tolerant to the patch sizes, edge types, and isolation effects that have resulted in species extinctions in other ecosystems (Buskirk et al., *this volume*).

We are no longer in pre-European settlement times, however. Modern human land use has dramatically altered vegetation patterns across much of the Rockies. While logging has further fragmented habitats in some locations, livestock grazing and fire exclusion have resulted in a pronounced expansion of closed-canopy coniferous forest elsewhere (Arno 1980, Gruell et al. 1982). In more productive valley bottoms, agriculture and rural residential development have altered habitats, landscape connectivity, and biotic processes like predation (Theobald, *this volume*; Hansen and Rotella, 1999).

The relative effects of these different human-driven trajectories of landscape change on native species are poorly understood in the Southern Rocky Mountains. Certainly, understanding will not be gained by only considering a simple story of the forest being fragmented and replaced by expanding agriculture. Rather, in the Rockies we should examine interactions among species life histories, abiotic factors, natural disturbance, and human land use.

We explore the influence of these changes in landscape patterns on Southern Rocky Mountains birds in the context of two hypotheses. Hansen and Urban (1992) and Hansen et al. (1992) suggested that the effects of habitat fragmentation on biodiversity reflect: (1) the life history attributes of the species in the community, and (2) the specific trajectory of landscape change. In this chapter, we first compare the life history attributes of birds in the Southern Rocky Mountains to those in other biomes to evaluate their likely sensitivities to landscape change. We then describe three common trajectories of landscape change in the Southern Rockies and review current knowledge of bird responses to these landscape trajectories. Finally, we draw conclusions for management and future research. As we shall see, forest fragmentation by logging is only one of the challenges that landscape managers will face in the Southern Rocky Mountains.

LIFE HISTORY ATTRIBUTES

Life history attributes (LHA) such as migratory strategy, reproductive potential, and home range size set constraints on the types and spatial and temporal scales of resources that organisms can exploit. Examples of bird species that are sensitive to forest fragmentation in eastern forests include neotropical migrants with low reproductive potential that have nest types that are vulnerable to nest predators and brood parasites (Whitcomb et al. 1981). Hansen and Urban (1992) hypothesized that communities from different geographical locations have different suites of LHA and that these differences will cause commu-

nities to respond differently to landscape change. In comparing the LHA of birds in the Pacific Northwest (PNW) to those in the EDF, Hansen and Urban found that no species in the Pacific Northwest had the set of traits that characterized the group of birds most sensitive to forest fragmentation in the Eastern deciduous forest. They concluded the Pacific Northwest bird community was likely to be less sensitive to forest fragmentation than the Eastern deciduous forest community.

What LHAs characterize birds in the Southern Rockies? Based on pre-European settlement landscape dynamics in the Rockies, we predict that Southern Rocky Mountains bird communities have the following traits (presented relative to traits of Eastern deciduous forest birds):

1. Relatively more species dependent upon structurally complex, open-canopy habitats because of the high disturbance frequency here.
2. Relatively fewer closed-canopy forest associates because of abundance of nonforest and open forest habitats.
3. Relatively fewer conifer edge or interior specialists because the gradient from early-seral to late-seral habitats is less extreme here.

The rationale for the first two predictions is that many species in a community are adapted to the most common habitat types. Disturbances such as wildfire and abiotic constraints resulted in structurally complex, open-canopy habitats being common across the Rockies in pre-European settlement times, while closed canopy conifer forests were likely less common (Veblen, *this volume*).

The logic behind the third prediction is based on what we term the Biomass Accumulation Hypothesis (Fig. 10.1). According to this hypothesis, species will more finely partition resources from forest edge to forest interior when there is high contrast in biomass accumulation along the gradient. In the Pacific Northwest, for example, the equitable environment allows mature and old-growth forests to have relatively high net primary productivity and accumulate very high levels of vegetative biomass relative to early successional forests. Vegetation abundance strongly influences microclimate, ecological processes, and distribution of organisms (e.g., Franklin and Forman 1987). Further, while moving between early-successional and mid-to-late successional patches, wind speed and light levels are reduced while soil moisture increases (Chen et al. 1995). These changes in microclimate influence decomposition rates (Klein 1989) and the structure and composition of understory vegetation (Ranney et al. 1981). Even biotic interactions like predation vary with vegetation structure (Martin 1993). The

result is a steep gradient in resources and conditions from forest edge to forest interior. This steep gradient should allow for resource specialization and niche partitioning, such that some species specialize on either edge or interior habitats. In the Southern Rocky Mountains, in contrast, abiotic factors constrain net primary productivity and biomass accumulation to lower levels and mid-to-late seral forests often have relatively open canopies. Consequently, we expect less of a difference in vegetation structure, microclimate, and ecological processes between forest edge and interior. Hence, we predict that fewer species in the Southern Rocky Mountains will specialize on either forest edges or interiors. As forest fragmentation benefits edge specialists and hinders

BIOMASS ACCUMULATION HYPOTHESIS

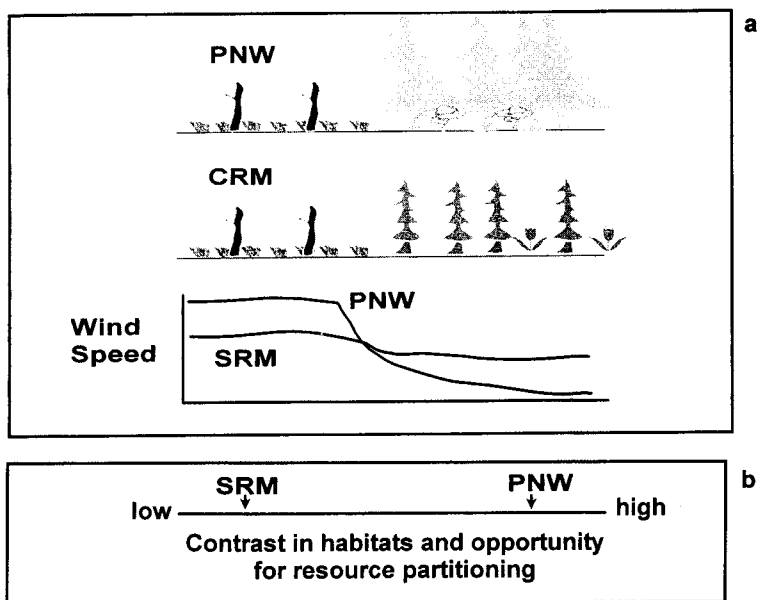


Fig. 10.1. The Biomass Accumulation Hypothesis predicts that differing biomass accumulation influences relative differences in forest edge and interior habitats and the number of species that specialize on edge or interior habitats. (a) Biomass accumulation is greater in late-seral forests compared to early seral habitats in the PNW than in the SRM. Consequently, microclimate and ecological processes differ more along the gradient from edge to interior in the PNW than SRM. Consequently (b), more species are likely to specialize on either edge or interior habitats in the PNW and other ecosystems with high biomass accumulation.

interior specialists, we expect fewer species to respond to fragmentation in the Southern Rocky Mountains compared to the PNW and other ecosystems with high biomass accumulation.

We examined these predictions by drawing on five studies that rated the LHA of birds in different locations. Hansen and Urban (1992) compared the LHA of an Eastern deciduous forest bird community from southern Maryland (Whitcomb et al. 1981) with a Pacific Northwest bird community from western Oregon. Miller and Knight (1995) did a similar analysis of LHA of birds in the Colorado Rocky Mountains. These studies were used to estimate the number of bird species from each of these three communities in each of three life history guilds: structurally complex open-canopy specialists, closed-canopy specialists, and fragmentation-sensitive species as defined by Whitcomb et al. (1981). To assign species to a fourth guild (closed-canopy interior specialists) we drew on Hansen et al. (1994), who quantified bird abundances along transects from clear-cuts to mature and old-growth forest interiors in western Oregon, and on Rufenacht (1997), who did a similar study in conifer forests of the Colorado Rockies. As each of these previous works are case studies with no estimates of variance, it was not possible to assess the statistical significance of differences in species distributions among guilds.

The results indicated that a substantially larger percentage of the species from the Southern Rocky Mountains were associated with open-canopy forests that contained large trees or snags than was the case for the Eastern deciduous forest or Pacific Northwest communities (Table 10.1). Also as predicted, relatively fewer species were associated with

Table 10.1. Representation of species in life history guilds in three forest biomes: the Southern Rocky Mountains (SRM), the Eastern Deciduous Forest (EDF) and the Pacific Northwest (PNW). Data for the first three guilds come from Hansen and Urban (1992a) and Miller and Knight (1995). Data for the last guild are from Whitcomb et al. (1981), Hansen et al. (1994), and Rufenacht (1997).

Guild	SRM (98 Species)	EDF (74 Species)	PNW (75 Species)
Structurally complex	4 (14%)	6 (8%)	6 (8%)
Open-canopy	19 (19%)	22 (30%)	25 (33%)
Closed-canopy			
Fragmentation sensitive	1 (1%)	8 (11%)	0 (0%)
Closed-canopy interior	2 of 30	15 of 62	2 of 20
	species studied (6%)	species studied (24%)	species studied (10%)

closed-canopy forests in the Southern Rocky Mountains than in the Pacific Northwest or Eastern deciduous forest. Moreover, only one Southern Rocky Mountains species (the veery) had the suite of LHA that Whitcomb et al. (1981) found characterized the eight Eastern deciduous forest species that were most sensitive to forest fragmentation. Finally, a lower percentage of species in the Southern Rocky Mountains were significantly more abundant in forest interiors than near forest edges created by clear-cuts (6%, brown creeper and red-breasted nuthatch) than was the case in the Pacific Northwest (10%, Swainson's thrush and Stellar's jay) or the Eastern deciduous forest (24%).

Forests in the Eastern deciduous forest study area were fragmented by agriculture and residential development, rather than by clear-cuts, as was the case in the other two biomes. As discussed later in this paper, we would expect stronger negative edge effects in human-dominated landscapes such as those found in the Eastern deciduous forest. Our analysis suggests that the bird community in the Southern Rocky Mountains is characterized by LHA that may cause the community to be less sensitive to forest fragmentation and more sensitive to lack of natural disturbance (such as wildfire) than the communities in the Eastern deciduous forest or Pacific Northwest. The LHA of the Southern Rocky Mountains community may reflect both the prevalence of forest/grassland ecotones in pre-European settlement times and the relatively small difference in biomass accumulation between early- and late-seral forest patches in the Southern Rocky Mountains. Because relatively few studies of these topics have been done in the Pacific Northwest and Southern Rocky Mountains, these conclusions should be seen as preliminary.

TRAJECTORY OF LANDSCAPE CHANGE

Hansen et al. (1992) suggested that forest fragmentation by agricultural land uses is only one of several trajectories of landscape change occurring around the world. They additionally modeled bird response to forest fragmentation by forest plantations and afforestation following abandonment of agriculture. They found that the bird community responded very differently to each of these landscape trajectories. Hence, knowledge of the nature of landscape change is critical to understanding long-term biodiversity trends. What are the typical trajectories of landscape change in the Southern Rocky Mountains today? Below we describe three trajectories: (1) expansion of conifer forests resulting from fire exclusion, (2) forest fragmentation due to logging, and (3) habitat

conversion and alteration from rural residential development. Fire, as a natural agent of forest fragmentation, is the oldest type of landscape trajectory; logging has been the most prevalent type in recent history and has been the most studied form of landscape change; and residential development is the most recent. We summarize the changes in landscape pattern associated with each trajectory and predict the response of the Southern Rocky Mountains bird community. We then review relevant studies on actual bird responses to these changes.

Fire Exclusion

Studies of fire scars on trees have revealed that the fire frequency has shifted from relatively high to very low throughout the Rockies, especially at low to mid elevations (Arno et al. 1997, Swetnam and Baisam 1996). This dramatic reduction is thought to be the product of both fuel reduction from livestock grazing and human fire suppression. Vegetation has responded dramatically to this change in fire regime. Photo comparisons have revealed substantial encroachment of grasslands by forests and an increase in tree density and canopy cover in conifer stands in southwest Montana (Gruell 1983). Simultaneously, deciduous forest types have declined in abundance in many areas. For example, Gallant et al. (1998) reconstructed vegetation composition and structure in a watershed in the Centennial Mountains, Idaho, from 1850 to present. They found that aspen cover was reduced by about 80% over this time period, while mature conifer forest increased in area, patch size, and connectivity. Moreover, this response of vegetation to fire exclusion appears to be ongoing. Simulation studies in Zion National Park, Utah, suggest that conifer forest expansion may continue for another 100 years under the current fire regime (D. Roberts, *personal communication*). This increase in forest area and fuel loads is likely to eventually lead to an increase in large, severe fires (Veblen, *this volume*).

Hence, the likely landscape change under this trajectory is an increase in the area, patch size, connectivity, and density of mature conifer forest and a concomitant fragmentation of grasslands and deciduous forest types (Table 10.2). Severe fires would reverse this trend and lead to an overall increase in the grain size of the landscape (Veblen, *this volume*). Therefore, we predict an increase in the abundance of species associated with dense conifer forests and large forest patches and a reduction in species specializing on early seral conifer forests, grasslands, and deciduous stands. Habitats for this latter group of species would increase following the infrequent severe fires. However, these

early successional habitats may be too isolated in space and time to support viable populations of these species.

Existing studies suggest that this landscape change will strongly influence the bird community. Deciduous habitats including aspen, cottonwood, and willow stands were found to support substantially higher species richness than any other cover type in a study area in the Greater Yellowstone Ecosystem (Hansen et al., 1999). Several bird species specialized on these habitat types and were not present in other habitats. Similarly, several grassland specialists are found in the Rockies, and many of these species exhibited substantial population reductions in recent decades (Dobkin 1992). As deciduous and grassland habitats are reduced, several bird species are likely to suffer increasing rates of local extinction.

Table 10.2. Predicted changes in landscape pattern and bird responses under three landscape trajectories in the Southern Rocky Mountains.

<i>Trajectory</i>	<i>Landscape Pattern</i>	<i>Bird Reponse</i>
Fire Suppression	Non-Fire Periods: Increase in mature conifer area, patch size, connectivity, stand density; decrease in grassland and deciduous area, patch size, connectivity. Severe Fire Periods: expansion of grasslands and deciduous; contraction of coniferous forest.	Non-Fire Periods: Increase in species associated with conifer habitats and large conifer patches; decrease in early seral conifer, grassland, deciduous species. Severe Fire Periods: Increase in early seral conifer, grassland, deciduous species. Long term: Reduction in species richness due to spatial/temporal isolation of habits.
Logging	Decrease in mature conifer area, core area, patch size/shape variation, connectivity, stand structural complexity; decrease in disturbance patch structural complexity, variation in patch size/shape.	Loss of closed-canopy species, forest-interior species, structural-complexity associated species; expansion of early-seral, structurally-simple associated species.
Rural Residential Development	Habitat conversion, reduced patch size, simpler patch shape, reduced connectivity for native species, increased connectivity for invasive species, more abrupt ecotones, altered biotic interactions.	Increase in some nest predators/brood parasites; lowered reproductive success in deciduous-associated species; loss of deciduous-associated species.

Another consequence of fire exclusion is a reduction in stand-replacement fires and early-successional forest habitats. Hutto (1995) studied birds in several recent burns in Montana and Idaho. Of 87 species detected in these burns, 15 species were strongly associated with them, being found more frequently in recent burns than other cover types. Some of these species, such as the black-backed woodpecker, were virtually restricted to recently burned sites. Habitat area, patch size, and connectivity is likely greatly reduced for these species in post-settlement times. Even if fire exclusion leads to major fires over the next 50 years, it is not clear if local populations can persist during the long intervals between fires.

Another possible consequence of fire exclusion is loss of species associated with open-canopy mature conifer forests such as ponderosa pine forests. These forests were maintained by frequent ground fires and are now undergoing invasion by Douglas fir and true fir and dramatic increases in stand density. Unfortunately, we are not aware of any studies of bird response to increases in stand density in ponderosa pine forests. We also predict that closed-canopy forest species will expand under fire exclusion. However, key studies have yet to be done.

In summary, conifer expansion under fire exclusion is a very prevalent trajectory of landscape change throughout the Rocky Mountains. Conservationists and landscape managers have only recently begun to acknowledge the substantial changes in vegetation associated with this trajectory and research on ecological consequences remains underdeveloped. Initial studies suggest substantial impacts on bird species abundances.

Logging

A second common trajectory of landscape change in the Rockies is driven by clear-cut logging. Staggered-setting clear-cut logging has been widely employed on some of the national forests in the region. Its effects on landscape patterns have been similar to those documented in other regions in fragmenting conifer forests and reducing within-stand structural complexity (e.g., Hansen et al. 1991, Ripple et al. 1991, Mladenoff et al. 1993). For example, Reed et al. (1996) quantified landscape change under logging during 1950–1993 in the Medicine Bow National Forest in southeast Wyoming. They found a decrease in forest mean patch size and mean patch shape and an increase in total edge.

How might landscape patterns under logging compare with those of pre-European settlement times? A. J. Hansen and R. Patten (*unpub-*

lished data) compared spatial patterns created by clear-cut logging in Targhee National Forest, Idaho, during 1950–1990 with those created by wildfire in the adjacent Yellowstone National Park. Approximately 50% of each landscape remained in closed-canopy forest. Because wildfire burned in large linear strips as driven by wind, the forest remaining in the burned landscape was much less fragmented than that in the logged landscape. Mean core area (area >100 m from an edge) was about five times greater in the burned landscape. Disturbance patches also differed between the two landscapes. Patches created by fire were larger, more variable in size, more complex in shape, and better connected than those created by logging units. They also had much higher levels of within-stand heterogeneity for variables such as live trees, snags, and fallen trees.

Selective timber harvest is also common in the Rockies. However, we are not aware of studies quantifying the effects of this type of logging on landscape patterns. We predict that staggered-setting clear-cut logging would lead to a loss of species associated with within-stand structural complexity and interiors of closed-canopy forests (Table 10.2).

In our evaluation of current knowledge of bird response to fragmentation due to logging, we recognize three components of landscape change associated with fragmentation: loss of total area of the habitat, decrease in patch size and associated increase in edge, and increasing patch isolation. Each of these components of fragmentation due to logging may elicit unique responses from species and communities. Because relatively few studies of bird response to fragmentation have been completed in the Southern Rocky Mountains, we reviewed studies of logging effects in conifer forests from throughout western North America.

Area of Habitat. Most ecologists assume that the average abundance of a species in a landscape is related to the area of suitable habitat across the landscape. Thus, as the area of a habitat is reduced through fragmentation, we expect that species abundances will drop and some species will suffer local extinction. The best test of these ideas in western coniferous forests was by McGarigal and McComb (1995) working in coastal Oregon (Table 10.3). They found that the abundance of 10 of 15 late-seral associated bird species was significantly ($p < 0.10$) related to area of late-seral forest. Hence, in western forests, as elsewhere, we can expect species to be reduced in abundance if the area of their habitats is reduced through habitat fragmentation.

Patch Size and Edge. As stated earlier, several species of birds have been found to be rare or missing from small forest patches in the East-

ern deciduous forest (Terborgh 1989). This loss of species could result from altered microclimate, nutrient cycling, vegetation structure, and/or predation rates due to loss of interior habitat with decreasing patch size (Ranney et al. 1981, Robinson and Wilcove 1994). However, such strong effects of decreased patch size have generally not been found in coniferous forests in western North America (Table 10.3). In each of four studies we reviewed, only a small percentage (7–20%) of species exhibited significantly lower abundance in small patches or near forest edges. No species showed a significant response to patch size or edge across all of the studies, and no species were absent from small patches. Similarly, species richness was not found to be significantly related to patch size or distance from edge. The two studies that examined predation on artificial nests found that rates did not differ from forest edge to interior, quite in contrast to similar studies in the Eastern deciduous forest (e.g., Wilcove 1985, Small and Hunter 1988).

Patch Isolation. The third component of fragmentation, patch isolation, sometimes reduces species abundances and richness due to reduced immigration. However, the two studies on isolation in western coniferous forests found little or no effect on species abundances or diversity (Table 10.3).

In total, studies on patch size, edge, and patch isolation suggest that the spatial configuration of habitat (controlling for area) does not influence birds in western coniferous forests as much as in some other biomes. This result may be at least partially explained by the nature of land use in the expanding matrix (Schmiegelow et al. 1997). The agricultural and rural residential development that fragments the Eastern deciduous forest favors nest predators and brood parasites (brown-headed cowbirds) that strongly influence birds in forest fragments (Terborgh 1989). In all the studies we reviewed from western coniferous forests, natural factors or logging were the agents of fragmentation. Nest predators and cowbirds were not found to be more abundant in more fragmented landscapes in these studies. These results suggest that research in the West should focus on potential differences in the effects of fragmentation between landscapes driven by logging and those driven by agriculture and rural residential development.

Landscape Setting. An often overlooked aspect of landscape pattern that is relevant to the impacts of fragmentation is the location of habitats relative to biophysical gradients (Hansen and Rotella, 1999). The Rocky Mountains are characterized by strong gradients in topography, climate, and soils. Ecological processes like primary productivity vary across these abiotic gradients. Both abiotic patterns and the

Table 10.3. Summary of studies of bird response to forest fragmentation in coniferous forests of western North America.

Study	Design	Species Responses	Community Responses
<i>Habitat area</i> McGarigal and McComb 1995, (Oregon Coast Range)	30 subbasins stratified by area and spatial configuration of late-seral forest.	Abundance of 10 of 15 late-seral associates related to habitat area.	Not studied.
<i>Patch Size and Edge</i> Keller and Anderson 1992, (southeastern Wyoming) Schmiegelow et al. 1997, (north central Alberta)	Compared natural true fir stands with those fragmented by logging. Compared isolated fragments of 4 sizes, connected fragments, and controls.	Abundance of 2 of 15 species showed significant negative relationship with fragmentation. Abundance of 6 of 30 species was lower in connected fragments than controls; abundance of 7 of 37 species was lower in isolated fragments than controls.	Not studied. Species richness did not differ among three treatments.
Zweifel 1997, (Colorado Rockies)	Compared edge and interior habitats for meadow/forest and clear-cut/forest edges.	Abundance of 5 of 39 species was higher in forest interior than on meadow/forest edge; abundance of 2 of 30 species was higher in forest interior than on clear-cut/forest edge.	Predation on artificial nests not differ between edge and interior.
Zega 1993, (Oregon Cascades)	Examined artificial nest predation from clear-cut/forest edge to forest interior.	Not studied.	Predation did not differ between edge and interior.
Schieck et al. 1995, (Vancouver Is., British Columbia)	Compared old-growth forest tracts of different size.	The abundance of 1–3 (depending on statistical test) species of late-seral associates was related to patch size.	Richness of late-seral associates was not related to patch size.
McGarigal and McComb 1995, (Oregon Coast Range)	30 subbasins stratified by area and spatial configuration of late-seral forest.	Abundance of 1 of 15 late-seral associates was higher in less fragmented subbasins.	Not studied.
<i>Patch Isolation</i> Schmiegelow et al. 1997, (north central Alberta)	Compared isolated fragments of 4 sizes, connected fragments, and controls.	Percent of species with lower abundance in fragments and controls did not differ between isolated and connected fragments.	Slightly less species turnover connected than isolated fragments.
Fruchi et al. 1995, (Colorado Rockies)	Compared aspen patches differing in isolation.	Not studied.	Species richness was not related to patch isolation.

related ecological processes can strongly influence the distribution and abundance of vertebrates. For example, in mature lodgepole pine forests in the Greater Yellowstone Ecosystem, we found that the abundances of several species and species richness significantly related to elevation, snowmelt date, and normalized difference vegetation index, a measure of vegetation productivity (Hansen et al., *in review*). Moreover, initial demographic studies suggest that some low-elevation forests serve as population source habitats for some bird species (Hansen et al., *in review*). These results suggest that low-elevation conifer forests may merit special consideration in managing biodiversity. Logging has often been centered on more productive, low-elevation forests, presumably with negative effects on some forest birds. The challenge is to tailor timber harvest to biophysical gradients to better optimize biodiversity and wood-production objectives.

RURAL RESIDENTIAL DEVELOPMENT

The most rapidly expanding land use in many locations in the Rockies is rural residential development. Population growth in the Rockies is among the fastest in the United States (Riebsame et al. 1997), and many of the immigrants are choosing to live in rural locations (Theobald, *this volume*). Initial studies suggest that rural residential development results in conversion of natural habitats; reduced patch size, shape complexity and connectivity of native habitats, and increased connectivity for invasive species (Theobald et al. 1996).

Perhaps as important as what landscape changes result from this development is where in the landscape these changes are occurring. We have hypothesized that people in the northern Rockies have disproportionately settled in those places in the landscape that are most important for native species (Hansen and Rotella, 1999). These places tend to be the productive valley bottoms that are well watered and support deciduous forests or productive conifer forests.

Consequently, we predict that rural residential development will result in reduced habitat area for bird species, especially those specializing on deciduous forests and low-elevation conifer forests. Many of these species may also suffer local extinction due to increased nest predation and brood parasitism.

Relatively few studies have quantified the effects of rural residential development on birds in the Rockies. The few that have show striking results. V. Saab (1999) examined bird communities in cottonwood forests of different sizes along the South Fork of Snake River in southeast Idaho. The 57 patches were stratified by the surrounding landscape

matrix: either seminatural habitats or agriculture and rural residential development. Saab found that 71% of the variation in bird species richness was explained by landscape matrix, patch size, patch proximity, and patch vegetation structure. Large, well-connected patches in a seminatural matrix were highest in species richness. The abundances of many individual bird species showed similar trends. Saab also found that nest predators and brood parasites were most abundant in cottonwood patches in the agricultural and rural residential matrix.

In the Greater Yellowstone Ecosystem, we found (Hansen et al., 1999) that bird abundance and richness were significantly higher in deciduous forests (cottonwood, aspen, willow) than in other cover types. We speculated that these "hot spot" habitats act as population source areas for some species due to the high vegetation structure and productivity in these habitats. Preliminary field studies of nest success and population modeling revealed that this was the case for aspen habitats. However, cottonwood stands appeared to be population sinks. In this study area, aspen occurs in a seminatural matrix while cottonwood is surrounded by agriculture and rural residential development. These intense land uses favor nest predators and brood parasites and have likely caused these cottonwood stands to change from a population source habitat for some native birds to a population sink.

As rural residential development expands in the Rockies, we can expect local extinctions of bird species as population source habitats are increasingly converted to sink habitats. To the extent that rural residential development is disproportionately focused on deciduous habitats and low-elevation coniferous forests, we may find that local extinctions occur even in landscapes where average human density is relatively low.

INTERACTIONS AMONG LANDSCAPE DRIVERS

While many landscapes in the Southern Rocky Mountains may be experiencing only one of these trajectories of change, some places are likely subjected to two or even three trajectory types. Interactions among these trajectories may lead to complex relationships. For example, logging near rural residential development will possibly have a larger effect than logging in seminatural forests because the predators and parasites favored by this development will be able to penetrate logged forest. Also, fire exclusion may be more vigorous near residences, hastening the loss of deciduous, grassland, and shrubland habitats. Understanding these interactions among landscape drivers will be a challenge.

CONCLUSIONS

How do birds respond to forest fragmentation in the Southern Rocky Mountains? Perhaps this question is a subset of those we should ask to better understand the influence of human activities on Rocky Mountain ecosystems. The more general questions are what are the major factors that affect landscape change in this region, what are the resulting trajectories of landscape change, and how are ecological processes and native species responding to this change?

Forest fragmentation by logging is the trajectory of change best studied in the Southern Rocky Mountains. There is good reason to expect that reductions in the area of forest habitats resulting from logging will lead to reductions in some species abundances and ultimately to local extinctions. However, the influence of forest spatial configuration on native birds here appears to be rather weak, based on current studies. These studies have not yet identified any particular species that are obviously sensitive to forest spatial configuration. Bird community-scale responses have also been weak in these studies. These results may be due to the fact that species in the region have developed life history attributes that are well adapted to the natural fragmentation that was typical over much of the Southern Rocky Mountains in pre-European settlement times and to the lower biomass accumulation in this region. However, the results could also be due to too few studies being completed to date or to the possibility that landscapes studied have not yet undergone sufficient fragmentation to cause strong responses by native species. How extensive is forest fragmentation by logging in Southern Rocky Mountains? Key studies on this topic are yet to be done. Substantial fragmentation has been documented on particular national forests such as the Medicine Bow in Wyoming (Reed et al. 1996) and the Targhee National Forest in Idaho. In some other national forests, however, timber harvest has been minimal, or partial logging has been used instead of clear-cutting.

We speculate that much more land area in Southern Rocky Mountains is likely undergoing forest expansion under fire exclusion than is being influenced by logging. Again, key data on forest expansion are not available. Because the expansion has been occurring over decades and is slow relative to our individual observation times, we often do not perceive the radical change in forest area, forest density, and loss of grasslands and deciduous forests. This trajectory is likely having a large impact on native species. Even with logging as mentioned above, net habitat area for closed-canopy conifer associates has likely experienced a substantial net increase across the region. At the same time, species

requiring structurally complex early successional conifer forest habitats, grasslands, shrublands, and deciduous forests have likely declined dramatically. Over the longer term, this trajectory is likely to lead to major changes in the grain size of the landscape (Veblen, *this volume*). The less frequent fires of the future are likely to be much larger in size and more severe. Hence, the landscape dynamic is changing from frequent, small, lower severity fires in pre-European settlement times to infrequent, large, high severity fires in future times. The consequences of this change for ecological processes and native species are not well known.

Rural residential development likely covers less area than either logging or forest expansion across the region. However, such development may be having a larger effect than its area would suggest because it may be concentrated on the places in the landscape that are hot spots for native species abundance and richness, and function as population source areas (Hansen and Rotella, 1999). Through habitat conversion and alteration of biotic interactions (e.g., predation) within remaining hot spot habitats, the value of these habitats for maintaining viable populations of native species may be substantially reduced.

How can we better understand and manage these changes? This book is evidence that we need to expand our research paradigm to better understand the drivers, types, and rates of change in landscape patterns, and consequences for species and processes. The simple model of forest fragmentation derived from the EDF is insufficient here in the Southern Rocky Mountains, and research needs to be better tailored to the regional situation. We would also benefit from better understanding the influence of abiotic factors on ecological processes, biodiversity, and human settlement in the region. To the extent that strong gradients in topography, climate, and soils strongly influence ecological and socioeconomic patterns in the region, management plans should consider these gradients. Hansen and Rotella (1999) offer several guidelines for land use allocation and silviculture in landscapes with strong abiotic controls. (An example of landscape-scale management is offered in Romme et al., *this volume*). Similarly, Hansen et al. (1999) offer an approach for managing biodiversity at local to regional scales that focuses increasing research and management on the species and places in a planning area that are most at risk.

Beyond attempting to maintain key habitats, future management will likely be increasingly focused on restoration of degraded habitats. Excellent opportunities exist to use prescribed fire and ecological forestry to expand the area of aspen groves, grasslands, and early successional, structurally complex seral stages (e.g., Aplet, *this volume*).

Managing the rate and consequences of rural residential development offers a special challenge because development occurs mostly on private lands. Increasingly, scientists and public land managers need to work with local government officials to develop knowledge, data, and management alternatives that include suites of incentives and regulations to meet biodiversity, socioeconomic, and other objectives.

Fortunately, viable populations of native species still remain in many Rocky Mountain landscapes, and we have time to engage in this new era of cooperative research and management.

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