

Quantifying loss and degradation of former American marten habitat due to the impacts of forestry operations and associated road networks in northern Idaho, USA

Samuel A. Cushman and Tzeidle N. Wasserman



American marten in northern Idaho, USA. © Michael Lucid

Introduction

The global human population has more than tripled in the past century, reaching seven billion in 2012. The total footprint of humanity on the biosphere has more than doubled since the mid-twentieth century (Vitousek et al. 1997). Every year globally more than 14 million hectares of natural forest are converted to other land uses (FAO 2011), and many other ecosystems, such as temperate grasslands, are

mere remnants of their original area. More than 30% of Earth's annual primary productivity is utilized directly by humans (Vitousek et al. 1986) and between one-third and one-half of Earth's land surface has been transformed by human action. As a result, many scientists estimate that between 33% and 50% of all species of mammal may become extinct by the end of the twenty-first century (Leakey and Lewin 1996; Wilson 2002).

Habitat loss and fragmentation are without question the most important drivers of the global biodiversity crisis (Saunders et al. 1991; Myers and Knoll 2001; Balmford et al. 2003). Each species performs best near an optimum value of its key resource requirements and cannot survive when this value diverges beyond its tolerance (Schwerdtfeger 1977); thus habitat is best thought of as species-specific and multidimensional (Hutchinson 1957). Each species has a unique ecological niche that differs from that of all other species. Multidimensionality arises because there are typically a suite of environmental variables that define each species' habitat. It is also multi-scale because each of these environmental variables is likely to be related to resource use at different spatial scales (e.g. Grand et al. 2004; Sánchez et al. 2014; Shirk et al. 2014).

Most studies of habitat loss and fragmentation have used a simplified model of habitat known as the 'island biogeographic perspective' (Forman and Godron 1986). This assumes that one can represent the environmental characteristics that are important to an organism as a single map class, defined as 'habitat', and that all locations that are 'non-habitat' are equivalent and can be treated in a uniform manner (Turner et al. 2001). This simplistic view of habitat, however, is usually insufficient to reflect the multidimensional nature of habitat structure for most species (e.g. Cushman et al. 2010). Reliable assessment of the effects that habitat loss and fragmentation have on a population depends on defining habitat in a way that is biologically meaningful and represents environmental features at scales that determine suitability for the species.

When a habitat is defined as a single cover type, it is easy to define habitat loss as the reduction in the extent of the cover type, and habitat fragmentation as the breaking of habitat into pieces. When there is no focal habitat type, and the landscape instead is represented as a mosaic of different patch types, it is substantially harder to define habitat loss and fragmentation. Ultimately, when habitat is represented as gradients of varying quality, there are no patches at all (e.g. Cushman et al. 2010). In such situations the question becomes: should habitat loss be defined as a reduction in the total aggregate quality of habitat across the study area, or a reduction in the proportion of area meeting a certain threshold of quality, or something else?

The overall purpose of this case study is to illustrate how habitat quality is impacted by the effects of landscape change, through land use, and how this can be

assessed quantitatively for a species with strong, multidimensional and multi-scale habitat relationships, the American marten (*Martes americana*).

Predicting habitat suitability

Due to their dependence on extensive, unfragmented forest landscapes and microhabitat structures associated with late successional forest (Buskirk and Ruggiero 1994; Hargis et al. 1999), American martens are sensitive to fragmentation of late seral forest habitats, such as that resulting from timber harvest and associated extraction route/road building (e.g. Cushman et al. 2011). Previous studies have consistently shown that American marten habitat requirements include forests with high canopy cover (Hargis and McCullough 1984; Wynne and Sherburne 1984), abundant near-ground structure (Chapin et al. 1998; Godbout and Ouellet 2008), high prey densities (Fuller and Harrison 2005), and sufficient snow depth to provide subnivean spaces during winter (Wilbert et al. 2000). These habitats are thought to provide opportunities for foraging, resting, denning, thermoregulation, and avoiding predation. Perturbations such as timber harvest remove canopy cover, reduce coarse woody debris, change mesic sites into xeric sites, remove riparian dispersal zones, and change prey communities (Buskirk and Ruggiero 1994). American martens avoid areas with even relatively low levels of forest fragmentation and rarely use sites where more than 25% of forest cover has been removed (Hargis et al. 1999). Highly contrasting edge habitats, such as borders between late successional forest and harvested patches, and areas of open canopy are strongly avoided (Buskirk and Ruggiero 1994; Hargis et al. 1999; Cushman et al. 2011).

Recently, Wasserman et al. (2012a) predicted and mapped habitat suitability for American marten in northern Idaho, USA. They used multiple scale habitat suitability modelling with logistic regression on a data set of marten presence/absence locations collected non-invasively using genetic (hair) samples across a 3884 square kilometre region to quantify the relative importance of topographical, forest cover, and road density variables in predicting marten occurrence. Wasserman et al. (2012a) exposed strong and consistent relationships with various measures of landscape fragmentation: marten occurrence was positively associated with landscapes that contained high canopy closure, low road density of all roads (including small forest roads), few past clear-cuts, and extensive late

seral forest. Several of these variables had maximum influence on marten probability of occurrence at fairly broad spatial scales. For example, probability of occurrence was diminished by road density at distances more than 2 km from a road. These long-distance, diffuse effects suggest that habitat fragmentation and forest loss can have cumulative effects that extend across broad landscapes and can reduce probability of marten occurrence over large extents.

At scales approximately the size of marten home ranges (500–1000 m radius; Tomson 1999) within our study area, American marten select landscapes with high average canopy closure, low road density, and low forest fragmentation (Wasserman et al. 2012a). Within these low-fragmentation landscapes, marten select foraging habitat at a fine scale (90 m) within middle-elevation, late-seral, mesic forests, often with a large component of western red cedar (*Thuja plicata*). This is consistent with the results of previous studies, which have shown high sensitivity to landscape fragmentation and perforation by non-stocked clear-cuts (Hargis et al. 1999; Cushman et al. 2011), and strong preference of American marten in northern Idaho for mesic riparian forest conditions in unfragmented watersheds (Tomson 1999; Shirk et al. 2014).

Wasserman et al. (2012a) also revealed several new insights that have substantial implications for conservation and management of American marten. From approximately 1960 to the early 1990s there was a very high rate of timber harvest across the study area. Wasserman et al. (2012a) noted that most past timber harvest in the study area had occurred in lower and middle elevations, and was often concentrated in the most productive western red cedar cover types. Western red cedar covers approximately 15% of the study landscape (Evans and Cushman 2009), and forms optimal habitat for American marten. Specifically, Wasserman et al. (2012a) noted that past timber management in northern Idaho seemed to have been implemented in a way that affected marten habitat quality disproportionately, due to the: (1) pervasive timber extraction road (<10m wide/dirt track/unpaved) network, (2) dispersed clear-cutting in small patches (3–10 ha), and (3) importance of middle-elevation cedar forest to marten occurrence.

Forest management

Private land, which comprises 25.3% of the study area, has been heavily managed for more than 100 years. Much of the private land is in agricultural valleys that

were cleared of forest in the 1880s and 1890s. About half of the private land is forested, most of which has been heavily harvested, often several times, in the past century. Approximately 13.1% of the study area is State Trust Land, which is timber land owned by the State of Idaho and managed with the goal of maximizing economic return. The portions of these lands that are suitable for harvest (e.g. not steep slopes) have been heavily managed with intensive timber harvest in the past 60–80 years. The US Forest Service (USFS) manages 58.8% of the study area. In the post-World War II era, the USFS adopted a land management model based on regulated forests. The goal was to exert full control over timber harvest and wildfire across the land base not excluded from active management (such as official road-less or Wilderness Areas). The first step in implementing a regulated forest was installation of an extensive road network. Roads were built throughout National Forest System (USFS-managed) lands, except for administratively withdrawn areas such as congressionally designated Wilderness or areas that were too topographically extreme for road construction. This resulted in a pervasive network of roads throughout National Forests: currently there are approximately 837,000 kilometres of roads (including classified Forest Service roads, public, private, and unclassified, unauthorized roads) within the 78.1 million hectare US National Forest System. Wasserman et al. (2012a) surmised that, given the long-range effect of road density on habitat quality, this road network may have had a large negative effect on landscape-level habitat suitability for American marten.

Timber harvest on National Forest System lands from the late 1950s until the 1990s was based on dispersing relatively small clear-cuts (3–10 ha) widely across the landscape. However, while the intended benefits of this approach were to avoid the ecological impacts associated with very large cut blocks, an unintended negative consequence was that this style of management maximizes forest fragmentation and edge density (Wallin et al. 1994). Forest fragmentation and perforation are among the greatest negative impacts on marten habitat quality and occurrence measured in habitat suitability studies (e.g. Hargis et al. 1999; Cushman et al. 2011). Indeed, Cushman and McGarigal (2007) showed that simulated timber harvest patterns involving dispersed clear-cutting led to much more rapid and more severe loss of habitat suitability for martens than aggregated harvest blocks.

These factors led Wasserman et al. (2012a) to propose that marten habitat quality in northern Idaho may have been substantially reduced by timber harvest

and road building in the past 100 years. To test this hypothesis, however, it was necessary to reconstruct the historic conditions of the landscape variables (canopy cover, late seral forest patches, clear-cut patches, cedar-dominated forest types, elevation) included in the Wasserman et al. (2012a) habitat model and apply the model to predict the availability of American marten habitat under both pre-harvest (prior to 1900) and current conditions. Our goal in this case study was thus to quantify likely habitat loss due to timber harvest practices over the last century.

Northern Idaho study area

The study area is a 3884 km² section of the Selkirk, Purcell, and Cabinet Mountains, encompassing the Bonners Ferry and Priest River Ranger Districts of the Idaho Panhandle National Forest (2282 km²) and adjacent non National Forest System lands, including private land (986 km²), state (508 km²), tribal- and other federal agency-owned land (Figure 12.1). The topography is mountainous, with steep ridges, narrow

valleys, and many cliffs and cirques at the highest elevations. Elevation ranges from approximately 700 m to 2400 m above sea level. The climate is characterized by cold, moist winters and dry summers. The average daily maximum temperature at Bonners Ferry, the largest town in the study area, in the coldest month (January) is 0.2 °C, while that of the warmest month (July) is 27.8 °C. Average precipitation in the wettest month (December) amounts to 7.84 cm, while that of the driest month (July) is 2.33 cm, with an average annual total of 56.4 cm.

The area is heavily forested, with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) co-dominant above 1300 m, and a diverse mixed forest of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western red cedar, western larch (*Larix occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*) dominating below 1300 m.

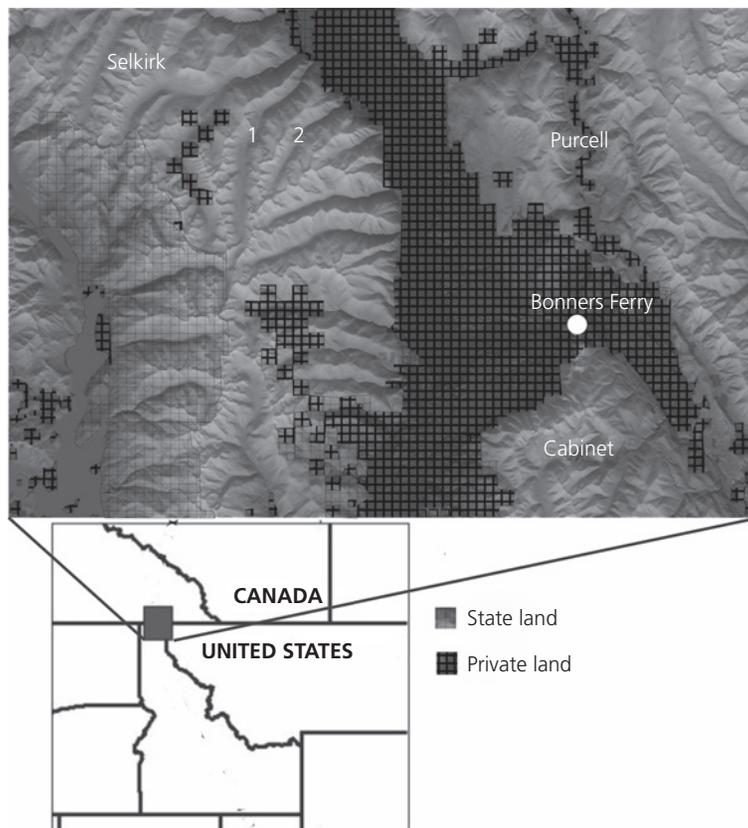


Figure 12.1 The study area consists of an approximately 3800 km² region in the United States northern Rocky Mountains in the State of Idaho, including portions of the Selkirk, Purcell, and Cabinet Mountains. Areas in dark cross-hatching are private lands; areas in light cross-hatching are state lands; areas with no cross-hatching are National Forest Lands. 1—Long Canyon, 2—Parker Creek.

Methods and analyses

Habitat model

We utilize a multi-scale habitat suitability model produced by Wasserman et al. (2012a), who used multi-scale logistic regression modelling to predict habitat suitability from a presence/absence data set collected non-invasively through hair snaring (e.g. Wasserman et al. 2010). To obtain data on American marten presence, Wasserman et al. (2010) deployed hair snare stations at 361 locations across topographical and ecological gradients, across the study area, over three winter seasons (2005, 2006, and 2007; one survey per site). Genetic analysis confirmed detection of American marten at 159 individual hair snare stations. Wasserman et al. (2012a) selected variables a priori known to be related to American marten occurrence based on previous research (Buskirk and Ruggiero 1994; Hargis et al. 1999; Tomson 1999), including elevation, percent canopy closure, road density, patch density, percentage of the landscape occupied by late seral forests, percentage of the landscape occupied by non-stocked clear-cuts, and probability of occurrence of each major tree species (western red cedar and six other species) at each cell of the landscape. The first step undertaken by Wasserman et al. (2012a) was to use bivariate scaling (Thompson and McGarigal 2002; Grand et al. 2004) to identify the scale at which each of these independent variables was most strongly related to American marten occurrence. This resulted in reduction of the model to seven variables significantly related to marten occurrence (Table 12.1). Wasserman et al. (2012a) then used logistic regression to test all combinations of these predictor variables and used model averaging, based on AIC weights, to produce parameter estimates for a final model predicting probability of marten occurrence. This model was then used to evaluate the impacts of past timber harvest and road building on the extent and quality of available marten habitat.

Developing pre-harvest landscape conditions maps

The key new analyses needed to infer effects of past land management on marten habitat quality involved mapping each predictor variable, as per Wasserman et al.'s (2012a) habitat model, as it would have existed in the landscape prior to road building and timber harvest (approximately 1900). Removal of road effects was accomplished by digitally 'filling' the pixels

Table 12.1 Variables included in the final habitat model, their spatial scale and effect on marten probability of occurrence. Each variable was quantified at the spatial scale (focal extent) at which it most strongly affected probability of occurrence. Effect size was measured as the percent change in the probability of marten occurrence as the associated variable changed from the 10th to the 100th percentile value in the data set, holding the other variables constant at their medians.

Predictor variable	Spatial scale (m)	Effect size
Elevation	1400	+ 19.78
Road density	1980	-53.05
Percent canopy cover	990	+ 61.05
Patch density	990	-46.26
Percentage of the focal landscape in large sawtimber	90	+ 13.21
Percentage of the landscape in non-stocked conditions	990	-35.99
Western red cedar	90	+ 77.21

in the landscape lying on roads with forest, using GIS filtering to merge patches of forest fragmented by roads. Reconstructing the canopy cover, patch density, and percent of landscape in non-stocked clear-cuts and late seral forest were more challenging tasks. For this we developed a classification algorithm that identified patches of past timber harvest and reclassified them as forest with age-class corresponding to the forest patches surrounding them. Specifically, we noted through visual inspection of the maps, with reference to our intimate knowledge of the study area, that areas that had been harvested within the past 50 years were in non-stocked, seedling/sapling, or pole conditions. Furthermore, we noted that the patch shapes of these areas were highly angular and compact, rather than the more complex and amoebic shapes produced by natural disturbances. Thirdly, we noted that past timber harvest patches were generally larger than 7 ha and less than 856 ha. These observations allowed us to use GIS to identify all patches that were likely to have resulted from timber harvest in approximately the past 50 years. We then reassigned the seral stage of each such patch according to the seral stage of the forest in the largest adjacent patch. Canopy closure values for all cells in the patch were similarly re-assigned as being equal to the average value of the forest cells immediately conterminous. This produced a retrospective seral stage map and canopy closure map from which we calculated pre-harvest percentage of the landscape in late seral and non-stocked forest, and canopy closure, respectively.

Predicting changes in extent, quality, and fragmentation of marten habitat

To predict changes in the extent, quality, and fragmentation of marten habitat, we applied our empirical logistic regression equation developed in Wasserman et al. (2012a) to predict probability of marten presence across the landscape at both dates. We quantified changes in predicted habitat by reclassifying the two predicted probability maps into bins (all cells greater than 50% probability of marten occurrence classified as moderate to high quality; all cells greater than 70% probability classified as high quality). We then used FRAGSTATS (a spatial pattern analysis program, McGarigal et al. 2012) to calculate several landscape metrics quantifying landscape configuration and composition. Landscape metrics are statistical measures of particular spatial attributes of a landscape mosaic. We calculated four landscape metrics, including the percentage of the landscape covered by habitat in that suitability class (PLAND), which gives a total measure of the amount of habitat in the two maps at each suitability level (moderate to high quality, or high quality). We also calculated the largest patch index (LPI, which measures the extent of the largest single patch of habitat as a proportion of the landscape), the area weighted mean patch size (AREA_AM, measuring the expected value of patch area when selecting a pixel of a particular habitat type from the map at random), and correlation length (GYRATE_AM, measuring the area-weighted extensiveness of patches of that cover

type) of habitat, which all describe different attributes of habitat extensiveness across the landscape. These metrics were chosen based on their utility in predicting habitat occupancy and gene flow in fragmented landscapes in various studies on a number of other species (e.g. Cushman et al. 2013). For more information on landscape pattern analysis with Fragstats with applications to habitat assessments, see Cushman and McGarigal (2007), Cushman et al. (2013), and McGarigal et al. (2012).

Effects of timber harvest and road building on extent and fragmentation of marten habitat

Overall pattern of habitat loss

There were striking differences in the extent, pattern, and quality of habitat predicted in the historic landscape prior to road and timber harvest effects (Figure 12.2a) compared with the current condition of the landscape (Figure 12.2b). In the pre-harvest and pre-road landscape we predicted extensive and well connected areas of high suitability habitat (white areas, Figure 12.2a) that spread dendritically from middle elevation, mesic valleys across large extents of the three mountain ranges. In contrast, the current landscape is characterized by a general reduction in habitat suitability and increased fragmentation due to timber harvest and roads (Figure 12.2b). The extent and pattern of this reduction in habitat suitability is best seen in the map

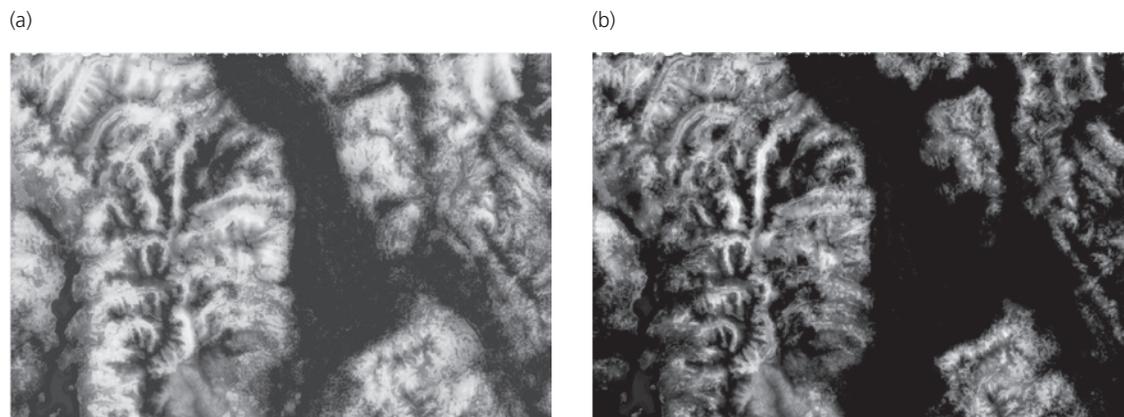


Figure 12.2 Comparison of mapped probability of occurrence for (a) predicted marten habitat removing the effects of roads and past timber harvest (b) current predicted marten habitat. In both maps full white represents the maximum predicted probability of 0.828, and full black represents 0.0 probability, of marten occurrence in any given cell.

depicting the difference between predicted probability of occurrence without roads or logging retrospectively, and the current situation (Figure 12.3). This difference map shows reductions in predicted habitat suitability concentrated in middle elevation valleys and spreading across adjacent ridges. The severity of habitat loss appears to have been highest in the eastern part of the Selkirk Range and throughout the portion of the Purcell Mountains included in the study area. In contrast, the predictive model implied relatively less reduction in predicted habitat suitability over the northern portion of the Selkirk Range and the Cabinet Mountains, as well as in the road-less area that runs along the Selkirk Crest and encompasses the drainages of Long Canyon and Parker Creek, which was predicted to suffer virtually no reduction in habitat suitability. These areas retained high suitability due to very low amounts of harvest and road building compared to the majority of the study area.

Proportional changes in habitat suitability by ownership category

A simple way to quantify these changes is to summarize the average probability of occurrence in the pre- and post-harvest landscapes, by land ownership. The average pixel probability of occurrence for martens across the entire study area declined from 46% in the pre-harvest to 28% in the post-harvest landscape (Table 12.2). The pre-harvest average suitability of state and USFS lands were roughly the same (55% and 57% respectively) and declined by similar proportions (to 34% and 36% respectively). In contrast, private land had relatively low pre-harvest average probability of marten occurrence (21%) and a proportionally larger reduction (to 9%; Table 12.2).

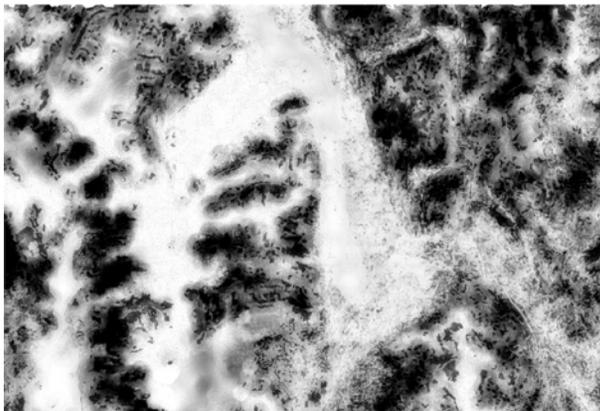


Table 12.2 Marten probability of occurrence, averaged across all pixels, for pre- and post-harvest landscapes by ownership category

	USFS	Private	State	Total
Pre-harvest	0.57	0.21	0.55	0.46
Post-harvest	0.36	0.09	0.34	0.28
Difference	0.21	0.13	0.22	0.18
Relative difference	0.37	0.60	0.39	0.39

Changes in landscape metrics across ownership categories

Percentage of the landscape covered by moderate to high, or high, quality habitat

Across the full study area extent, we predicted a decrease in the extent of moderate to high quality habitat (areas with greater than 50% probability of occurrence) from 38.5% in the pre-harvest to 22.6% in the current landscape, amounting to a relative decrease of 41% (Figure 12.4a). The proportional loss of habitat was higher for the highest quality habitat (areas with greater than 70% probability of marten occurrence). Specifically, the extent of high quality habitat decreased by 67% from 12.8% of the pre-harvest, to 4.3% of the current, landscape (Figure 12.4b). There were marked differences in the amount of habitat loss among the different ownership categories. For moderate to high quality habitat, there was proportionately less habitat loss in USFS lands (−37.2%), followed by state lands (−52.0%), with private lands showing the highest habitat loss (−78.1%; Figure 12.4a). Even more severe relative loss was seen in the high quality habitat, with a proportional decline of 62.6% for USFS, 80.2% for state, and 93.0% reduction in the extent of

Figure 12.3 Change in predicted probability of marten occurrence as a result of road building and timber harvest. Full black represents the largest reduction in predicted probability of marten occurrence of -0.710 , and full white represents no change in predicted probability of occurrence.

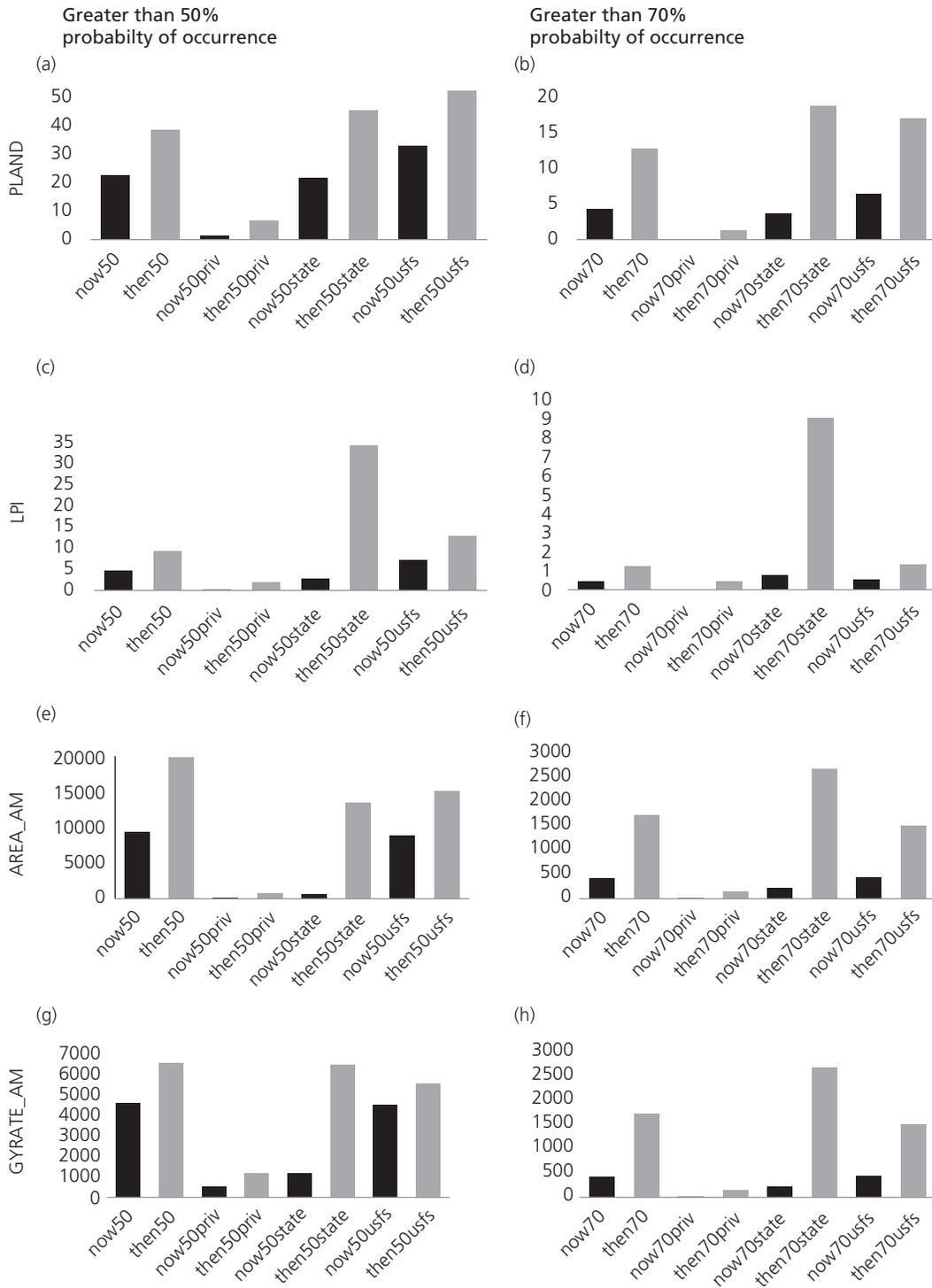


Figure 12.4 Comparison of four FRAGSTATS metrics between pre- (black bars) and post-harvest (grey bars) landscapes, calculated on moderate to high quality habitat (left panels), and high quality habitat (right panels), for the full landscape and for the different ownership categories. The metrics are: PLAND—percentage of the landscape covered by habitat, LPI—extent of the largest patch of habitat as a percentage of the landscape, AREA_AM—area-weighted mean patch size of habitat, GYRATE_AM—correlation length of habitat. The ownership categories are: full study area (first two bars), privately owned land (third and fourth bars), state-owned land (fifth and sixth bars), US Forest Service land (seventh and eighth bars).

high quality habitat in private lands as a result of logging and road building (Figure 12.4b).

Largest Patch Index

We predicted large declines in the extent of the full landscape covered by the largest patch of moderate to high quality habitat. Specifically, in the pre-harvest landscape the largest patch of moderate to high quality habitat covered 9.4% of the study area, and decreased to 4.7% in the current landscape (Figure 12.4c), a relative decline of 50.2%. The Largest Patch Index declined even more for the highest quality habitat (from 1.2% to 0.3%, a relative decline of 72.5%; Figure 12.4d). The degree of decline in the Largest Patch Index differed among ownership categories. For moderate to high quality habitat, there was proportionately much less reduction in the size of the largest single habitat patch in USFS lands (−43.5%) than state (−92.1%) or private lands (−84.6%; Figure 12.4c). The relative decline of the Largest Patch Index of high quality marten habitat was also much greater for private and state lands than USFS land (Figure 12.4d).

Area-weighted mean patch size

The area-weighted mean patch size of moderate to high quality habitat was predicted to decline by 52.7% from the pre-harvest to the current landscape (Figure 12.4e), with proportionately larger declines in the area-weighted mean patch size of high quality habitat across the full study area (−75.4%; Figure 12.4f). As with the other metrics, the decline in the area-weighted mean patch size of moderate to high quality habitat was lowest for USFS lands (−41.9%) and much higher for state (−95.2%) and private (−84.0%) lands (Figure 12.4e). The relative decline of area-weighted mean patch size of high quality habitat was substantially greater than that of moderate quality habitat in USFS lands (−70.3%; Figure 12.4f), while state and private lands had similar reductions in high quality (−92.0% and −86.8% respectively) as for moderate to high quality habitat (Figure 12.4f).

Area-weighted extensiveness of patches

We predicted a decline of 29.3% in the area-weighted extensiveness of patches (correlation length) of moderate to high quality habitat from the pre-harvest to the current landscape (Figure 12.4g), with proportionately larger declines in the high quality habitat across the full study area (49.3%; Figure 12.4h). The decline in the correlation length of moderate to high quality habitat was much lower for USFS lands (−18.9%) than

for state (−81.8%) and private (−53.9%) lands (Figure 12.4g). The relative decline of correlation length of high quality habitat in USFS lands was substantially greater than that of moderate quality habitat (−43.1%; Figure 12.4h), while state and private lands had similar reductions in high quality (−92.0% and −86.8% respectively) as compared to moderate to high quality habitat (Figure 12.4h).

Ecological implications for marten conservation

While it is widely known that timber harvest and road construction have negative impacts on American marten habitat quality, most past studies have not quantified the synoptic spatial effects of past land use change on extent and pattern of marten habitat. This study is valuable in providing explicit quantification of reduction in habitat quality, and, most importantly, spatially explicit mapping of the severity and location of these reductions, which is essential to understand the population-level implications and drivers of these changes.

The goal of our analysis was to quantify the apparent effects of past road building and timber harvest on the extent, quality, and pattern of American marten habitat in three mountain ranges in northern Idaho, and compare changes among ownership categories. Our results strongly suggest three things. First, it appears that road building and past timber harvest have had dramatic effects on reducing the extent of moderate/high quality marten habitat in each of the three mountain ranges, with the western Selkirk and Purcell Mountains most impacted.

The second main finding of our study is that timber harvest and road building have been most concentrated in the portions of the landscape that previously were of highest quality for marten habitat (e.g. middle elevation mesic valleys), and that the dispersed cutting pattern and extensive road network amplify the negative effects of the past landscape changes on the extent, pattern, and quality of marten habitat. This provides further support for the conjecture (see Wasserman et al. 2012a) that the dispersed nature of timber harvest on a fully regulated forest road network, with harvest disproportionately concentrated in middle elevation mesic valleys, would have a synergistic negative effect on marten habitat beyond that expected from the area of harvest alone. Since the early 1990s there has been little timber harvest on National Forest lands in the study area, but harvest rates have increased on state

and private land in the region, leading to a net reduction in harvest and road building, and a shift to the lower elevations and the western Selkirk Range (state land).

The third important result of our analysis is that there are large differences among private, state, and Forest Service land in terms of the extent and pattern of habitat loss resulting from timber harvest and road building. We predicted relatively low extent of quality marten habitat on private land in the pre-harvest landscape, largely because much of these lands are concentrated in low elevation agricultural valleys that probably did not support large marten populations in pre-settlement times. However, the private timber lands in the higher elevations have been heavily logged, and this has resulted in large relative declines in the extent, and large increases in fragmentation, of marten habitat on private lands. State Trust timber lands were predicted to have quite high extent and low fragmentation of marten habitat prior to road building and timber harvest, and to have experienced very large proportionate habitat loss and very large increases in fragmentation. Forest Service lands were predicted to have similar pre-harvest habitat extent and connectivity as state lands, but experienced proportionately smaller reductions in habitat extent and smaller increases in habitat fragmentation. The degree of habitat loss in Forest Service lands, however, was still quite high with 37% decline in the extent of moderate to high quality habitat and a decline of over 62% in the extent of high quality habitat, with similarly large increases in the metrics measuring habitat connectivity and fragmentation (LPI, AREA_AM, GYRATE_AM). These results overall suggest very large decreases in marten habitat extent and increases in fragmentation across the study area, with state and private lands showing particularly extreme declines in habitat extent and increases in fragmentation.

In Wasserman et al. (2010) we found that gene flow of martens in the study area was related to climatic gradients, with high gene flow (low landscape resistance) at middle to high elevations and reduced gene flow in warm valleys. In Wasserman et al. (2012b) we used an ensemble of Global Circulation Models to project future climate in the study area, extrapolated expected landscape resistance in those conditions, and applied individual-based, landscape genetic simulation modelling to investigate the potential impacts of habitat loss and fragmentation due to climate change-driven decreases in dispersal. We found that climatic warming predicted by the year 2080 would be expected to

substantially reduce the extent of the marten population in the study area. Applying landscape genetic simulation models to these landscape changes, we (Wasserman et al. 2012b) predicted that allelic richness would decline linearly with reduction in habitat area and that heterozygosity would decline non-linearly with increasing fragmentation and decreasing habitat extensiveness. The large reductions in habitat area we predicted in the analyses reported here were likely therefore to have been accompanied by declines in allelic richness in the population, and the decline in habitat extensiveness and increase in fragmentation would be expected to have reduced observed heterozygosity as well.

Cushman et al. (2011) used path-level movement modelling of extensive empirical snow-tracking data to infer the effects of habitat loss and fragmentation on movement path selection of American martens in the central US Rocky Mountains. That study found that, in a landscape characterized by large and well connected patches of high quality habitat (such as we predict for the study area prior to road building and timber harvest), martens selected movement paths that efficiently maximized time spent in the forest types that have the highest density of prey. In contrast, after intensive road building and logging, marten paths became much more tortuous and were placed to avoid crossing open clear-cuts, resulting in probable loss of foraging efficiency, increase in energy use, and increase in predation mortality risk (due to increased exposure in open areas, longer distances traversed, and higher density of coyote [*Canis latrans*] and bobcat [*Lynx rufus*] in these areas). The large habitat loss and increase in fragmentation due to road building and timber harvest we predict in the current study would likely result in similar reductions in foraging efficiency, increases in energetic demands in integrating fragmented home ranges, and increased predation risk. These factors could be the proximate drivers of potential past population declines that may have driven the current pattern of heterogeneous occurrence across the study area and local reductions in genetic diversity in areas that had the highest habitat loss. We infer population declines from the observed low detection rates and low genetic diversity in areas we predicted to have had the largest decreases in habitat suitability.

These expectations are supported by Wasserman et al. (2010; 2012a). Specifically, the areas predicted to have undergone the highest reduction in habitat quality historically were also those with the smallest number of marten detections (Wasserman et al. 2012a) and

lowest local genetic diversity (Wasserman et al. 2010), while detection rates and genetic diversity were by far the highest in the northern Selkirks and Cabinet Mountains. For example, we (see Wasserman et al. 2012a) detected few martens in the western Selkirk (dominated by heavily logged state land) and Purcell Mountains (USFS land with heavy logging and high road density). Conversely, detection rates were more than twice as high as in the northern Selkirk and Cabinet Mountains (USFS land with large road-less and unlogged areas). Likewise, we (Wasserman et al. 2013) found that allelic richness was 25% lower in the western Selkirk and the Purcell Mountains than in the parts of the study area where marten detection rates were higher. This suggests that the apparent historic habitat loss and fragmentation modelled in this analysis may be associated with long-term local population declines linked to reduction in genetic diversity, and that these population declines are concentrated in areas with high levels of past logging and road building.

Comparisons with other mustelids

These species-specific habitat changes for marten can be compared to other mustelids. While there have been no habitat models done for other mustelid species in the study area, modelling efforts in other parts of the US northern Rocky Mountains have indicated that fisher (*Pekania pennanti*) occurrence is also strongly related to forest cover and fragmentation, and sensitive to habitat loss and fragmentation (e.g. Olson et al. 2014). Fishers are more strongly associated with lower elevation forest than are martens, and appear to be more strongly associated with riparian areas and cedar forest types (Olson et al. 2014), thus it is likely that fishers have been affected even more severely than martens. In contrast, Copeland et al. (2007) predicted that wolverine habitat quality was primarily related to elevation zone and overall forest cover, with high suitability in high elevation landscapes with high forest cover. These are the areas with the lowest change in our study area, suggesting that this species was probably less affected by forest harvest and road building than the others. Second, it shows the protective benefit of road-less status, as the large central Selkirk road-less area suffered nearly no reduction in predicted habitat quality. It is well known that road access is highly related to hunting and trapping pressure, which, along with increased predation and competition from other

carnivores, such as coyote and bobcat, in highly roaded areas, probably contributes to the observed relationship with road effects.

Changes in the size and isolation of mature forest patches at a particular scale may have little or no detectable impact on species that perceive and respond to landscape patterns at a different scale or that select habitat on the basis of other environmental variables (e.g. shrub cover, litter depth) or that use a broad range of habitats (i.e. generalist species), while they might have large, negative consequences on probability of occurrence of a late-seral forest-dependent species, such as American marten. For example, as noted above, wolverines (Copeland et al. 2007) are likely to have responded very differently than martens to these changes, given their lesser sensitivity to forest cover and forest fragmentation, and association with high elevation locations where landscape change has been less, while fishers likely have been impacted even more (Olson et al. 2014), given their stronger association with lower elevation, late-seral, riparian forest, which has been disproportionately impacted by timber harvest and road building.

These inferences to fisher and wolverine are based on published models developed elsewhere in the region, and thus are uncertain until verified with rigorous assessment in this study area, as we did with the marten. The method we describe in this chapter could be applied generally to a wide range of species and provides the ability to quantify the effects of landscape changes on the probability of occurrence across large landscapes. Successful use of this approach, however, will depend on the development of robust, multivariate, and multi-scale models predicting probability of occurrence, which are not available for most species. Nevertheless, once such models are available they can then be used to guide conservation strategies to restore degraded habitats in the locations where they would have the largest positive impact, or limit future development in places that would have the largest negative effects on the population. There are large differences among private, state, and Forest Service land in terms of the extent and pattern of habitat loss resulting from timber harvest and road building. Our results overall suggest very large decreases in marten habitat extent and increases in fragmentation across the study area, with state and private lands showing particularly extreme declines in habitat extent and increases in fragmentation.

Conclusion

Our analysis provides a quantitative assessment of the effects of past timber harvest and road building on the extent and fragmentation of American marten habitat across three mountain ranges in Northern Idaho, USA. We found that road building and past timber harvest have had dramatic effects on reducing the extent of moderate/high quality marten habitat in each of the three mountain ranges, with the western Selkirk and Purcell Mountains most impacted. Timber harvest and road building have been most concentrated in the portions of the landscape that previously were of highest quality for marten habitat (e.g. middle elevation mesic

valleys), and dispersed timber cutting and extensive road networks amplify the negative effects of the past landscape changes on the extent, pattern, and quality of marten habitat. Habitat loss and fragmentation we predicted in this analysis seem to be associated with long-term local population declines linked to reduction in genetic diversity, and these population declines are concentrated in areas with high levels of past logging and road building.

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