Ecological Consequences of Forest Fragmentation in the Klamath Region

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ABSTRACT: We review the evidence for changes in species composition and population viability caused by forest fragmentation in one of North America's most biologically diverse regions, the Klamath region of northwestern California and southwestern Oregon. Our studies on small mammals and understory plant communities suggest that a number of species are restricted to, or closely associated with, remnant patches of late-successional or old-growth forest. Likewise, we found evidence for changes in population sizes in species that we studied in-depth: California red-backed vole (*Clethrionomys californicus* Merriam) and western trillium (*Trillium ovatum* Pursh.). We also identified many species that do not fit the island-ocean analogy that is often applied to habitat fragmentation. For example, some species were found mostly in remnants, while other species were restricted to clearcuts, or were ubiquitous across sites. Evidence from these studies suggests that the landscape matrix can provide important habitat for many species. The conservation of biological diversity in this region will require not only knowing which species are adversely affected by fragmentation and what role remnant habitat plays in the viability of populations; it will also require a better understanding of the role of matrix in providing both habitat and opportunities for dispersal of species between remnants. Studies of matrix conducted in the Cascade and Coast Ranges of Oregon and Washington provide relevant information, but there is a striking paucity of data concerning matrix in the Klamath region, where we predict that the drier, warmer growing season is likely to result in different, species-specific responses to fragmentation. Research on these responses would provide a vital contribution toward understanding how to conserve biological diversity in the Klamath region.

Index terms: edge effects, extinction, habitat fragmentation, island biogeography, Klamath region

INTRODUCTION

Most terrestrial ecosystems have been subject to patterns of human use that have subdivided once contiguous habitats into smaller, more isolated patches. Agriculture, housing development, intensive forestry, and road construction have all served to divide originally widespread habitat (Groom and Schumaker 1993). For species that are restricted to remnant habitat, this process of "habitat fragmentation" seems to increase the likelihood that some populations will become extinct and, thus, ultimately leads to a reduction in the number of species in the region or a change in species composition (Simberloff 1988, Harrison and Fahrig 1995). We present a summary of empirical evidence for these predictions, specifically concerning the fragmentation of forests, from one of the most biologically diverse regions of North America—the Klamath Mountains Region of northwest California and southwest Oregon.

Populations that become isolated in remnant forest fragments are subject to several changes that may increase their extinction probability. The most obvious changes are reductions in total amount of available habitat and increasing isolation of remaining populations (Saunders et al. 1991). Small, isolated populations are considered more susceptible to extinction than are large populations through the normal fluctuations in environmental conditions, birth rates, and death rates (Ewens 1990, Lawton 1995). Also, populations that are small and isolated should tend to lose genetic variability, due to both genetic drift and the lack of immigration from other populations (Lacy 1987). Thus, smaller populations are thought to be more likely to go extinct due to interactions between nongenetic factors as well as inbreeding depression—a reduction in the fitness of offspring derived from the mating of closely related individuals (Lande 1988, Mills and Smouse 1994).

Further, forest fragments are typically surrounded by a new habitat type, or matrix. The altered matrix often includes changes

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near forest edges that can influence population viability. In general, the surrounding matrix (e.g., a clearcut) and the adjacent forest edge experience more solar radiation, stronger winds, drier soil conditions, warmer daytime temperatures, and cooler nighttime temperatures than forest interiors (Saunders et al. 1991, Chen et al. 1995). These conditions can change food resource levels, alter the physical environment, and favor disturbance-oriented species that compete with interior-associated species (Matlack 1994, Mills 1996, Frost 1997). Such effects may reduce available habitat and decrease population viability (e.g., Jules 1998). Also, reduced population viability can result near edges from increases in environmental fluctuations that may influence birth and death rates (e.g., increased variability in microclimate; see Murcia 1995).

In sum, evidence from both theoretical and empirical studies of forest fragmentation suggests that the extinction probability for some populations increases with (1) a decrease in habitat size, (2) an increase in habitat isolation, and (3) an increase in the ratio of edge to interior habitat (reviewed in Simberloff 1988, Murcia 1995). This paper summarizes the findings of several empirical studies that address the ecological effects of forest fragmentation in the Klamath Mountains Region, a topographically complex region of northwest California and southwest Oregon comprising numerous interconnected mountain ranges, including the Siskiyou, Marble, Yolla Bolly, Scott Bar, Salmon, and Trinity Mountains. High biological diversity in the Klamaths is generally attributed to extreme heterogeneity in topography, climate, and substrates (Whittaker 1960, Smith and Sawyer 1988). We begin our summary with an overview of the patterns of forest fragmentation that have occurred in the region, and then discuss evidence of fragmentation-related effects on small mammals and understory plant species. Based on data from several case studies, we examine how well species conform to the island analogy used for forest fragments, and we discuss the role of matrix in the maintenance of biological diversity.

FOREST FRAGMENTATION IN THE KLAMATH REGION

Forested landscapes in the Klamath region have been fragmented by nearly a century of logging, agriculture, and road building. Low-elevation forests, which have been in private ownership since white settlers entered the area, were logged heavily starting in the late 1800s. By World War II, most of the forests in private ownership had been converted either to farmland or to early successional forest stands (Hirt 1994, McKinley and Frank 1995). In contrast, mid- and high-elevation forests in the Klamath region are managed by the U.S. Forest Service. Little logging occurred on these federal forest lands (including the Siskiyou, Klamath, Rogue River, Shasta-Trinity, Six Rivers, and Mendocino National Forests) before the 1940s, but logging increased dramatically after World War II in response to increasing timber demands and the reduced supply available from private lands (Clary 1986). For example, the Siskiyou National Forest, in Josephine County, Oregon, produced an average of less than 2.4 million board feet (mbf) per year during the period 1906–1941. This rose to 43.3 mbf in 1951, 45.9 mbf in 1961, and 60.9 mbf in 1969 (Wall 1972).

In a local study of forest fragmentation patterns in the region, Jules (1997a) documented annual rates of logging in the Sucker Creek watershed. This watershed, approximately 250 km^2 in size, forms the eastern boundary of the Illinois River drainage in southwestern Oregon. Most of the watershed (190 km^2) is managed by the Siskiyou National Forest, and the history of management within the area is representative of the rapid fragmentation that occurred on federal lands in the Klamath region. In 1948, 53% of the federal land in the Sucker Creek watershed was in four large patches of mid-successional, late-successional, or climax old-growth forest. These patches were 6,594 ha, 2,075 ha, 892 ha, and 731 ha in size and were embedded in a landscape mosaic that included early successional forests (U.S. Forest Service 1995).

During the 1940s, only 27 ha were clearcut in the watershed. The rate rose sharply thereafter (Figure 1). Clearcut sites in this region have experienced the following management regime: clearcut logging, prescription burning to remove woody debris and vegetation, and planting of conifer seedlings (mostly Douglas-fir, *Pseudotsuga menziesii*). Clearcutting accounted for 72% of the logged area in the watershed; the remaining 28% was thinned or logged using a "shelterwood" method that retains three to six green trees per hectare for a few years after the initial cutting. Today, 35% of the watershed contains uncut forest of mid-successional, late-successional, or climax forest—a reduction of 34% since 1950 (U.S. Forest Service 1995). None of the large patches of older forest mentioned above survive in the watershed; the remaining forest fragments

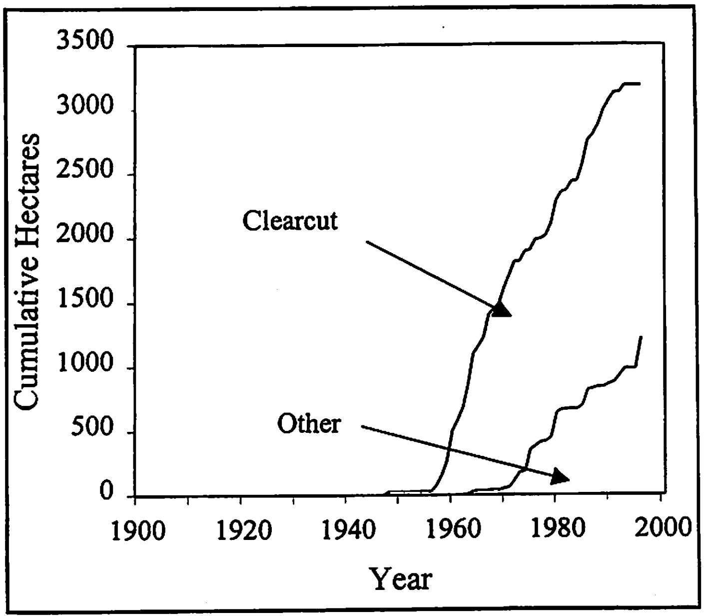

Figure 1. Area clearcut and area thinned or shelterwood cut ("Other") in the Sucker Creek watershed, 1900 to present. Data from U.S. Forest Service, Grants Pass, Oregon.

range in size from 0.3 ha to approximately 1,000 ha (Mills 1995, Jules 1997*b*). Only two fragments of about 1,000 ha each exist. These are at the very highest elevations of the watershed, and they represent 8% of the watershed area.

SMALL MAMMALS AND HABITAT FRAGMENTATION

Studies concerning the effects of habitat fragmentation have often focused on small mammals because they are usually abundant, easily captured, and live in habitats that can be manipulated for scientific investigation. Small mammal studies have been exceptionally useful in gaining insight into the effects of habitat fragmentation because they can be conducted at many geographical scales, ranging from the individual to the population, and up to the community and landscape levels.

Close association of a small mammal species to a given habitat type, coupled with a large degree of habitat fragmentation and isolation relative to historic levels, may result in negative effects on that species. In contrast, some species may be quite well adapted to habitat fragmentation and show increased fitness as a result of habitat fragmentation. For example, Bowers et al. (1996) found positive "edge effects" for meadow voles (*Microtus pennsylvanicus*) in experimentally fragmented habitat. That is, females along the edges of habitat fragments weighed more, had longer residence times, and reproduced more frequently than individuals in habitat fragment interiors. Nupp and Swihart (1996) found that the density of white-footed mice (*Peromyscus leucopus*) in woodlot fragments was inversely related to woodlot size, and that these populations showed no evidence of isolation. Moreover, body mass of adult males was inversely correlated to woodlot size, suggesting no negative effects of increased mouse density on individual mice. In contrast, our studies of California red-backed voles (*Clethrionomys californicus*) in the Siskiyou Mountains of southwestern Oregon, discussed below, suggest some negative effects of habitat fragmentation for this species.

Small Mammals on Forest Remnants in the Siskiyou Mountains

We briefly describe the results of studies on the effects of forest fragmentation on small mammals in the Siskiyou Mountains conducted by Mills and colleagues (Tallmon and Mills 1994; Clarkson and Mills 1994; Mills 1995, 1996). In 1990 and 1991 we studied 5 unfragmented "control" forests and 16 forest remnants surrounded by clearcuts 3 to 30 years old. Thirteen of these remnants were of appropriate size and characteristics to use in an analysis of edge effects. Live traps were placed in a measured, regularly spaced trapping grid on the control and remnant sites; and four lines of four traps each, with the same spacing, were placed in the middle of the clearcuts surrounding each remnant (for greater details on the sampling design see Mills 1995).

The primary species of interest was the California red-backed vole, and only individuals of this species were individually marked upon capture. However, indices of relative abundance for other species suggested that the response of small mammals to forest fragmentation varies greatly across species. For example, deer mice (*Peromyscus* spp.) showed a positive response, with more than twice as many mouse captures in clearcuts as in forest remnants, and more captures on remnant edges than in remnant interiors. Trowbridge shrews (*Sorex trowbridgii*) responded neutrally to forest fragmentation.

In contrast, California red-backed voles appeared to be negatively affected by forest fragmentation. In 1990 and 1991 voles were very rare in clearcuts and had much lower densities near the edges of remnants relative to forest interior (Figure 2). The edge effect resulted in decreased vole densities across the entire distance (from the forest edge) that we considered (1–90 m). In 1997 Tallmon and Mills (unpubl. data) revisited 11 of the same forest remnants, plus one additional remnant and two nonfragmented control sites. Only 32 voles were captured on forest remnants—a sam-

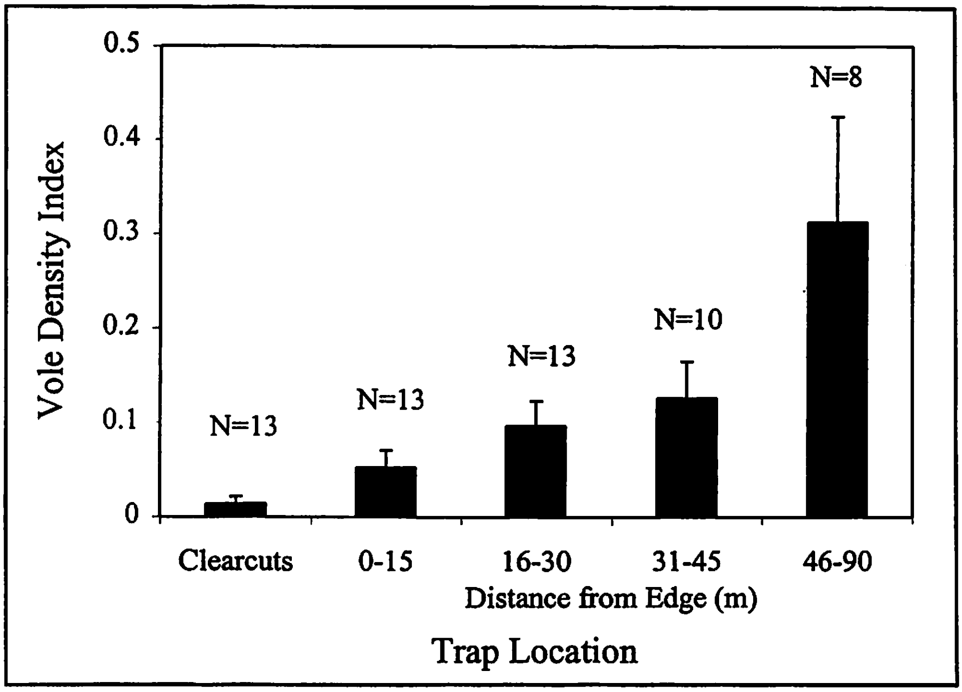

Figure 2. Mean density index (and standard errors) for the California red-backed vole (number of different voles captured per trap in four nights of trapping) in southwestern Oregon, 1990 and 1991 (from Mills 1995). The N refers to the number of sites trapped. Small remnants often did not have any area farther than 30 m from an edge. The density index is significantly lower for the clearcut compared to remnants ($P = 0.003$), and there is a significant negative edge effect ($P = 0.003$; statistical tests described in Mills 1995).

ple size too small to test for edge effects. In general, vole abundances were much lower than in 1990–91 on both remnant and control sites.

The mechanism of California red-backed vole response to forest fragmentation in the Siskiyous appears to be related to the distribution of the voles' primary food. More than 60% of the voles' diet is truffles, the below-ground fruiting bodies of many mycorrhizal fungi (Maser et al. 1978, Ure and Maser 1982). In 1990 and 1991 Mills and his colleagues first investigated whether the negative edge effect for voles could be explained by the density or biomass of logs, or coarse woody debris, which has been closely correlated with abundance of red-backed voles (Hayes et al. 1987, Tallmon and Mills 1994). Log density and biomass per se could not explain the negative edge effect on voles, because log density was found to increase toward the edges of forest remnants, probably as a result of trees falling into the remnant during harvest or postharvest blow down (Mills 1995). A solution to this paradox—whereby voles prefer logs but are least abundant on edges where logs are most common—was offered by detailed study of voles in one forest remnant (Tallmon and Mills 1994). These voles strongly preferred logs in later stages of decay, while logs on the edge are typically of recent origin and little decayed. In addition, truffles were more common in the moister microclimate under logs than they were away from logs, more common in interiors than at edges, and more common in remnants than in the relatively hot, dry clearcuts surrounding remnants (Clarkson and Mills 1994, Mills 1996; see also Amaranthus et al. 1994).

Another related factor of probable importance to truffles and voles is the soil organic layer, which decreases following clearcutting and burning (Rosenburg et al. 1994). The near absence of California red-backed voles and truffles from young clearcuts that have been burned may lead to the isolation of some populations of voles. Because very low levels of connectivity or immigration between populations can minimize the loss of genetic variation on forest remnants, we have begun to investigate whether the observed ecological isolation translates into a loss of genetic variation.

Changes in California red-backed vole movement could have negative feedback on mycorrhizae formation because spores of some mycorrhizae are dispersed primarily by small mammals (see Johnson 1996). In turn, forest regeneration may be affected because most woody plants depend upon mycorrhizal associations for water and soil nutrients (Perry et al. 1987). Thus, a number of different components are linked in normally functioning forest ecosystems: trees depend on mycorrhizae for survival and vice versa, some mycorrhizae depend on small mammals for dispersal, and small mammals rely on mycorrhizal sporocarps for an important food source. These biotic interactions are so strong that the mycorrhizae and voles have been labeled "keystone" or "strongly interacting" species in these forests (Mills et al. 1993, Power et al. 1996).

The effects of forest fragmentation on California red-backed voles appear to be negative and strong. However, the effects of fragmentation on other small mammals in the Siskiyou Mountains range from neutral to positive. It appears that the effects of forest fragmentation are species-specific and difficult to generalize across taxonomic groups. These results caution against the uncritical application of an island analogy to forest remnants in a matrix of cut-over lands in the Klamath region (Doak and Mills 1994, Mills 1996).

UNDERSTORY PLANTS AND FOREST FRAGMENTATION

The effects of habitat fragmentation on plants have most often been assessed indirectly by testing for a correlation of species diversity with fragment size and/or isolation (e.g., Carleton and Taylor 1983, Gibson et al. 1988, Dzwonko and Loster 1989). In general, such studies indicate that larger fragments tend to support a larger number of species. However, results from these studies are often difficult to interpret due to some general problems in experimental design. High variability in physical characteristics among remnant fragments can confound statistical relationships between fragment attributes and community diversity (Doak and Mills 1994), and the lack of historical (prefragmentation) data on plant distributions limits the conclusions that can be drawn from analysis of existing landscape patterns (Zimmerman and Bierregaard 1986). On the other hand, studies of individual species lend strong evidence that effects associated with edges and reduced fragment size can influence various life-history stages of plants. These include studies of seed set (Sork 1983, Aizen and Feinsinger 1994), plant-pollinator interactions (reviewed in Rathcke and Jules 1993), and herbivory (Andrén and Angelstam 1993, Santos and Telleria 1994). It is significant, however, that none of these studies have related changes in life history to actual changes in extinction probability. Here we focus on the effects of clearcut-forest edges in the Klamath region on understory community composition.

Edge Effects on Understory Plants in the Western Marble Mountains

To determine the impacts of fragmentation and edge effects on plant diversity in the Klamath region, we investigated the composition of forest understory communities along transects running from clearcuts into the interior of adjacent old-growth forest stands (Frost 1992, 1997). The study was carried out in mixed conifer forests located between 1,100 and 1,400 m elevation on the western slope of the Marble Mountains, Siskiyou County, California (Frost 1992). Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) dominate the overstory in this forest type, and incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and ponderosa pine (*Pinus ponderosa*) are frequent secondary associates. The herb layer is very rich and well developed, with many of the most common species characteristic of mesic environments (Waring 1969). Dispersed clearcutting (generally 10–20 ha in size) of forests in the study area began in the 1960s. Over time, this management regime has resulted in a checkered mosaic of late-successional forest patches, regenerating clearcuts, and managed tree plantations, thereby increasing the amount of edge-influenced area (Jimerson and Hoover 1992). Planted conifers are present in most of the plantations but are generally less than 5 m in height and have not reached the closed-canopy stage.

Within this study area, understory composition was sampled at 11 sites (6 with northerly aspects and 5 with southerly aspects) along clearcut-to-forest-interior gradients, and in 4 unfragmented control sites (2 with northerly aspects and 2 with southerly aspects) located in the nearby Bridge Creek Research Natural Area (Keeler-Wolf 1990). Sites were selected to control for variation in topography, soils, and other environmental variables. The age of clearcuts and edges sampled ranged from 18 to 26 years. At each site, five 10-m x 100-m transects were laid out perpendicular to the forest edge at 10-m intervals. For each transect, 10-m x 10-m plots were delineated at 0, 15, 30, and 60 m into the forest, and 15 and 30 m into the adjacent clearcut. Within each plot the presence of all vascular species in the shrub and ground layers was recorded, and both percentage cover and abundance of each species were estimated using standard cover class scales. Vascular plant nomenclature follows Smith and Sawyer (1988).

Comparisons of understory composition were made among all plot locations along clearcut-to-forest-interior transects. North and south-facing aspects were analyzed separately. To detect individual species' responses to forest edges, frequency of occurrence (constancy), mean abundance, and mean percentage cover for all species were calculated at each plot location. Cover and abundance class values were transformed into means by converting to the midpoints of the intervals, then averaged from plots at the same distance from the forest edge, across all sites with the same aspect. Chi-square goodness-of-fit tests were used on both the pooled constancy and cover data to assess whether the species were uniformly distributed over the six plot locations. Cover and constancy profiles of species with significantly nonrandom distributions along the clearcut-to-forest-interior transect were inspected for trends and assigned into one of seven response groups, based on the plot location(s) with the highest constancy and mean cover (Table 1).

Table 1. Generalized distribution patterns used to categorize plant species into seven response groups. Relative importance by plot location indicated as follows: x = present with low constancy/cover values, X = moderate constancy/cover values, XX = highest constancy/cover values.

	Clearcut		Edge	Forest Interior		
Species Response Group	30 m	15 m	0 m	15 m	30 m	60 m
Clearcut-oriented	XX	X	x	x	x	x
Clearcut-restricted	XX	X				
Edge-oriented	x	x	XX	X	x	x
Forest interior-oriented	x	x	x	x	X	XX
Forest interior-restricted				x	X	XX
Clearcut/forest interior-oriented	XX	X	x	x	X	XX
Ubiquitous	x	x	x	x	x	x

The results of this study indicate that edges created by clearcutting had pronounced effects on the composition of understory plant communities in adjacent old-growth stands. Of the species sampled sufficiently to allow statistical analysis, 50% (73 species) and 65% (60 species) showed a significant ($p < 0.05$) plot location effect on north- and south-facing sites, respectively. The forest interior-oriented response was most common among all understory species exhibiting any edge effect, including a total of 7 woody and 31 herbaceous species. These species were sampled in clearcuts and near edges, but they exhibited significantly higher constancy in the interior-most forest plots. Species in this group include many of the more common herbs, such as *Achlys triphylla, Chimaphila umbellata, Linnaea borealis, Goodyera oblongifolia, Clintonia uniflora*, and *Trillium ovatum.*

In addition to the forest-interior-oriented group, 12 understory species were sampled in forest plots (15 m, 30 m, 60 m) but not in clearcuts or edges. This forest interior-restricted group includes three moisture-loving shrubs (*Ribes lacustre, Mahonia nervosa, Cornus nuttallii*), three orchids (*Calypso bulbosa, Listera caurina, Cephalanthera austiniae*), and six shade-tolerant herbs (*Asarum caudatum, Actaea rubra, Pyrola asarifolia, Maianthemum stellatum, Orthilia secunda,* and *Vancouveria hexandra*; summarized in Table 2). In contrast, 21 species were clearcut-oriented, including *Pteridium aquilinum, Rubus parviflorus*, and *Apocynum androsaemifolium.* Six species, including *Anaphilis margaritacea, Epilobium angustifolium*, and *Lotus crassifolius*, were clearcut-restricted.

The proportion of species that exhibited a forest interior-associated response was similar for both north- and south-facing sites, but some individual species responded differently with a shift in aspect. For example, *Whipplea modesta, Paxistima myrsinites,* and *Rosa gymnocarpa* reached their greatest abundance in forest interiors on south-facing sites, but exhibited no significant plot location effect on north-facing sites. Similarly, several forest interior-oriented species on north-facing sites became interior-restricted on south-facing sites. However, of the 52 species sampled on both north- and south-facing sites that showed a plot location effect, 36 (69%) exhibited the same pattern on both aspects.

The depth of edge influence on forest understory species can range considerably (0 m to more than 60 m in this study), depending on the species of interest. Changes in forest understory composition were most dramatic within 30 m of the clearcut boundary, but a number of species, such as *Tiarella trifoliata, Taxus brevifolia*, and *Anemone deltoidea*, continued to exhibit increased importance up to and probably beyond the 60-m maximum forest interior plot location sampled in this study. Based

Table 2. Constancy as a function of plot location for all forest interior-oriented (i) and forest interior-restricted (I) plant species sampled at both north-facing (N) and south-facing (S) sites. Values from contiguous forest locations at Bridge Creek (BC) are presented for comparison, but were not included in statistical analyses. Significance levels (*P*) from chi-square tests as follows: * = < 0.05, ** < 0.025, *** < 0.01, **** < 0.005, + < 0.001. Where significance was detected at both north- and south-facing sites, data from north-facing sites are presented first. Vascular plant nomenclature follows Smith and Sawyer (1988).

		Clearcut		Edge	Forest Interior				
Species	Site	30 m	15 m	0 m	15 m	30 m	60 m	BC	Sig.
SHRUB LAYER									
Calocedrus decurrens	N	10.0	10.0	6.7	23.3	30.0	43.3	30.0	+ i
	S	0	12.0	20.0	24.0	20.0	40.0	42.5	+ i
Cornus nuttallii	N	26.7	33.3	56.7	50.0	70.0	76.7	95.0	+ i
	S	0	0	0	8.0	28.0	48.0	45.0	+ I
Corylus cornuta	S	0	8.0	16.0	40.0	44.0	76.0	75.0	+ i
Mahonia nervosa	N	26.7	56.7	56.7	60.0	73.3	90.0	95.0	+ i
	S	0	0	0	4.0	16.0	32.0	27.5	+ I
Paxistima myrsinites	S	4.0	24.0	28.0	28.0	24.0	32.0	42.5	+ i
Ribes lacustre	N	0	0	0	6.7	16.7	20.0	20.0	+ I
Rosa gymnocarpa	S	44.0	52.0	64.0	72.0	76.0	76.0	80.0	** i
Taxus brevifolia	N	3.3	3.3	3.3	3.3	13.3	16.7	22.5	+ i
GROUND LAYER									
Achlys triphylla	N	56.7	76.7	86.7	93.3	100.0	100.0	100.0	*** i
	S	0	4.0	8.0	8.0	52.0	84.0	90.0	+ i
Actaea rubra	N	0	0	0	6.7	20.0	20.0	27.5	+ I
Adenocaulon bicolor	S	4.0	20.0	8.0	36.0	48.0	60.0	85.0	+ i
Anemone deltoidea	N	6.7	13.3	13.3	16.7	33.3	43.3	80.0	+ i
Asarum caudatum	N	0	0	0	3.3	13.3	20.0	20.0	+ I
Calypso bulbosa	N	0	0	0	6.7	16.7	13.3	10.0	+ I
Cephalanthera austinia	N	0	3.3	3.3	16.7	33.3	43.3	40.0	+ i
	S	0	0	0	8.0	12.0	24.0	17.5	+ I
Chimaphila menziesii	N	0	0	23.3	40.0	60.0	56.7	45.0	+ i
	S	0	0	16.0	20.0	48.0	52.0	50.0	+ i
Chimaphila umbellata	N	46.7	73.3	93.3	90.0	100.0	96.7	97.5	+ i
	S	28.0	52.0	88.0	100.0	100.0	100.0	100.0	+ i
Clintonia uniflora	N	13.3	23.3	13.3	40.0	63.3	93.3	90.0	+ i
Corallorhiza maculata	N	0	10.0	26.7	26.7	40.0	46.7	40.0	+ i
	S	0	0	12.0	20.0	32.0	32.0	27.5	+ i
Corallorhiza mertensiana	N	0	0	3.3	6.7	40.0	46.7	43.3	+ i
Disporum hookeri	N	43.3	50.0	66.7	76.7	83.3	83.3	75.0	+ i
	S	0	0	8.0	8.0	16.0	40.0	27.5	+ i
Fragaria vesca	S	8.0	12.0	4.0	12.0	28.0	24.0	45.0	+ i
Gaultheria ovatifolia	N	0	3.3	3.3	0	6.7	16.7	20.0	+ i
Goodyera oblongifolia	N	3.3	10.0	56.7	56.7	90.0	90.0	87.5	+ i
	S	0	0	8.0	28.0	52.0	68.0	85.0	+ i
Iris purdyi	S	32.0	48.0	32.0	60.0	60.0	60.0	25.0	+ i
Lilium washingtonianum	N	0	3.3	0	3.3	23.3	13.3	10.0	+ i
Linnaea borealis	N	13.3	33.3	33.3	50.0	70.0	86.7	100.0	+ i
Listera caurina	N	0	0	0	0	13.3	16.7	17.5	+ I
Maianthemum stellatum	N	0	0	0	0	16.7	16.7	20.0	+ I
Orthilia secunda	N	0	6.7	23.3	33.3	60.0	70.0	57.5	+ i
	S	0	0	0	4.0	28.0	44.0	45.0	+ I
Osmorhiza chilensis	N	0	0	3.3	16.7	40.0	53.3	57.5	+ i
Phlox adsurgens	N	3.3	13.3	6.7	30.0	36.7	60.0	30.0	+ i
	S	0	8.0	8.0	24.0	40.0	60.0	32.5	+ i

continued

Table 2, *Continued.*

		Clearcut		Edge	Forest Interior				
Species	**Site**	**30 m**	**15 m**	**0 m**	**15 m**	**30 m**	**60 m**	**BC**	**Sig.**
Polystichum munitum	N	0	0	3.3	13.3	16.7	30.0	27.5	+ i
Pyrola aphylla	S	0	0	4.0	8.0	24.0	24.0	15.0	+ i
Pyrola asarifolia	N	0	0	0	0	10.0	20.0	15.0	+ I
Pyrola picta	N	13.3	33.3	60.0	73.3	76.7	83.3	60.0	+ i
	S	12.0	16.0	52.0	76.0	72.0	76.0	87.5	+ i
Stellaria jamesiana	S	12.0	16.0	16.0	24.0	36.0	24.0	20.0	**** i
Tiarella trifoliata	N	0	3.3	0	3.3	23.3	26.7	37.5	+ i
Trillium ovatum	N	0	10.0	6.7	30.0	43.3	70.0	65.0	+ i
Vancouveria hexandra	N	36.7	50.0	36.7	66.7	93.3	96.7	90.0	+ i
	S	0	0	0	0	12.0	32.0	25.0	+ I
Viola glabella	N	30.0	43.3	50.0	46.7	70.0	80.0	62.5	+ i
	S	0	16.0	32.0	56.0	88.0	88.0	77.5	+ i
Viola lobata	S	0	0	4.0	24.0	28.0	24.0	15.0	+ i
Viola sempervirens	N	0	10.0	20.0	53.3	70.0	80.0	67.5	+ i
Viola sheltonii	S	0	0	4.0	12.0	12.0	28.0	27.5	+ i
Whipplea modesta	S	4.0	4.0	8.0	4.0	12.0	24.0	22.5	+ i
Mycotroph group [a]	N	0	0	6.7	6.7	33.3	33.3	27.5	+ i
	S	0	0	0	4.0	24.0	28.0	25.0	+ I
Orchid group [b]	N	0	0	0	3.3	13.3	26.7	20.0	+ I

[a] Seven species included in mycotroph group: *Allotropa virgata*, *Hemitomes congestum*, *Monotropa hypopitys*, *Pityopus californica*, *Pleuricospora fimbriolata*, *Pterospora andromedea*, and *Sarcodes sanguinea*.

[b] Three species included in orchid group: *Piperia unalascensis*, *Listera convallarioides*, and *Corallorhiza striata*.

on these data and those reported in studies conducted elsewhere in the Pacific Northwest (Chen et al. 1992, Halpern and Spies 1995, Luoma and Thies 1997), we conclude that negative edge effects on the understory can penetrate far into the adjacent forest. It follows that species with affinities for forest interior conditions could be experiencing population declines in highly fragmented forest landscapes within the Klamath region.

The potential mechanisms of negative edge effects in understory plants were reviewed by Frost (1997). Given the reduced abundance or complete absence of a number of understory herbs near forest edges, four different causal mechanisms seem most plausible. First, negative responses to edge-induced environmental changes, such as increased water stress, are likely to influence plants adapted to mesic sites. Second, the establishment and growth of aggressive disturbance-adapted species, such as many of the species frequently sampled in clearcuts, can result in increased competition for interior-oriented species. Third, interspecific interactions can change as a result of edge formation and result in reduced abundance of some herbs. For example, higher herbivory levels, decreased effectiveness of pollination, reduced presence of mycorrhizal associates, and increased seed predation may occur as a result of the creation of edges. Fourth, plant species with poor tolerance to physical disturbances associated with logging will decline near edges. The case study described below illustrates how complex these mechanisms can be, as well as how limited our ability to identify them will be without comprehensive analyses.

A Case Study: Trillium and Forest Fragmentation

One particular understory herb, western trillium (*Trillium ovatum*), has been the subject of several studies concerning forest fragmentation in the Klamath region because of some unique life history traits (Jules 1997a, 1997b, 1998). Annual stem production in trillium creates a constriction on the underground rhizome, such that the age of individuals can be estimated by excavated the rhizome and counting the constrictions (excavation does not kill the plants). The ability to age plants, as well as their long life span (up to 72 years), make trillium an ideal organism for demographic studies related to fragmentation. The studies of trillium described here were conducted in the Sucker Creek watershed, in forests that are very similar in structure and composition to those sampled by Frost (described above).

In an initial study to determine how logging had affected the general distribution of trillium, eight clearcuts (now young plantations; mean size = 11.4 ha) were surveyed for trillium, and the age of each plant was estimated. The data on plant abundance from this survey were compared to data collected at the same elevations in the same watershed by Whittaker in 1948 (published in 1960). This comparison suggested that the process of clearcutting and subsequent plantation development has resulted in the mortality of almost all trillium plants (ca. 97.6%). Essentially no recruitment of new plants has occurred in plantations; of the few plants that were found, most were at least as old as the clearcut in which they were sampled. Thus, trillium is generally, but not entirely, restricted to forest fragments in the Sucker Creek watershed, and the relictual plants in clearcut sites appear to be unable to successfully reproduce.

In a second study designed to investigate the effects of fragmentation on trillium within forest fragments, eight populations (ca. 15 m x 15 m each) were located in eight separate fragments surrounded by clearcuts and/or plantations. Populations were selected such that they varied in several key attributes, most importantly fragment size and distance to the edge of the fragment. In each population, the age of all individuals was estimated for the purpose of calculating demographic measures of recruitment for comparison with key attributes. Our comparisons showed no relationship of fragment size with recruitment of younger plants. However, recruitment of younger plants was significantly lower near edges as compared to forest interior. In fact, populations within about 65 m of the edge had almost no new recruitment since the edge was created, and these populations appear to be declining toward extinction.

In a final study, several potential mechanisms that might explain reduced recruitment of trillium were tested using the same eight populations. Survivorship of extant plants, flowering phenology (timing), seed production, pollination- and resource-limitation of seed set, seed dispersal, seed predation, and germination were compared with edge distance and recruitment of younger plants. Two processes were significantly different near edges and were highly correlated with decreased recruitment: seed production had decreased due to changes in pollination, and seed predation by rodents had increased. Pollinators, including common beetles and bees, appeared to be either less abundant or less effective near edges (Jules and Rathcke, 1999), and increased seed predation probably result from significantly higher densities of deer mice in clearcuts and along edges (Mills 1996). The other ecological factors were eliminated as possible mechanisms responsible for reduced recruitment. In this case, plant population declines associated with fragmentation are due to subtle but pervasive changes in interspecific interactions, rather than to direct alteration of the physical environment.

DISCUSSION

During the past 30 years, habitat fragmentation has been the focus of an enormous amount of theoretical and empirical work in ecology. Since this work began, the conceptual model used for understanding fragments of habitat embedded in a new "matrix" has been the analogy of islands surrounded by an ocean (e.g., MacArthur and Wilson 1967). Early work that focused on correlations of species diversity with fragment size and isolation treated habitat remnants just as the analogy suggests—isolated in a sea devoid of terrestrial life (Doak and Mills 1994). Perhaps due to both statistical and logistical problems inherent in such studies, much of the focus has shifted toward population-level studies. The result of this shift has been, among other things, a slow breakdown in the island-ocean analogy, and the acknowledgment among ecologists that many species do not operate as if they are restricted entirely to habitat remnants. Similarly, we have found a wide range of responses to the fragmentation of forests in the Klamath region.

Our review offers strong evidence for several different categories of species' responses to fragmentation. For example, for species like the California red-backed vole that are closely associated with or restricted to remnants of old forest, the island-ocean analogy is appropriate. In addition, a number of understory herbs are either restricted to or reach their greatest level of abundance in forest interior sites located away from the edges of clearcuts. For these species, we expect that the predictions described in our Introduction are likely to hold true—their populations are probably smaller and more isolated, and more likely to experience extinction in highly fragmented landscapes. Detailed studies on trillium as well as red-backed voles lend strong support for predicted consequences of fragmentation, such as population declines. Other species are likely to exhibit a neutral or even positive response to fragmentation, in that they are found in equal or greater abundance in the new matrix of disturbed habitats that has been created as a result of human activity in the Klamath region. Deer mice and dusky-footed woodrats (*Neotoma fuscipes*) as well as numerous disturbance-adapted plant species are found in greater abundance in clearcuts and plantations, and for these species the island-ocean analogy clearly is not appropriate (Mills 1996).

The view that habitat fragmentation leads only to islands of remnant habitat needs to be revised in light of the case studies presented here. The models describing isolated populations and the predictions concerning reduced population viability in fragmented landscapes are appropriate, but only for a subset of the regional biota; a whole suite of other organisms are not restricted to habitat remnants and are not adversely affected by current levels of fragmentation. Most important, the abundance of these organisms in a given region, as well as the number of species in each response group, is dependent on two main factors. First and most obvious, the amount of fragmentation that has occurred will strongly influence species composition. For example, very small and isolated clearcuts in a large contiguous forested landscape can lead to minimal edge and area effects for forest interior-associated species, while leaving little habitat for disturbance-oriented species. As clearcuts become more numerous and connected, however, the number of species that exhibit edge effects (both positive and negative) will increase.

The abundance of species and the relative number in each response group will be strongly influenced by a second factor—the type of fragmentation that has occurred.

Here we mean not only the shape of the matrix units (and thus of remnants), but also the characteristics of the matrix itself. As our work has shown, many species that are interior-oriented are occasionally present in clearcuts. The importance of these individuals may be great in that they may have the potential to disperse between remnants (or disperse their seeds to remnants), mitigating the adverse effects of inbreeding and of stochastic environmental and demographic events. Generally however, the island-ocean analogy has not encouraged very much consideration of the relictual or occasional individuals found in matrix. In fact, dispersal between remnant habitat, a key variable in models of population persistence, is almost always viewed as a function of distance between patches, with no regard to the type of habitat between patches (Harrison 1994). It is clear, though, that a remnant surrounded by a young plantation will differ markedly from one surrounded by an agricultural field. The significance of this oversight is that population-level studies in fragmented habitats have lost some of their potential and practical uses by focusing attention only on remnants and the creation of habitat "corridors" between remnants; the role of matrix has been largely overlooked as an important consideration (Franklin 1993, Vandermeer and Perfecto 1997).

One region in which numerous studies of matrix characteristics have been conducted is the Cascade and Coast Ranges of Oregon and Washington. This work has included documentation of a wide array of factors related to fragmentation, including (1) the extent of fragmentation at the landscape scale (Ripple et al. 1991, Rasmussen and Ripple 1998), (2) resulting abiotic changes (Chen et al. 1992, 1995), (3) changes in coarse woody debris (Spies and Cline 1988), and (4) shifts in biological diversity (Hansen et al. 1991, Halpern and Spies 1995). In an analysis of 23 bird species in 67 stands, including several kinds of managed and natural stands, Hansen and coworkers (Hansen et al. 1995) found significant habitat preferences for 18 of the species. They suggested that these birds can be classified into four guilds (open-canopy, open-canopy with dispersed large trees, structurally complex closed-canopy, or structurally simple closed-canopy), implying a diversity of responses to managed matrix. Halpern and Spies (1995) showed that vascular plant diversity can recover quickly after clearcutting, although some local extinction does occur. In sites that were intensively burned, diversity was depressed for up to two decades. Also, chronosequence studies of unmanaged stands suggest that plant diversity peaks in old-growth forest (see also Schoonmaker and McKee 1988). This and other ongoing studies, however, are limited by the absence of older, managed forests that could be used to assess long-term trends in managed matrix (Hansen et al. 1991, Halpern and Spies 1995).

This work on matrix has direct implications for forests in the Klamath Mountains Region because of the similarities in species and community structure. Most important, the studies in the Cascade and Coast Ranges suggest that the kind of matrix management (e.g., burning intensity) and the resulting structural characteristics (e.g., snag and large tree retention, levels of woody debris) can be important for many taxa. However, differences between the two regions, such as drier, warmer growing seasons and the resulting higher frequency fire regime (Franklin and Dyrness 1973), are likely to result in different, species-specific responses to fragmentation in the Klamath region.

Given the importance of both patterns of fragmentation and matrix characteristics in determining species' distributions, we conclude that the likelihood of maintaining biological diversity in forested landscapes found in the Klamath region will increase by protecting the relatively scarce remnants of remaining late-successional/old-growth forest, minimizing the fragmentation of the landscape, and managing clearcuts and plantations in such a way that they are most likely to serve as viable dispersal habitat between remnants and/or be colonized by organisms that depend upon older forests. More research on matrix in the Klamath region is needed. Our own studies indicate that the rapid fragmentation of Klamath region forests has had strong negative effects on a number of species, and we strongly suspect that there are many more organisms, such as fungi, insects, birds, and lichens, for which we have no data. These negative effects are found alongside an array of neutral and positive responses that do not fit the traditional view of fragmentation. The existence of these other responses suggests that the discussion regarding fragmentation should be broadened to include consideration of the actual distributions of organisms, as well as the potential roles of all habitats.

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