

## LANDSCAPE-LEVEL PATTERNS OF AVIAN DIVERSITY IN THE OREGON COAST RANGE

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**Abstract.** We used a comparative mensurative landscape-level experiment to quantify the relative importance of mature forest area and fragmentation and differences among watersheds in influencing avian community diversity in the Oregon Coast Range, USA. Our study design included three large hydrological basins, two levels of fragmentation, and six levels of mature forest area. We recorded 82 species of birds in a total of 1046 plots in 30 landscapes. Our four response variables were species richness, species density, species evenness, and total bird density. We used a combination of factorial ANOVA and partial canonical variates analysis to quantify the relative importance of differences in mature forest area, fragmentation, and basin in influencing each response variable and community diversity overall.

Bird community diversity was influenced by both the extent and fragmentation of mature forest at the landscape level. Species richness and density responded more strongly to mature forest area than to fragmentation and were significantly lower in landscapes that were completely dominated by mature forest than in landscapes with a mixture of seral stages. This reflected a selective loss of a number of early-seral species when mature forest completely blanketed the landscape. Species evenness was more strongly related to fragmentation than to area of mature forest at the landscape level. In fragmented landscapes, the most dominant species decreased in abundance, whereas moderately abundant species increased in relative abundance. This resulted in bird communities that were more even in fragmented landscapes. Unlike several other studies, we did not find that the relative strength of fragmentation effects increased as habitat area decreased. Total bird density, in contrast, was not related to either mature forest area or fragmentation, but it varied significantly among basins. In summary, although both area and fragmentation of mature forest at the landscape level were strongly related to bird community diversity, they had qualitatively different effects. These results must be interpreted within the scope of this study, which took place in a forest-dominated landscape. Our results provide an interesting view of the factors that are related to bird diversity in a spatially complex seral mosaic but may not reflect the patterns that would exist in a high-contrast forest–nonforest landscape.

**Key words:** *bird communities; habitat diversity; intermediate disturbance hypothesis; landscape pattern; mature forest area; mature forest fragmentation; Oregon Coast Range; species diversity; species evenness; watershed.*

### INTRODUCTION

Determining the factors that influence community diversity remains one of ecology's most persistent and controversial issues. The general question of what drives community diversity is theoretically interesting, while understanding how anthropogenic changes to ecological systems affect species diversity and abundance is central to effective conservation planning. The idea that local ecological characteristics determine local diversity has been dominant for decades (Cody 1985, Blake and Karr 1987, Soulé et al. 1992). However, it has become increasingly clear that species diversity is determined by multiple factors acting at multiple scales (Turner 1989, Wiens 1989, Turner and

Gardner 1991). Patch, landscape, and regional patterns and processes must be accounted for if scientists wish to fully account for species diversity at any given location.

There have been many studies of patch-level influences on species diversity and abundance. These studies followed from MacArthur and Wilson (1967), who proposed that the number of species in island habitats is determined by an interaction of island size and isolation. A major assumption of the application of their island biogeographic theory to terrestrial habitats is that effects of patch size and isolation are independent of landscape context. This assumption rests on the premise that populations are separated into patches of suitable habitat within an unsuitable matrix (Merriam et al. 1991, Opdam 1991, Debinski et al. 2001). This assumption is unlikely to be justified in real systems. Evidence from studies of metapopulation dynamics

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(Levins 1970, Hanski and Gilpin 1997, Holt 1997), source-sink dynamics (Pulliam and Danielson 1991), and mass effects (Shmida and Wilson 1985, Auerback and Shmida 1987, Kunin 1998) strongly suggest that the landscape context of a patch can strongly mediate the diversity of organisms that reside there. For example, mass effects may dilute species-habitat or species-area relationships by altering the frequency of species colonization of suboptimal habitats from outside source pools, due to differences in regional species density and productivity (Shmida and Whittaker 1981). Thus, studies that do not account for the influences of landscape-level factors may make erroneous predictions about the relative influences of local and patch-level processes on species diversity (Allen and Starr 1982, Wiens 1989, 1994).

There has been increasing interest in the influences of landscape-level patterns and processes on species diversity and abundance (Askins et al. 1987, Ricklefs 1987, Ricklefs and Schuller 1993, Andr en 1994, Kareiva and Wennergren 1995, Robinson et al. 1995, Flather 1996, Flather and Sauer 1996, Bolger et al. 1997, Fahrig 1997, 1998, Augermeir and Winston 1998, Trzcinski et al. 1999, Villard et al. 1999, Drapeau et al. 2000). Most studies of landscape-level influences on species diversity have been conducted in landscapes with strong contrast between habitat fragments and less suitable matrix (Opdam 1991). The majority of these studies found negative effects of habitat fragmentation on species diversity and abundance. Some of these studies have shown a general trend toward lower species diversity following habitat loss and fragmentation, whereas others have found that diversity may peak at intermediate disturbance levels (Connell 1978, Jokimaki and Suhonen 1993, Blair 1996). However, relatively few studies have been undertaken in landscapes that are not subject to semipermanent conversion to less suitable habitat. For example, relatively little is known about how the spatiotemporal dynamics in forest seral stages at the landscape level influence species diversity in managed forest landscapes (e.g., McGarigal and McComb 1995).

In addition, at the landscape level, many factors covary in their influences on species diversity and abundance. For example, a number of studies have shown that the size, number, and distribution of habitats has an important influence on species diversity (Freemark and Merriam 1986, van Dorp and Opdam 1987, Donovan et al. 1995, Freemark et al. 1995, Robinson et al. 1995, Bolger et al. 1997, Drapeau et al. 2000, Howell et al. 2000). However, the degree of habitat fragmentation (i.e., the subdivision and isolation of habitat fragments) in a landscape is usually highly confounded with the amount of habitat (Fahrig 1997, 1998, Trzcinski et al. 1999, Villard et al. 1999). In other words, as habitat is lost in a landscape due to disturbance, the degree of spatial fragmentation of the remaining habitat often increases. As a result, it has proven very difficult

to robustly quantify the relative importance of different factors at the landscape level.

The key to separating the confounded effects of landscape-level factors on community diversity is to conduct replicated and controlled studies with landscapes as experimental units. However, remarkably few empirical field studies of species diversity have been replicated and controlled at the landscape level (McGarigal and Cushman 2002). Replicated and controlled studies that have landscapes as the experimental units are necessary to rigorously assess landscape-scale effects on species diversity and decompose the influences of important covarying landscape factors such as habitat area and fragmentation (Fahrig 1997, Villard et al. 1999, McGarigal and Cushman 2002). Only through such rigorous separation can scientists know with confidence the importance of habitat fragmentation vs. simple habitat loss at the landscape level, a question that is at the heart of a number of major debates in community ecology and conservation biology.

### *Hypotheses*

Our major goal in this research was to quantify how the area and fragmentation of mature forest (hereafter also referred to as late-seral forest) in Oregon Coast Range landscapes influence the diversity of birds at the landscape level, as measured by species richness, species density (number of species per ha), evenness, and total bird density. Specifically, we sought to separate the effects of mature forest area and fragmentation, and differences among large hydrological basins, on these diversity variables. Our research was motivated by four primary hypotheses.

First, we hypothesized that total bird density across all species would peak in landscapes with low mature forest area, as many early-seral birds tend to occur at higher densities than most late-seral birds in the Oregon Coast Range (Brown 1985). We reasoned that this was probably an evolutionary legacy of the dominance of late-seral forests in this landscape. Because early-seral habitats are relatively ephemeral, these species probably maximize fitness through a combination of high reproduction and rapid dispersal. As a result, early-seral species tend to occur at higher densities in their optimal habitats than do mature forest species, which live in more continuous and relatively stable habitats and are likely to maximize fitness through competitive superiority. In addition, we expected that fragmentation of mature forest habitat also would increase total bird density, because increasing edge habitats and decreasing interior habitat area, at a given level of mature forest area, will generally favor early-seral species, which occur at high densities relative to late-seral species.

Second, we hypothesized that species richness, density, and evenness would peak in landscapes with intermediate levels of mature forest cover and high fragmentation. This prediction follows from the interme-

diate disturbance hypothesis (Paine 1966, Connell 1978) and habitat diversity hypothesis (Wiens 1989), which predict that landscapes with an equitable and interspersed mixture of early- and late-seral forests should have both more diverse and more equitably abundant resources than landscapes that are dominated by either early- or late-seral forest.

Third, we hypothesized that mature forest area and fragmentation would be partly confounded in their effects on bird diversity at the landscape level. Consequently, when effects of mature forest area are statistically removed from the diversity measures, the multivariate separation between fragmented and unfragmented landscapes should decrease. Similarly, when effects of fragmentation are removed from the diversity measures, the separation among levels of area should decrease. In contrast, when the influences of interbasin differences are statistically removed, multivariate separation among levels of area and between levels of fragmentation should increase because differences among basins in bird diversity are not expected to be related to differences in mature forest area or to the degree of fragmentation. Removing the basin effect should remove variance in the diversity variables that is not related to differences among levels of forest area or levels of fragmentation, and thus should increase the proportion of remaining variance that is related to differences among these groups.

Fourth, we hypothesized that mature forest area would be a better predictor of all four diversity measures than would fragmentation. This contention was based partly on our earlier findings for individual species (McGarigal and McComb 1995) and partly on other published studies (e.g., Villard et al. 1999, Trczinski et al. 1999), from which there has emerged a general picture that for most species in most systems, the amount of habitat at the landscape level is usually more important than its spatial configuration (Fahrig 1997, 2001). It follows that when the effects of confounding factors are statistically removed, area of mature forest should have a stronger relationship with overall bird diversity than does fragmentation. Several researchers have found that spatial configuration of habitat matters most when habitat area is low, for example, roughly <30% of the landscape (Fahrig 1997, 1998, 2001, Jansson and Angelstam 1999, With and King 1999b). Consequently, we also hypothesized that mature forest fragmentation will be relatively more important when the percentage of the landscape covered by mature forest is low, and that there will be little effect of fragmentation at high levels of forest area.

## METHODS

### *Study area*

The study area is described in detail in McGarigal and McComb (1995); here we provide only a brief description. The study area consists of three major hydrological basins (Drift Creek, Lobster Creek, and Nes-

tucca River basins) in the central Oregon Coast Range, USA (Fig. 1). Elevation ranges from sea level to 968 m. Climate is maritime with mild, wet winters and cool, dry summers. The study area is characterized by steep slopes and deeply cut drainages and lies almost entirely within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973). The natural forest overstory is dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and red alder (*Alnus rubra*). Western redcedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyllum*) are also common. Understory vegetation is variable in composition and distribution. Common species include salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), Oregon grapes (*Berberis* spp.), huckleberries (*Vaccinium* sp.), and swordfern (*Polystichum munitum*).

The entire area experienced a series of catastrophic wildfires in the mid-1800s and regenerated naturally (Spies and Cline 1988). Over the past 45 years, federal land managers have used a dispersed-patch system of clear-cut logging, which maximizes fragmentation of the late-seral forest matrix (Franklin and Forman 1987). As a result, the area currently has a bimodal age distribution dominated by early-seral forests (<40 yr old) and mature forests (100–150 yr old). Mid-aged (40–100 yr old) and old-growth (>150 yr old) forest are poorly represented. For the purpose of this study, we defined late-seral forest as large sawtimber (>20% overstory cover composed of trees with a mean dbh >53.3 cm) as well as remnant old growth (>20% overstory cover composed of trees with a mean dbh >81.3 cm and multistory canopy).

The study area contains some private lands (primarily industrial forestland), but is dominated by public lands administered by the USDA Forest Service and USDI Bureau of Land Management. In portions under public ownership, the landscape consists of a matrix of late-seral, unmanaged forest dominated by Douglas-fir and red alder perforated by many small (8–25 ha), young, even-aged Douglas-fir plantations. In private land, the landscape consists largely of extensive, young (0–40 yr old), even-aged Douglas-fir plantations, with isolated patches of late-seral forest. Consequently, a wide range of landscape structural conditions exists in the study area, particularly with respect to the extent and fragmentation of late-seral forest.

### *Landscape mapping*

We used color infrared aerial photos to map 27 different patch types across each basin (McGarigal and McComb 1995). Late-seral forest, as defined previously, included hardwood-, mixed-, and conifer-large sawtimber. In some landscapes, late-seral forest also included scattered remnant old-growth trees and patches. We defined minimum patch size as 0.785 ha and >50 m wide in the narrowest dimension. This minimum

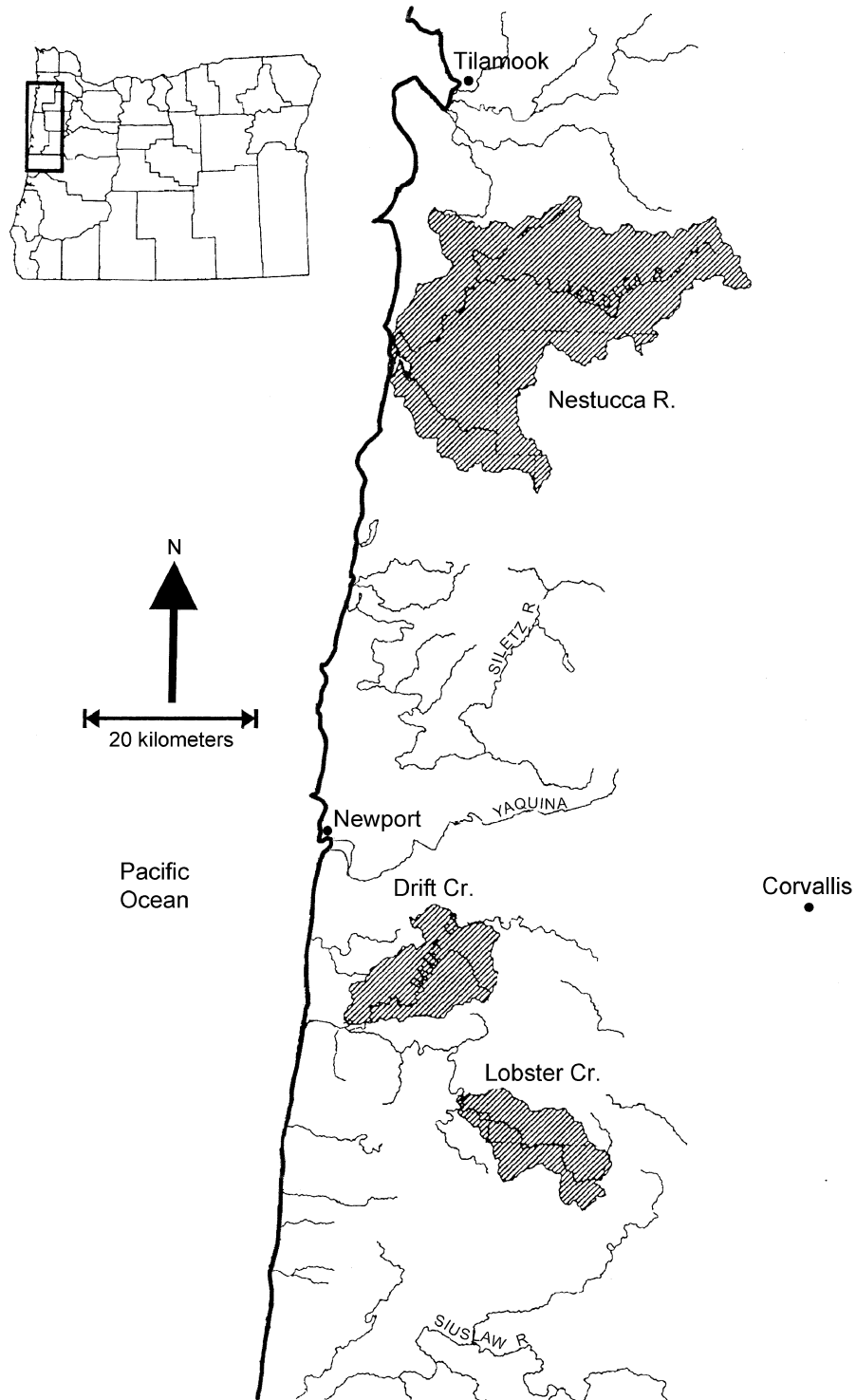


FIG. 1. Study area orientation map depicting the location of the three study basins in the Oregon Coast Range.

area corresponds roughly to the smallest estimated home range size of any bird species found in the study area (Brown 1985). We then used FRAGSTATS (McGarigal and Marks 1995) to measure the area and

fragmentation of mature forest in each landscape. We used the results of this landscape mapping to guide selection of replicate landscapes in our study design, as we will describe.

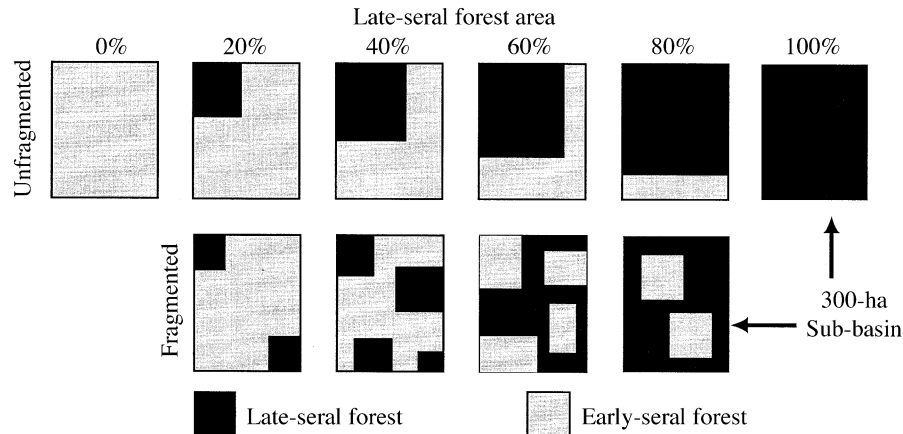


FIG. 2. Study design schematic. Late-seral forest includes all conifer-, mixed-, and hardwood-large sawtimber. Early-seral forest includes all other patch types, including all forest types <100 years old.

### Study design

Our study design included three basins, two levels of mature forest fragmentation, and six levels of mature forest area. Within each basin, we selected 10 landscapes to provide replicates for each combination of mature forest fragmentation and mature forest area (Fig. 2). Thus, there were three replicates of each combination of area and fragmentation level, one from each basin, and 10 replicates for tests of differences among basins (Fig. 2). The landscapes ranged from 250 to 300 ha in size and corresponded to hydrologic sub-basins. Landscapes of this size reflected a compromise between landscape size and sample size. We chose the largest landscape size that still provided sufficient sample size for multivariate analyses. The six levels of mature forest area were 0, 20, 40, 60, 80, and 100% of the landscape. The fragmentation classes were defined simply as “fragmented” and “unfragmented,” based on the density of mature forest edge. Within each level of area in each basin, we selected the landscape with the lowest mature forest edge density as the “unfragmented” sample and the landscape with the highest mature forest edge density as the “fragmented” sample. We examined the interaction of each level of area with each level of fragmentation, except for 0% and 100% area, which were only present in the “unfragmented” level of fragmentation. Thus, in each of the three basins there were four landscapes with high fragmentation, one for each of 20, 40, 60, and 80% cover of mature forest, and six landscapes with low fragmentation, one for each of 0, 20, 40, 60, 80, and 100% cover of mature forest (Fig. 2). Landscapes were our replicate unit and all statistics were calculated at that level.

From this experimental design, we can produce two two-way unbalanced linear models to test Area (A), Fragmentation (F), Basin (B),  $A \times B$  interaction, and  $B \times F$  interaction effects, but no three-way factorial, and no test of the  $A \times F$  interaction, as follows:

$$Y_{ijk} = A_i + B_j + AB_{ij} + e_{ij(k)}$$

$$Y_{ijk} = B_j + F_l + BF_{jl} + e_{jl(k)}$$

where  $Y$  is the diversity measure, and  $e$  is residual error. Area and Fragmentation are fixed factors because we are interested only in differences among these particular levels of these factors. We limit our conclusions to differences among these three particular basins; therefore, we treat Basin as a fixed factor also. As a result of all factors being fixed, all tests use the error strata as the denominator of the  $F$  ratio.

### Bird sampling

We systematically located sample points in a uniform grid at 200-m intervals along transects spaced 400 m apart in each landscape. Based on an effective detection distance of 50 m, each sample point corresponded to an effective sample area of 0.785 ha, and the grid provided a uniform sample of ~10% each of landscape area. At this sampling intensity, we acquired between 32 and 38 sample points per landscape, for a total of 1046 points.

We sampled diurnal breeding birds in Drift Creek, Lobster Creek, and Nestucca River basins in 1990, 1991, and 1992, respectively. Confounding of year and basin was not significant (McGarigal and McComb 1995). Each year, we sampled birds four times in each of the 10 landscapes at regular intervals between 1 May and 12 July. Surveys began 15–20 min before sunrise and ended within 4 h after sunrise. On each visit, observers waited 2 min to allow birds to resume normal activity and then recorded all birds detected within 50 m during an 8-min sampling period (Fuller and Langslow 1984, Verner 1988). Only new detections during the sample of a landscape were included in the analysis. The resulting database included 82 bird species and an average of 2693 individual bird detections per replicate landscape, for a total of 80 794 bird detections.

*Landscape-level measures of species diversity*

Standard diversity indices, such as Shannon's or Simpson's diversity, confound the signals of total abundance, species evenness, and species richness. Evenness and richness reflect categorically different aspects of community structure and should be analyzed separately (Gotelli and Graves 1996). Thus, we did not analyze any composite diversity indices, but rather the responses of four different diversity variables measuring species richness, species density, species evenness, and total bird density. Traditional measures of species richness, density, and evenness are biased for comparison among landscapes because of differences in overall bird density, total abundance, differences in area sampled, and differences in landscape size (Gotelli and Graves 1996, Gotelli 2000). We computed an unbiased measure of species richness using rarefaction. Rarefaction is a resampling method that estimates the expected species richness of an assemblage for a given number of sampled individuals. For each of the 30 landscapes, we computed rarefaction curves using EcoSim software, with 1000 iterations (Gotelli and Entsminger 2002). Second, we computed species density from the rarefaction curves and the total area sampled in a landscape. Briefly, using rarefaction, we computed the expected number of species per number of birds sampled and divided that by the area of the landscape. To facilitate this calculation, we fit third-order regressions of rarefaction estimates on log-transformed total abundance levels. The regressions were all forced through the origin. For all basins, the regressions were significant at  $P = 0.0001$  and all had  $R^2$  values  $>0.999$ . We then produced species density curves for each basin for the number of species expected at 0.1–50 ha. Third, we computed an unbiased evenness index, the probability of interspecific encounter (PIE; Hurlbert 1971), given as the probability that two randomly selected individuals in a landscape (in this case) are from different species. It has several advantages as a measure of evenness: it has an easily understood, intuitive meaning and is a stable and unbiased estimator of species evenness (Gotelli and Graves 1996). We conducted Monte Carlo simulation of PIE values for each landscape across a range of bird abundances from 0 to 3000 using EcoSim using 1000 iterations. Fourth, we computed total bird abundance per hectare simply by dividing the total bird count per landscape by the number of sample plots multiplied by the area per plot.

We tested these variables for multicollinearity with pairwise Pearson's correlation. The only variables that were highly correlated were species richness and species density ( $r = 0.94$ ). No other combinations of variables were correlated to a greater degree than  $r = 0.45$ . Despite the high correlation, we included both species richness and species density, as suggested by Gotelli and Graves (1996), because of the important ecological difference between species per number of sampled in-

TABLE 1. Contrasts used to test predictions of hypothesis 1 at different levels (0–100%) of mature forest area.

	Area level of mature forest (%)					
	0	20	40	60	80	100
–5	1	1	1	1	1	1
–2	–2	1	1	1	1	1
–1	–1	–1	1	1	1	1
–1	–1	–1	–1	–1	–1	5
1	0	0	0	0	0	–1
1	0	–1	–1	0	0	1

dividuals and species per unit area. The collinearity of these variables is not an issue for univariate analyses, and the multivariate analyses that we used are quite robust to collinearity (ter Braak and Smilauer 1998).

*Test for spatial autocorrelation*

Comparative mensurative field experiments at the landscape scale face the difficult challenge of obtaining replicate samples that are spatially independent in terms of the measured response variables. In landscape analyses, positive spatial autocorrelation of response variables among sample landscapes is the most common kind of dependence. In the presence of positive autocorrelation, computed statistical tests too often declare differences to be significant.

We tested for spatial autocorrelation in each of the four diversity measures using Moran's  $I$  (Legendre and Legendre 1998). We calculated spatial autocorrelation overall, across all three sampled basins, and within each basin, across a range of lag distances. We calculated the geographical center of each landscape and calculated Moran's  $I$  for each of five inter-centroid distance classes using the R-Package (Legendre and Vaudor 2001). Correlogram significance values were corrected using the Bonferroni procedure.

*Tests of hypotheses*

We used a combination of factorial ANOVA, general contrasts, weighted-averaging canonical variates analysis (CVA), and partial weighted-averaging CVA to test our predictions.

*Hypothesis 1.*—We tested the differences in total bird abundance among levels of area, fragmentation, and basin using factorial ANOVA and general contrasts. We used the same two unbalanced two-way models previously introduced:  $Y_{ijk} = A_i + B_j + AB_{ij(k)} + e_{ij(k)}$  and  $Y_{ijk} = B_j + F_l + BF_{jl} + e_{j(k)}$ . We tested the significance of all terms using the GLM procedure and Type III sums of squares using SAS software version 8.0 (SAS Institute 2001), because our design is unbalanced in terms of replication within cells. After ascertaining that the area  $\times$  basin interaction was nonsignificant in the first model, we constructed the contrasts shown in Table 1 to test specific predictions. We note that these contrasts, although they test the particular differences in which we are interested, are not orthogonal. Thus,

TABLE 2. Contrasts used to test predictions of hypothesis 2 at different levels (0–100%) of mature forest area.

Area level of mature forest (%)					
0	20	40	60	80	100
-1	-1	2	2	-1	-1
-2	1	1	1	1	-2
-1	0	1	1	0	-1
5	-1	-1	-1	-1	-1
-1	-1	-1	-1	-1	5
2	2	-1	-1	-1	-1
-1	-1	-1	-1	2	2
-1	0	0	0	0	-1

we controlled for experiment-wise Type I error using a sequential Bonferroni procedure. For the second model, no contrasts were needed, as there are only two levels in the factor fragmentation.

*Hypothesis 2.*—We tested the predictions for this hypothesis using a combination of factorial ANOVA and general contrasts. Separate analyses were done for each dependent diversity variable (i.e., species richness, density, and evenness). Contrasts were constructed only for area because there are only two levels of fragmentation. After ascertaining that the area × basin interaction was nonsignificant, we constructed the contrasts in Table 2 to test the specific predictions of hypothesis 2.

In addition to using univariate ANOVA, we tested the multivariate differences among levels of area and

fragmentation with canonical variates analysis (CVA). Canonical variates analysis is an eigenvector technique that constructs linear combinations of independent variables that maximally separate classes of a grouping variable in multivariate space. In this case, the independent variables include the four diversity variables and the grouping variable is either mature forest area (six levels) or fragmentation (two levels). The sample sizes of our study design violate the sample-to-variable ratio requirements of classical CVA. However, a weighted-averaging solution to CVA does not require this assumption (Chessel et al. 1987, Lebreton et al. 1988, ter Braak and Verdonschot 1995, ter Braak and Smilauer 1998). We conducted weighted-averaging CVA in CANOCO 4 (ter Braak and Smilauer 1998) to test whether species diversity can effectively discriminate among levels of mature forest area and between fragmentation levels of mature forest. Canonical variates analysis in CANOCO 4 has the further advantage that the significance of group discrimination can be tested with Monte Carlo simulations, which have much less restrictive assumptions about the distribution of the data than do classical significance tests (ter Braak and Smilauer 1998).

*Hypotheses 3 and 4.*—We tested the predictions of hypotheses 3 and 4 using weighted-averaging CVA and partial weighted-averaging CVA. For these tests, we developed 11 CVA models (Table 3), all of which used the four diversity variables (species richness, density,

TABLE 3. List of the 11 canonical variates analysis models used to test hypotheses concerning the ability of several measures of species diversity to discriminate among six levels of mature forest area, two levels of mature forest fragmentation, and three basins in the Oregon Coast Range.

Model acronym	Discriminant class†	Effects removed‡	Factors discriminated
A	area	none	Levels of mature forest area based on the four raw diversity variables
A(B)	area	basin	Levels of mature forest area based on the four diversity variables, after removing the effect of basin
A(F)	area	fragmentation	Levels of mature forest area based on the four diversity variables, after removing the effect of fragmentation
A(BF)	area	basin and fragmentation	Levels of mature forest area based on the four diversity variables, after removing the effect of basin and fragmentation
F	fragmentation	none	Levels of mature forest fragmentation based on the four raw diversity variables
F(B)	fragmentation	basin	Levels of mature forest fragmentation based on the four diversity variables, after removing the effect of basin
F(A)	fragmentation	area	Levels of mature forest fragmentation based on the four diversity variables, after removing the effect of area
F(BA)	fragmentation	basin and area	Levels of mature forest fragmentation based on the four diversity variables, after removing the effect of basin and area
B	basin	none	Difference among basins based on the four raw diversity variables
B(F)	basin	fragmentation	Difference among basins based on the four raw diversity variables, after removing the effect of fragmentation
B(A)	basin	area	Difference among basins based on the four raw diversity variables, after removing the effect of fragmentation

† The categorical class variable whose levels are being discriminated.

‡ This indicates the class variables that are entered as covariables in CANOCO 4 (ter Braak and Smilauer 1998) and whose effects on the diversity variables are removed.

and evenness, and total bird density) as the explanatory variables, and mature forest area (six levels), fragmentation (two levels), or basin (three levels) as the grouping variable. We used partial weighted-averaging CVA to remove the effects of particular class variables on the diversity variables (Table 3). The partial models were developed by inserting the class variables whose effects we wished to remove as covariables. For each model, we tested the overall significance of discrimination through Monte Carlo permutation tests of the significance of all canonical eigenvalues, with 199 permutations, and conducted a forward selection with Monte Carlo permutation tests of the significance of each explanatory variable in each model. The success of each model was also evaluated based on total variance explained and classification accuracy. The predicted class membership was calculated by computing the minimum squared Mahalanobis distance to each cluster centroid (McGarigal et al. 2000). We then computed an error matrix for each model and computed the chance-corrected accuracy using the  $\tau$  statistic (McGarigal et al. 2000). The significance of each explanatory variable in each model was evaluated based on its marginal (i.e., the variance accounted for by itself) and conditional (i.e., the additional variance accounted for after adjusting for the variance accounted for by variables already included in the model) effect to determine which diversity measures most discriminate between classes, and how removing the effects of certain class variables changes the contribution of a variable in a model. The conditional effect was tested for significance using a Monte Carlo permutation test. We also produced canonical plots to graphically display the patterns among the replicate landscapes across the different classes.

## RESULTS

### *Test for spatial autocorrelation*

At the scale of differences among basins, there was no significant spatial autocorrelation. This is not surprising, as landscapes in the three different basins were separated by ~50 km. We also tested for autocorrelation in each of the four diversity measures within each of the three basins. Species richness, species density, and species evenness were not significantly autocorrelated at any lag distance in any of the three basins. This shows that, at least in terms of spatial independence, the landscapes that we selected are sufficiently independent to be treated as replicates for these variables. Total number of birds per hectare showed significant spatial autocorrelation in the Lobster Creek basin. It was positively autocorrelated at lag distances  $\leq 4$  km and negatively autocorrelated at lag distances  $> 19$  km. There was no significant autocorrelation of birds per hectare in either of the other two basins. The fact that only one of the 12 combinations of variable by basin showed significant autocorrelation,

and then only at short or very long lag distances (relative to the distribution of inter-landscape distances) indicates that spatial autocorrelation among response variables does not invalidate our treatment of landscapes as independent replicates in this study.

### *Hypothesis 1*

We predicted that species associated with the earliest of seral stages (i.e., grass-forb and shrub-dominated communities) should occur at higher densities than species associated with mature forest. Although the most common species in either early- or late-seral patches occurred at equal densities, the vast majority of species found in early-seral patches occurred at higher densities than species found in late-seral patches (Fig. 3). In fact, the eight most abundant species known to be strongly associated with very early seral habitats (McGarigal and McComb [1995]; see bold points in Fig. 3) occurred at twice the densities of the eight most abundant species strongly associated with late-seral forests (57.8 vs. 24.5 birds/40 ha, respectively).

Despite these patterns, and contrary to our expectations, neither the area of mature forest nor fragmentation of mature forest at the landscape level had a significant overall effect on total bird density ( $P = 0.106$ ,  $P = 0.118$ , respectively), although the general contrasts indicated that total bird density was greater in landscapes with 0–20% mature forest cover than in landscapes with 40–100% mature forest cover (Table 4). The lack of a strong effect of mature forest area and fragmentation on total bird density was probably due to the fact that most of the “early-seral” component of these landscapes actually consists of young pole stands of timber that were comparatively depauperate of birds. Thus, the higher total bird densities in very early seral habitats were compensated for by the lower densities in the more extensive mid-seral habitats. Interestingly, for both area and fragmentation, there was a significant basin effect ( $P = 0.021$ ,  $P = 0.019$ , respectively), indicating that the basins differed among themselves in total bird density, but there were no significant differences in total bird density related to either levels of mature forest area or levels of fragmentation. None of the interaction terms was significant.

### *Hypothesis 2*

We predicted that habitat diversity should peak at intermediate levels of mature forest area. This was, in fact, the case, as measured by Simpson’s landscape diversity index (McGarigal and Marks 1995; see Fig. 4). Interestingly, habitat diversity exhibited remarkably little variability among landscapes with  $> 60\%$  mature forest, and relatively high variability when mature forest area was  $< 40\%$  (Fig. 4). This pattern reflected the fact that there were disproportionately large numbers of “early-seral” patch types, as opposed to “late-seral” patch types. Thus, landscapes dominated by early-seral patch types were highly variable in composi-

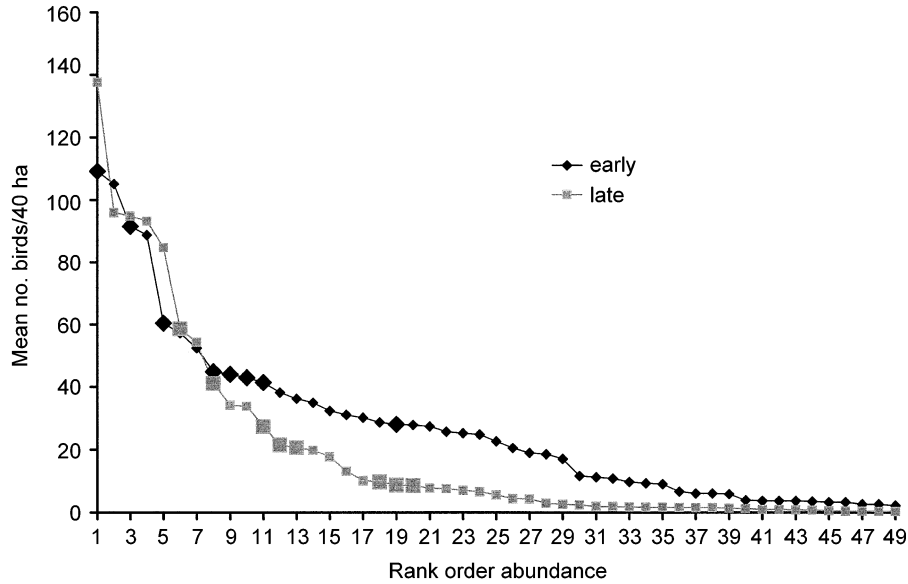


FIG. 3. Differences between the average density of individual species in very early-seral (i.e., grass-forb and shrub dominated) patches ( $n = 59$ ) and mature forest patches ( $n = 465$ ) in the Oregon Coast Range. The plot shows the mean number of birds/40 ha for the 50 most abundant species in early- and late-seral patches, in rank order of their abundance. The eight most abundant species in each habitat occurred at roughly equal densities. The eight species most strongly associated with early-seral forest (diamonds) and late-seral forest (squares) are plotted with larger symbols, revealing that the vast majority of early-seral species occurred at higher densities than did late-seral species.

tion and, therefore, patch diversity. In addition, we expected that species diversity should be strongly related to habitat diversity. This, too, was the case, although the relationship was not strong or consistent across all measures of species diversity. Species richness, for example, increased linearly with increasing patch type diversity ( $P < 0.001$ ), although the relationship was due primarily to consistently low richness at the lowest observed patch diversity levels (associated with 100% mature forest landscapes) and consistently high richness at the highest observed patch diversity levels (Fig.

5). At intermediate levels of patch diversity, species richness was highly variable.

Despite the general support for our predictions, species diversity did not peak significantly at intermediate levels of mature forest area. There were significant differences in species richness and density among levels of area, but richness reached its minimum in landscapes with 100% mature forest cover, rather than peaking at intermediate levels (Fig. 6). In fact, the contrasts indicated that the major difference among levels of forest area in terms of species richness and density was be-

TABLE 4. ANOVA results for the effects of mature forest area (A, six levels), basin (B, three basins), and area-basin (AB) interaction on species richness, density and evenness, and total bird density in the Oregon Coast Range ( $n = 30$  landscapes), based on the following model:  $Y_{ijk} = A_i + B_j + AB_{ij} + e_{ijk}$  where  $Y$  is the diversity measure and  $e$  is residual error.

Dependent variable	Area		Basin		Area $\times$ basin		Significant contrasts
	F	P	F	P	F	P	
Species richness	4.540	<b>0.015</b>	3.410	0.067	0.770	0.660	1-5 > 6, $P < 0.001$ ; 1-4 > 5-6, $P = 0.003$ ; 1 > 6, $P = 0.005$
Species density	5.540	<b>0.007</b>	3.260	0.074	1.390	0.292	1-5 > 6, $P < 0.001$ ; 1 > 6, $P = 0.002$ ; 1-4 > 5-6, $P = 0.002$
Species evenness	0.840	0.547	0.230	0.795	0.490	0.864	no significant contrasts
Bird density	2.340	0.106	5.320	<b>0.022</b>	1.660	0.201	1-2 > 3-6, $P = 0.017$

Notes: Significant relationships at  $\alpha = 0.05$  are given in boldface.  $P$  values are based on Type III sums-of-squares to account for the unbalanced design. In addition, significant contrasts associated with each diversity variable are given, where the numbers refer to the six levels of mature forest area (i.e., 1, 0%; 2, 20%; 3, 40%; 4, 60%; 5, 80%; and 6, 100%). For example, the contrast 1-5 vs. 6 shows differences between landscapes with 0-80% mature forest and landscapes with 100% mature forest.

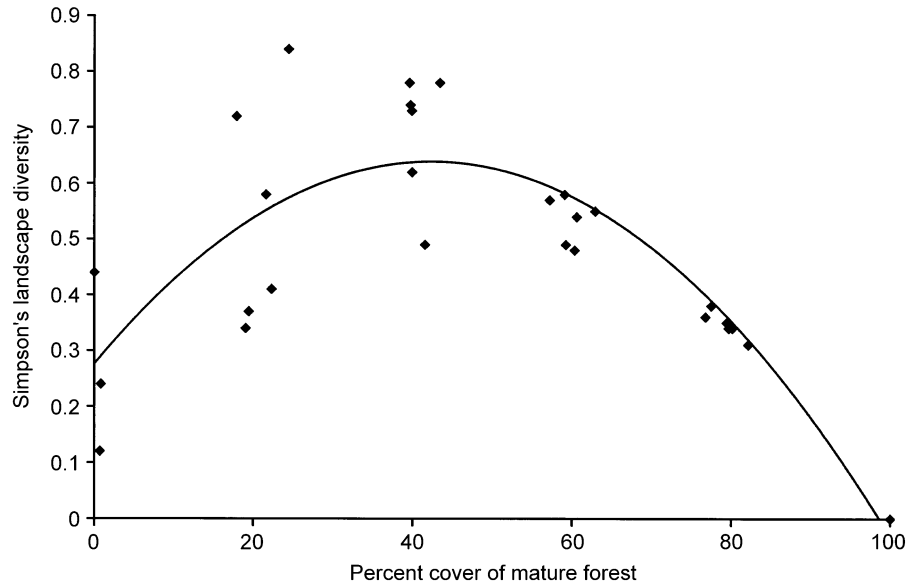


FIG. 4. Scatter plot of FRAGSTATS Simpson's diversity index vs. the percentage of landscape covered by mature forest in the Oregon Coast Range ( $n = 30$  landscapes). Simpson's diversity index was based on the number and areal extent of patch types in each landscape and was used as an index of habitat diversity at the landscape level. The solid line represents a second-order polynomial regression ( $y = 0.276 + 0.017x - 0.0002x^2$ , where  $y$  is Simpson's diversity index and  $x$  is the percentage of landscape covered by mature forest) and shows that habitat diversity exhibits a strong nonlinear relationship with the percentage of landscape covered by mature forest ( $P < 0.001$ ,  $R^2 = 0.77$ ), as predicted by the intermediate disturbance hypothesis.

tween landscapes with 100% mature forest cover and all other landscapes (Table 4). In contrast, total bird density and evenness (PIE) were not related to mature forest cover at the landscape level (Table 4). Basin and area  $\times$  basin interaction terms were nonsignificant in

all cases. These results indicated that intermediate levels of mature forest did not promote species richness in the Oregon Coast Range, and that species richness and density were lower in landscapes that were composed entirely of mature forests than in landscapes with

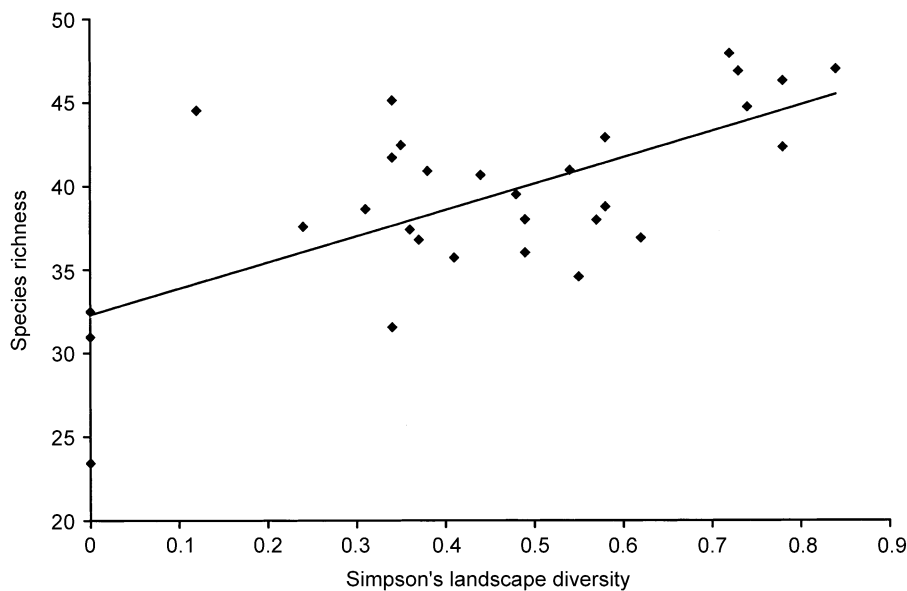


FIG. 5. Scatter plot of bird species richness vs. FRAGSTATS Simpson's diversity index in the Oregon Coast Range ( $n = 30$  landscapes). Simpson's diversity index is defined in Fig. 4. The solid line represents a linear regression ( $y = 32.290 + 15.713x$ , where  $y$  is species richness and  $x$  is Simpson's diversity index) and shows that species richness exhibits a positive linear relationship with habitat diversity ( $P < 0.001$ ,  $R^2 = 0.44$ ), as predicted by the habitat diversity hypothesis.

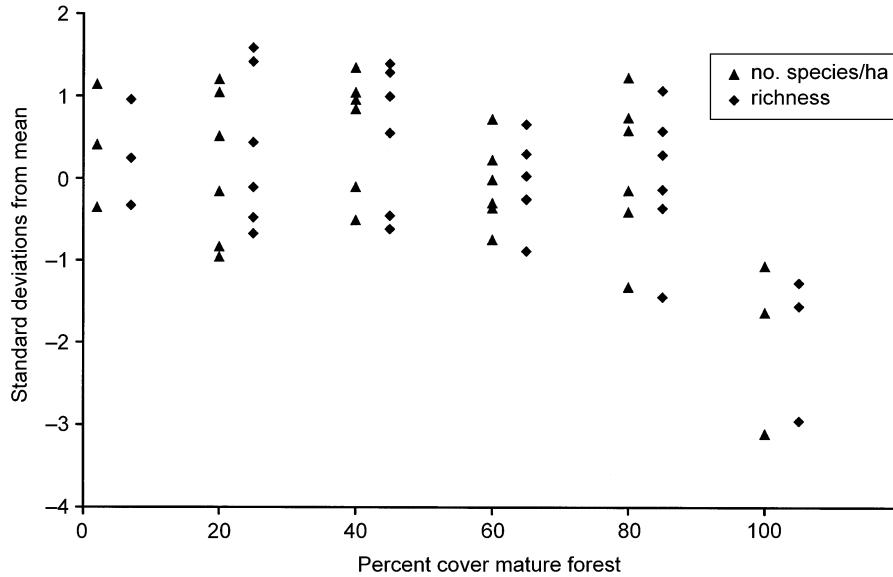


FIG. 6. Scatter plot of the number of species per hectare and species richness across the six levels of mature forest area in the Oregon Coast Range, showing the difference between landscapes with 100% mature forest cover and all other cover classes. All values for species/ha and richness are standardized to make their scales comparable for this figure.

a mixture of seral stages. Interestingly, these results also indicated that species evenness and total bird density did not follow the same pattern and were not related to the landscape cover of mature forests.

We investigated the causes of this pattern of diminished species richness in landscapes with 100% cover of mature forest, using chi-square contingency tables of species presence-absence at the landscape level. Seven species had significantly nonrandom distributions among the levels of area. All seven of these species were absent or rare in landscapes with 100% mature forest cover (Table 5). Furthermore, 12 out of the

13 species with chi-square probabilities <0.1 were absent or rare in landscapes completely covered in mature forest. Nearly all of these species were associated with early-seral or open-land habitats (Brown 1985). The only species to deviate from this trend was the Brown Creeper, which occurred more commonly in landscapes with high mature forest cover (Table 5). Thus, species richness drops in landscapes that are completely dominated by mature forest, through the selective loss of certain early-seral or open-land specialists.

In contrast, the CVA found no significant multivariate relationships between species diversity and levels of mature forest area ( $P = 0.095$ , based Monte Carlo permutations). This indicates that although the univariate relationships between mature forest area and species richness and density are clear, there is no strong, coordinated response of all diversity measures simultaneously to the amount of mature forest area at the landscape level, which reflects the lack of a relationship between evenness and total bird density and levels of mature forest area.

Our second hypothesis also led to the prediction that species richness, density, and evenness should all be greater in more fragmented landscapes. This prediction was supported by the data for species richness and evenness (PIE), which were both significant at  $P = 0.05$ , but species density and total bird density were not significantly related to fragmentation (Table 6).

As was the case for area, we augmented the univariate tests with CVA. In contrast to forest area, there were significant multivariate differences between levels of fragmentation based on the four diversity variables ( $P = 0.035$ , from Monte Carlo permutations). In these models, species evenness was the only significant

TABLE 5. Chi-square results for bird species presence across six levels of mature forest area at the landscape level in the Oregon Coast Range ( $n = 30$  landscapes).

Species	$\chi^2$ probability	Response to 100% forest cover
Rufous-sided Towhee	0.001	absent
Northern Flicker	0.002	rare
Orange-crowned Warbler	0.002	absent
McGillivray's Warbler	0.013	rare
White-crowned Sparrow	0.013	absent
Wrentit	0.015	rare
Willow Flycatcher	0.021	absent
Bush Tit	0.078	absent
Tree Swallow	0.095	absent
American Goldfinch	0.097	rare
Brown Creeper	0.097	common
Hutton's Vireo	0.097	rare
Song Sparrow	0.097	rare

Notes: Seven species had significantly nonrandom distributions at  $\alpha = 0.05$ . All of these species were absent or rare in landscapes with 100% mature forest cover. Out of the 13 species that had probability values of <0.1, 12 were rare or absent in landscapes with 100% forest cover.

TABLE 6. ANOVA results for the effects of mature forest fragmentation (F, two levels), basin (B, three basins), and fragmentation–basin (BF) interaction on species richness, density, and evenness and total bird density in the Oregon Coast Range ( $n = 30$  landscapes), based on the following model:  $Y_{ijk} = B_j + F_i + BF_{ji} + e_{j(i)(k)}$  where  $Y$  is the diversity measure and  $e$  is residual error.

Dependent variable	Fragmentation		Basin		Fragmentation × Basin		Differences
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Species richness	4.510	<b>0.044</b>	2.270	0.119	0.130	0.878	fragmented > unfragmented
Species density	3.210	0.086	1.360	0.269	0.040	0.957	
Species evenness	11.870	<b>0.002</b>	0.800	0.436	0.070	0.931	fragmented > unfragmented
Bird density	2.620	0.118	4.920	<b>0.019</b>	0.030	0.967	

Notes: Significant relationships at  $\alpha = 0.05$  are given in boldface. *P* values are based on Type III sums-of-squares to account for the unbalanced design. The direction of significant differences between levels of fragmentation is indicated in the last column.

variable, with  $\lambda = 0.32$  ( $P = 0.020$ ) in CVA. These results show that although there were significant multivariate differences among levels of mature forest fragmentation in terms of diversity, these differences were dominated by species evenness. Evenness was higher in fragmented landscapes and this difference was large enough to drive the multivariate responses.

We investigated the cause of the increased evenness in fragmented landscapes and found that several of the most abundant species, which were associated with mature forest, were less dominant in fragmented habitats. Also, many moderately abundant species were more abundant in fragmented habitats. As a result, overall species abundance was more equitable in fragmented than in unfragmented landscapes, leading to higher overall species evenness (Fig. 7).

These analyses together provide a detailed picture of how landscape-level bird diversity was influenced by mature forest area and fragmentation. Generally, species richness and density were lowest in landscapes with 100% cover of mature forest. Landscapes with 60–80% mature forest cover were next, followed by landscapes with 0, 20, or 40% mature forest cover, which had the highest species richness and density (Fig. 8). Although there was a clear gradient from landscapes with low (0–40%) mature forest cover, to landscapes with intermediate (60–80%) cover, there was substantial overlap among them. The only meaningful and statistically significant difference among area levels was between landscapes with 100% forest cover, which had the lowest richness and density, and all other landscapes (Table 4, Fig. 6). In contrast, species evenness was strongly related to mature forest fragmentation, with PIE peaking in landscapes with relatively low area and high fragmentation of mature forest cover, and lowest in landscapes that were unfragmented (Fig. 8).

### Hypothesis 3

Our third hypothesis led to several different predictions. First, as predicted, multivariate discriminant models with basin effects removed most effectively separated levels of area and levels of fragmentation on

the basis of species richness, density, and evenness, and total bird density (Table 7). The best discriminant model for area, which had basin, but not fragmentation effects removed, had a total classification accuracy of 67%, which was 60% better than chance, as measured by the  $\tau$  statistic (Table 7). In this model, both species richness and density had large marginal effects, and were the only variables that contributed significantly (Table 8, Fig. 9). Second, as predicted, the best discriminant model for fragmentation, which had basin, but not area effects removed, had a total classification accuracy of 73%, which was 53% better than chance (Table 7). In this model, evenness (PIE) was the only significant variable (Table 8). Also, as predicted, the model that most poorly discriminated among levels of area was that with fragmentation effects removed; the model that most poorly discriminated between levels of fragmentation was that with area effects removed (Table 7). However, contrary to our expectations, all three basin-discriminant models were significant based on Monte Carlo permutations (Table 7, Fig. 10). This indicates that there were significant differences among basins in terms of bird diversity, although inspection of the marginal and conditional effects of individual diversity variables indicates that the differences among basins were due primarily to differences in total bird density and not to species richness, density, or evenness (Table 8).

### Hypothesis 4

We predicted that mature forest area should have relatively more influence on bird diversity than does fragmentation. As predicted, the conditional area model was more successful than the conditional fragmentation model, in terms of chance-corrected accuracy and overall model significance (Table 7), suggesting that the independent effects of area on bird diversity were stronger than the independent effects of fragmentation. Interestingly, the same pattern was not evident in the full models. The full fragmentation model, which included the confounded effects of basin and area, was more successful than the full area model. The

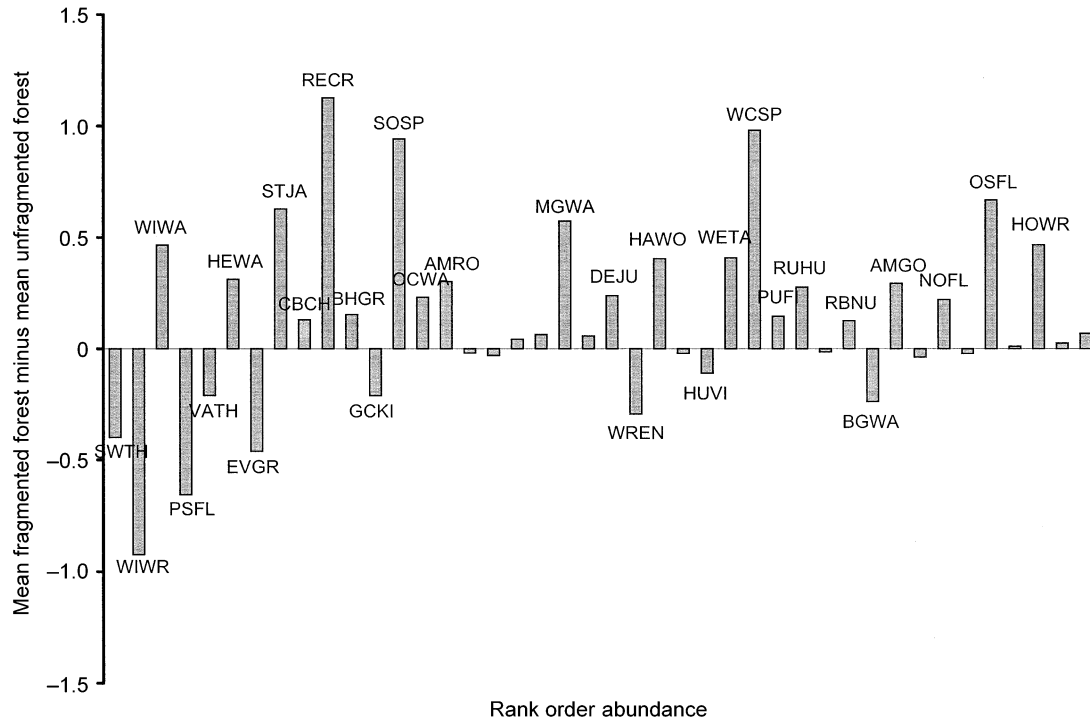


FIG. 7. Change in the abundance of individual species between fragmented and unfragmented landscapes in the Oregon Coast Range ( $n = 30$  landscapes). The plot shows the deviation between fragmented and unfragmented landscapes in mean abundance per plot for the 41 most abundant species, in rank order. Five of the seven most abundant species were less dominant (negative deviation scores), and many moderately abundant species were more abundant (positive deviation scores) in fragmented than in unfragmented landscapes, leading to overall higher community evenness in fragmented landscapes. Bird species codes are: SWTH, Swainson's Thrush; WIWR, Winter Wren; WIWA, Wilson's Warbler; PSFL, Pacific-slope Flycatcher; VATH, Varied Thrush; HEWA, Hermit Warbler; CBCH, Chestnut-backed Chickadee; GCKI, Golden-crowned Kinglet; BHGR, Black-headed Grosbeak; SOSP, Song Sparrow; OCWA, Orange-crowned Warbler; AMRO, American Robin; MGWA, McGillivray's Warbler; DEJU, Dark-eyed Junco; WREN, Wrentit; HAWO, Hairy Woodpecker; HUVI, Hutton's Vireo; WETA, Western Tanager; WCSP, White-crowned Sparrow; PUF, Purple Finch; RUHU, Rufous Hummingbird; RBNU, Red-breasted Nuthatch; BGWA, Black-throated Gray Warbler; AMGO, American Goldfinch; NOFL, Northern Flicker; OSFL, Olive-sided Flycatcher; HOWR, House Wren.

drop in variance explained and the chance-corrected accuracy from the full fragmentation model to the conditional fragmentation model measure the strength of confounding between fragmentation and area effects. This confounding has important implications about how to robustly measure the relationships among habitat area, fragmentation, and ecological responses.

Our second prediction that all four diversity variables should be more strongly related to mature forest area than to fragmentation was not supported for all diversity measures. Our prediction was supported for species richness and diversity, but not for evenness or total bird density (Table 8). In the area CVA, for example, species richness and density had the largest marginal effects ( $\lambda = 0.46, 0.47$ , respectively), whereas evenness and total bird abundance had substantially smaller influences ( $\lambda = 0.21$  each). Only species density had a significant conditional effect ( $P = 0.005$ , based on Monte Carlo permutations). In contrast, as already seen, fragmented and unfragmented landscapes were discriminated on the basis of species evenness, but not richness or density. Thus, species richness and

density were more strongly related to mature forest area, as we predicted. However, contrary to our expectation, species evenness was much more strongly related to mature forest fragmentation than to area.

Our final prediction was that the relative strength of the relationship between mature forest fragmentation and bird diversity should increase as the landscape area covered by mature forest decreases. To evaluate this, we compared the CVA scores of the full fragmentation model (Table 7) for fragmented vs. unfragmented landscapes grouped by levels of mature forest area. Recall that this CVA model derives an axis that best discriminates between fragmented and unfragmented landscapes on the basis of the four bird diversity variables, and that each landscape has a location or score on this axis. If the effect of fragmentation on diversity is great, then we would expect the fragmented landscapes to be widely separated from the unfragmented landscapes on this axis, because the diversity characteristics would differ greatly between fragmented and unfragmented conditions. Thus, the separation between fragmented and unfragmented landscapes on this axis provides a

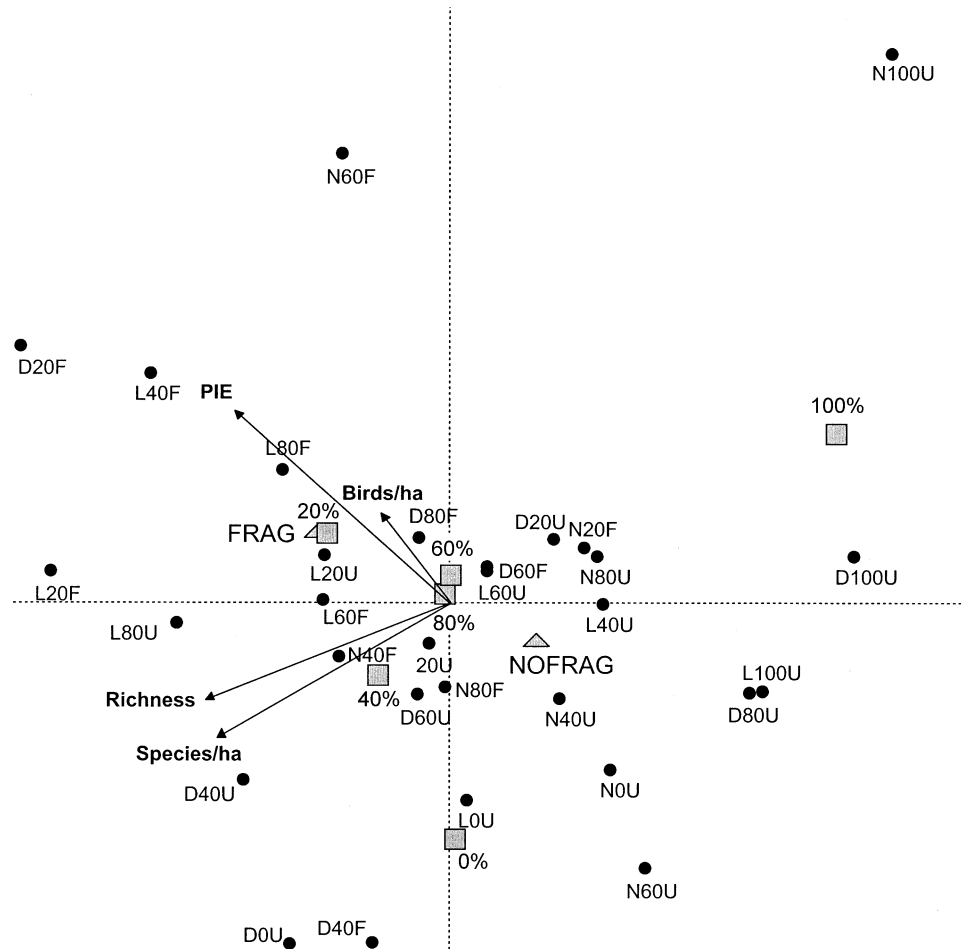


FIG. 8. Canonical variates analysis tri-plot obtained from CANOCO 4 (ter Braak and Smlauer 1998), showing the simultaneous discrimination among six levels of mature forest area and two levels of mature forest fragmentation, based on the diversity variables: species richness, number of species per hectare, probability of interspecific encounter (PIE), and number of birds per hectare; ( $n = 30$  landscapes). The black points correspond to the locations of individual landscapes in canonical space, and are labeled according to basin (D, Drift; L, Lobster; N, Nestucca), mature forest area level (0, 20, 40, 60, 80, 100%), and fragmentation level (U, unfragmented; F, fragmented). Plot distances are Mahalanobis distances. The plot shows that area levels are best discriminated by richness and number of species per hectare, and are not effectively discriminated by PIE or number of birds per hectare. Area levels are clearly ordered along a gradient of richness and number of species per hectare, with landscapes with low mature forest area having the highest richness and landscapes with 100% mature forest cover having the lowest. In contrast, fragmented and unfragmented landscapes are well separated on the evenness axis, with fragmented landscapes having higher evenness than unfragmented landscapes. No covariables were included in this analysis.

measure of the strength of the fragmentation effect. Based on our prediction, we expected that the separation between groups would be greatest at low levels of mature forest area. To test this, we used simple  $t$  tests, one for each level of mature forest area, with CVA scores as the dependent variable, and made the appropriate Bonferroni adjustments to control experiment-wise Type I errors. No tests were significant (all tests  $P > 0.286$ ), indicating that in the Oregon Coast Range there was no significant interaction between mature forest area and fragmentation, although we note that these tests have very low power to detect differences, considering the small sample sizes. Whatever effect mature forest fragmentation had on bird diver-

sity, it did not change significantly across the levels of area.

#### DISCUSSION

Although there is vigorous debate about the relative importance of different factors across the scale continuum from plot to landscape level and beyond, it is widely accepted that habitat extent and configuration at the landscape level can be important for many ecological processes (Askins et al. 1987, Turner 1989, Andrén 1994, Robinson et al. 1995, Trzcinski et al. 1999, Villard et al. 1999). Landscape influence on community diversity has been a particularly strong area of recent interest (Ricklefs 1987, Blair 1996, Flather 1996, Cam

TABLE 7. Results of 12 partial weighted-averaging canonical variates analyses (CVA) to discriminate among six levels of mature forest area, two levels of mature forest fragmentation, and three basins on the basis of four diversity variables (species richness, density, and evenness, and total bird density) in the Oregon Coast Range ( $n = 30$  landscapes).

Model	% Var <sup>†</sup>	Class Acc. <sup>‡</sup>	$\tau$ <sup>§</sup>	MC p <sup>  </sup>
Area of mature forest				
Area, full model	19.7	56.7	48.0	0.095
Area(frag)	17.3	50.0	40.0	0.210
Area(basin)	23.5	66.7	60.0	<b>0.010</b>
Area(fragbasin)	21.0	66.7	60.0	<b>0.035</b>
Fragmentation of mature forest				
Frag, full model	33.4	76.7	53.3	<b>0.035</b>
Frag(area)	21.5	70.0	40.0	0.130
Frag(basin)	37.3	76.7	53.3	<b>0.020</b>
Frag(areabasin)	24.2	73.3	46.7	0.120
Basin				
Basin, full model	23.5	63.3	45.0	<b>0.050</b>
Basin(area)	35.5	63.3	45.0	<b>0.010</b>
Basin(frag)	26.0	63.3	45.0	<b>0.025</b>

Notes: The full models discriminate among levels of the focal class variable without removing the effects of other class variables. In the partial models, the effects of class variables in parentheses were removed from the diversity measures.

<sup>†</sup> Percentage of variance explained by the CVA model.

<sup>‡</sup> Classification accuracy of the CVA in terms of percentage of correctly assigned landscape units.

<sup>§</sup> The percentage greater than chance accuracy of the classification.

<sup>||</sup> Monte Carlo permutation probability, the probability that the CVA results are no better than random; significant relationships at  $\alpha = 0.05$  are given in boldface.

et al. 2000, Drapeau et al. 2000, Lomolino and Perault 2000, Debinski et al. 2001). The influences of the rate of disturbance, habitat extent, and habitat configuration at the landscape level on community diversity are also central to several core ideas of ecological theory (Caswell 1978, Connell 1978, Chesson and Case 1986). Moreover, diversity correlates are widely used as justifications for various conservation planning strategies, such as The Nature Conservancy's ecoregional conservation planning approach (Groves et al. 2000). Despite the great interest and perceived importance of landscape-level studies of community diversity, there have been remarkably few controlled and replicated studies of species diversity at the landscape level (Fahrig 1997, Trzcinski et al. 1999, McGarigal and Cushman 2002).

Landscape-level mensurative studies are faced with numerous challenges (McGarigal and Cushman 2002). In particular, the choice of what cover class to control has important implications for the results of the analysis. For example, had we controlled for area and fragmentation of closed-canopy forest or open-canopy habitats, we probably would have found different patterns of response in the bird community. We chose mature forest as the focal class because of the recent focus on late-seral forest species in the Pacific Northwest (e.g., Swanson et al. 1990, Hansen and Urban 1992, Carey and Johnson 1995, Halpern and Spies 1995) and the fact that the major contrast between cover types in the Oregon Coast Range is between late-seral and early-seral forests, with relatively little in between (Spies and Cline 1988). Our study focused on variation of mature forest area and fragmentation among landscapes ranging from 250 to 300 ha in size, and our inferences are limited to this combination of factors and scales.

TABLE 8. Marginal (Marg.) effects sizes and conditional probabilities ( $P$ ) for the four diversity variables in each weighted-averaging canonical variates analysis in Table 6.

Model	Richness		Species density		Evenness		Bird density	
	Marg.	$P$	Marg.	$P$	Marg.	$P$	Marg.	$P$
Area of mature forest								
Area, full model	0.46	0.170	0.47	<b>0.005</b>	0.21	0.250	0.21	0.890
Area(frag)	0.06	0.910	0.43	<b>0.015</b>	0.15	0.480	0.23	0.210
Area(basin)	0.54	<b>0.005</b>	0.52	0.700	0.20	0.260	0.29	<b>0.050</b>
Area(fragbasin)	0.50	<b>0.005</b>	0.48	0.960	0.11	0.490	0.27	0.490
Fragmentation								
Frag, full model	0.14	0.840	0.11	0.390	0.32	<b>0.020</b>	0.07	0.680
Frag(area)	0.80	0.320	0.05	0.950	0.21	<b>0.045</b>	0.04	0.980
Frag(basin)	0.16	0.265	0.12	0.780	0.33	<b>0.005</b>	0.10	0.490
Frag(areabasin)	0.16	0.630	0.14	0.980	0.31	<b>0.010</b>	0.14	0.300
Basin								
Basin, full model	0.14	0.100	0.09	0.580	0.05	0.990	0.27	<b>0.025</b>
Basin(area)	0.25	<b>0.005</b>	0.17	0.690	0.05	0.870	0.34	<b>0.010</b>
Basin(frag)	0.16	0.085	0.10	0.440	0.06	0.985	0.29	<b>0.002</b>

Notes: The marginal effect is the variance that each variable accounts for by itself. Total variance for the area, fragmentation, and basin models are 5, 1, and 2, respectively. The conditional probability ( $P$ ) is the probability that the variable accounts for no additional variance after adjusting for the variance accounted for by variables already included in the model using forward selection in CANOCO 4 (ter Braak and Smilauer 1998); significant relationships at  $\alpha = 0.05$  are given in boldface.

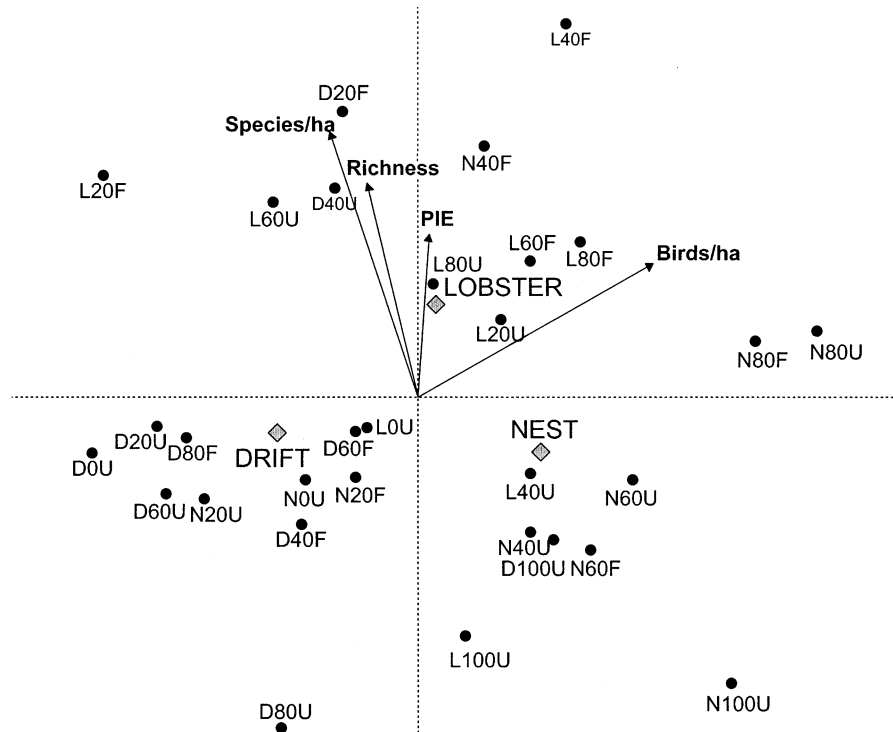


FIG. 9. Partial canonical variates analysis tri-plot obtained from CANOCO 4 (ter Braak and Smilauer 1998) for discriminating among three basins on the basis of the four diversity variables (species richness, number of species per hectare, probability of interspecific encounter (PIE), and number of birds per hectare) in the Oregon Coast Range ( $n = 30$  landscapes), after removing the effects of area. Plot symbols and scale are defined in Fig. 8. The plot shows that the basins differ in bird diversity, as measured by number of species per hectare, richness, PIE, and number of birds per hectare. In particular, Lobster Creek basin has higher evenness, species richness, and density than either Drift or Nestucca. In contrast, Nestucca Creek basin has the highest total bird density, followed by Lobster. Drift Creek has the lowest total bird density.

However, mature conifer forest is the dominant cover type in the region, it has been linked to the ecology of many species (Ruggiero et al. 1991, Johnson and O'Neil 2001), and it is at the heart of recent policy and conservation debates (FEMAT 1993). Therefore, we deemed it an appropriate control class for our experiment. However, it must be recognized that our results are from a spatially complex seral mosaic in a landscape dominated by coniferous forest, and may not reflect the responses of community diversity to fragmentation in other forest systems, or in systems that are dominated by a mosaic of forest and nonforest habitats interspersed with high-contrast edges. This latter class of landscape has been a focus of much conservation concern and ecological research, particularly in the eastern deciduous forest of North America (e.g., Whitcomb et al. 1981, Robbins et al. 1989, Terborgh 1989) and the tropics (e.g., Lovejoy et al. 1984, Bierregaard et al. 1992), and great care should be taken in extending our findings to those contexts.

#### *Patterns in total bird density*

We predicted that total bird density would peak in fragmented landscapes dominated by early-seral habitats, because we expected early-seral species to occur

at higher densities in their optimal habitats than mature forest species, and we expected fragmentation to differentially benefit early-seral species. Our results did not strongly support this prediction. However, this may have been due more to a limitation in our study design than to the absence of an actual effect. We found that species associated with the very early seral grass-forb and shrub-dominated habitats (i.e., recently disturbed areas) do, on average, occur at higher densities than species associated with mature forest, as we expected. However, this pattern is obscured and largely offset by species density relationships in other early-seral habitats. Recall that we explicitly controlled the area and fragmentation of mature forest in our study design, but did not control the character of the early-seral component. Yet this landscape component consists of several distinct habitats (e.g., grass-forb dominated, shrublands, open sapling-pole stands, closed-canopy pole stands, and nonforested wetlands). Consequently, landscapes with <100% mature forest varied markedly in the extent and distribution of specific early-seral habitats, which led to high variability in species diversity among landscapes with low mature forest cover.

Eight of the 10 most abundant bird species in landscapes with 100% mature forest cover, all of which are

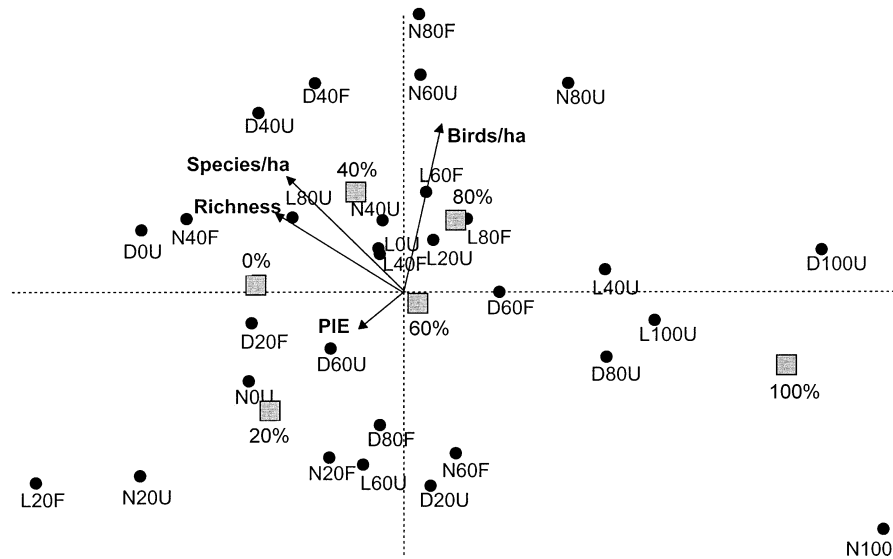


FIG. 10. Partial canonical variates analysis tri-plot obtained from CANOCO 4 (ter Braak and Smilauer 1998) for discriminating among six levels of mature forest area on the basis of the four diversity variables (species richness, number of species per hectare, probability of interspecific encounter (PIE), and number of birds per hectare) in the Oregon Coast Range ( $n = 30$  landscapes), after removing the effects of basin. This is the best model for area of mature forest. Plot symbols and scale are defined in Fig. 8. The plot shows that the best area model clearly separates levels of mature forest cover at the landscape level on the basis of species richness and species density. Landscapes with low mature forest cover have the highest species richness and density, whereas landscapes with 100% mature forest cover have substantially lower species richness and density. Evenness and total bird density are unrelated to the amount of mature forest.

associated with late-seral forest, had lower abundances in landscapes that were not completely dominated by late-seral forests (Fig. 11). These species, as a rule, remained common in all landscapes. Thus, although they reached peak abundance in landscapes dominated by late-seral forests, these species persisted at moderate densities in landscapes across the full area gradient because of their ability to utilize mid-seral forest (i.e., pole stands), which we lumped with early-seral forest (i.e., grass-forb and sapling stands) in our study. In contrast, many early-seral species were largely absent in landscapes with 100% mature forest cover and increased substantially when mature forest did not completely dominate the landscape (Fig. 11). There was a compensatory relationship between the decrease in abundance of late-seral species and the increase in abundance of early-seral species as the area of mature forest decreased.

These results suggest that species inhabiting very early seral patches do have high density relative to species in late-seral habitats, which is a hallmark of "fugitive" species. This suggests that very early seral patches may be perceived as ephemeral and relatively fragmented habitat from the perspective of the birds that live there. In addition, the compensatory responses of early- and late-seral species to changes in mature forest cover show that total bird density is insensitive to important details of community response to mature forest cover, and that further exploration of the responses of particular species is needed in order to in-

terpret the change, or lack of change, in overall bird density. In our case, interpretation of the density alone would indicate that changes in the area of mature forest in the Oregon Coast Range are not related to bird density, whereas, in fact, there are substantial, but compensatory, changes in species abundance.

#### *Intermediate disturbance and habitat diversity hypotheses*

We expected that bird species diversity would be higher in landscapes with intermediate levels of mature forest area than in landscapes with either very high or very low levels. This prediction follows from the intermediate disturbance hypothesis (Paine 1966, Connell 1978), which predicts peaks in species diversity at sites that have intermediate levels of disturbance, and from the prediction that species diversity will be maximum in landscapes with the highest habitat diversity. Although we are unaware of explicit tests of this hypothesis in dynamic forest landscapes, there have been several tests in urban landscapes. Some of these studies have provided evidence that species richness peaks at intermediate levels of urban development (Jokimäki and Suhonen 1993, Blair 1996), although others have noted a monotonic negative relationship between the level of urban development and species richness (e.g., Beissinger and Osborne 1982, Flather 1996, Cam et al. 2000). In the context of our study area, we would expect landscapes with moderate disturbance of mature forest to have higher total species

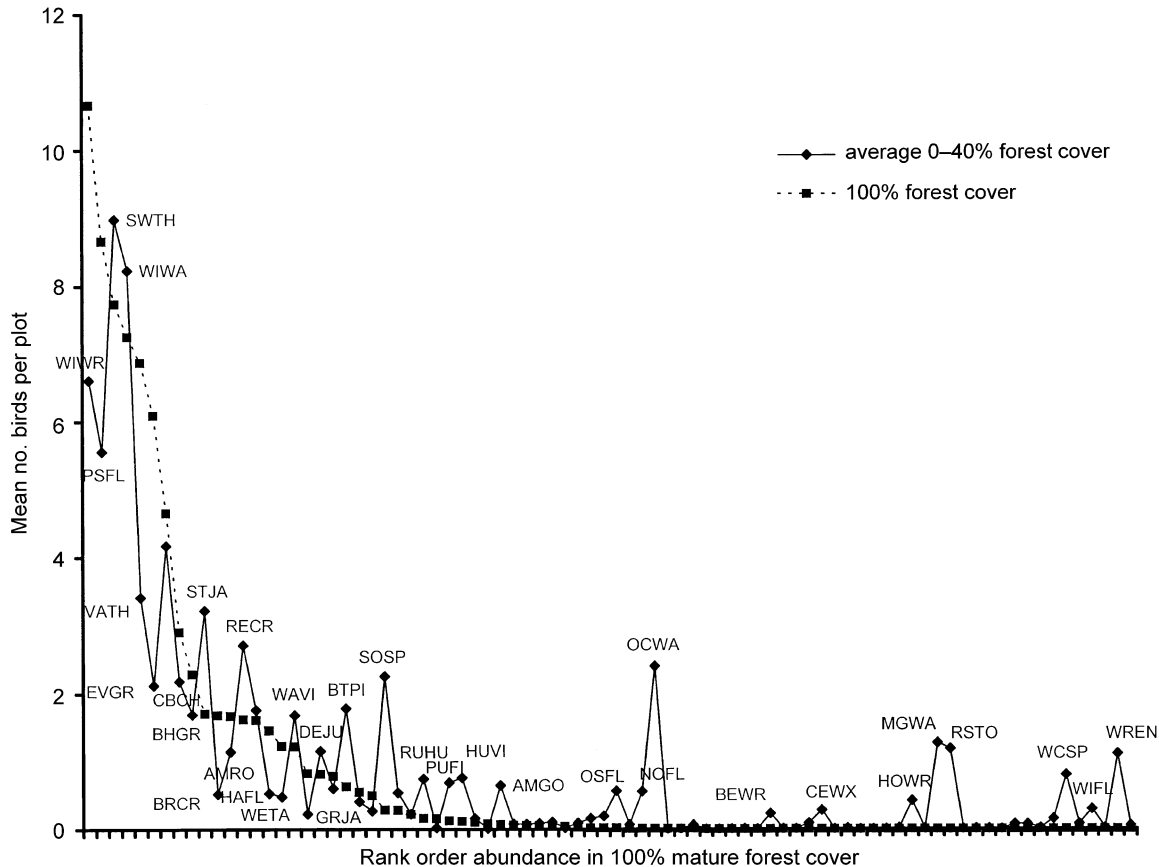


FIG. 11. Change in the abundance of individual species between landscapes with 100% mature forest cover and those with between 0% and 40% mature forest cover in the Oregon Coast Range ( $n = 30$  landscapes). The plot shows the mean number of birds per plot for each species across landscapes in each level of mature forest area, in rank order of their abundance in landscapes with 100% mature forest cover. The dashed line gives species abundances in rank order of abundance in landscapes with 100% mature forest cover. The solid line depicts average species abundances in landscapes ranging from 0% to 40% mature forest area, but preserves the rank order from the 100% level. Thus, species whose points are above the "hundred" line show positive responses to decreased mature forest cover, whereas those below the line show negative responses. Several of the most abundant species were less dominant in landscapes with low mature forest cover. In contrast, 11 species (OSFL–WREN) were absent in landscapes with 100% mature forest cover but were present in landscapes with other levels of mature forest. The drop in richness in landscapes with 100% mature forest cover is explained by the selective elimination of these early-seral, edge species, key to abbreviations: SWTH, Swainson's Thrush; WIWR, Winter Wren; PSFL, Pacific-slope Flycatcher; WIWA, Wilson's Warbler; VATH, Varied Thrush; EVGR, Evening Grosbeak; CBCH, Chestnut-backed Chickadee; STJA, Stellar's Jay; BHGR, Black-headed Grosbeak; RECR, Red Crossbill; BRCR, Brown Creeper; HAFL, Hammond's Flycatcher; WAVI, Warbling Vireo; WETA, Western Tanager; GRJA, Gray Jay; BTPI, Band-tailed Pigeon; DEJU, Dark-eyed Junco; SOSP, Song Sparrow; RUHU, Rufous Hummingbird; PUF1, Purple Finch; HUVI, Hutton's Vireo; AMGO, American Goldfinch; NOFL, Northern Flicker; OSFL, Olive-sided Flycatcher; BEWR, Bewick's Wren; OCWA, Orange-crowned Warbler; CEWX, Cedar Waxwing; HOWR, House Wren; MGWA, McGilivray's Warbler; RSTO, Rufous-sided Towhee; WCSP, White-crowned Sparrow; WIFL, Willow Flycatcher; WREN, Wren.

diversity than landscapes with either very high or very low disturbance rates. At low disturbance rates, mature forests would cover the full landscape and species that cannot persist in those habitats or compete with the dominant species would be excluded. In contrast, in highly disturbed landscapes with no mature forest, one might expect that species associated with mature forest conditions would be excluded. Similarly, the habitat diversity hypothesis predicts that species diversity will be correlated with habitat diversity, and that habitat diversity will be highest in landscapes with an equitable mixture of early- and late-seral habitats.

Our results are not fully consistent with these predictions, but do not necessarily refute the validity of the intermediate disturbance or habitat diversity hypotheses. In our study, neither richness nor evenness peaked at intermediate levels of mature forest. The major difference among levels of forest area was that richness was lower in landscapes with 100% mature forest cover than in landscapes with a mixture of early- and late-seral types. Thus, relatively low levels of disturbance and relatively small amounts of seral-stage interspersions at the landscape level are sufficient to achieve high species richness. In addition, species rich-

ness does not diminish with increasing dominance by early-seral habitats. This implies that most species that are dominant in mature forest can subsist in landscapes where mature forest is rare or absent. Our results do not preclude declines in richness at very high disturbance rates, where forest cover and habitat diversity are both reduced.

We did not find a significant relationship between evenness and mature forest area. This implies that the relative dominance of the landscape by mature forest does not affect the equitability of species abundances, whereas it does influence species richness. As mature forest area decreases, the dominance of species associated with mature forest also declines. This by itself would increase community evenness. However, as mature forest area drops from 100%, species richness increases as new species are introduced into the community. These new species are rare. This by itself would decrease community evenness. The lack of significant changes in evenness across levels of area reflects the balancing effect of these two processes. Fourteen out of the 25 most abundant bird species in landscapes with 100% mature forest cover are consistently less common in landscapes that are not completely dominated by mature forest (Fig. 11). Most of these species show significant relationships to mature forest area at the landscape level (McGarigal and McComb 1995). Simultaneously, when mature forest decreases from 100% cover, 10 species that are absent in landscapes with 100% mature forest cover begin to appear in the community. These species are associated with open and early-seral habitats (McGarigal and McComb 1995). The combination of decreases in the dominance of interior mature forest species and the appearance of uncommon early-seral species offsets any change in evenness. As a result, evenness does not change significantly among levels of area, although species composition and relative dominance of individual species do.

We also predicted increased species diversity in fragmented landscapes. At any level of mature forest area in fragmented landscapes, there will be less dominance of interior habitats. That is, fragmentation will reduce mature forest core area, which should reduce the dominance of mature forest interior species and should increase richness by allowing more edge and early-seral species to persist in the community. Evenness was the only diversity measure that was significantly related to fragmentation, with fragmented landscapes having a more even species distribution; dominant mature forest species becoming less dominant, and early-seral and edge species becoming more abundant. As a result of these simultaneous changes in abundance, total community evenness was higher in fragmented than in unfragmented landscapes.

It is important to recognize that our results easily could be misinterpreted if taken out of context to be used for management and conservation. Most species

of conservation concern in the Oregon Coast Range are associated with old-growth or late-seral forests (FEMAT 1993). Although insufficiently sampled to give significant trends, Northern Spotted Owls, Marbled Murrelets, and Pileated Woodpeckers, for example, were recorded at their highest densities in landscapes with 80–100% mature forest cover. Although we found strong patterns in species richness and density in relation to mature forest area, and in species evenness in relation to fragmentation, one must take great care in applying these patterns of species richness to conservation and management decisions.

#### *Habitat area vs. fragmentation*

One of the main motivations of this study was to separate the effects of habitat area and fragmentation at the landscape level on species diversity. Only by separating their confounding effects can we quantitatively describe how important habitat area is relative to habitat fragmentation (McGarigal and Cushman 2002). The general picture that has emerged is that for most species in most systems the amount of habitat at the landscape level is probably more important than its spatial arrangement or degree of fragmentation (McGarigal and McComb 1995, Fahrig 1997, 1998, Trzcinski et al. 1999, Villard et al. 1999, Schmiegelow and Monkkonen 2002). Our results provide an interesting test of these theoretical predictions for bird species diversity in temperate conifer forests.

First, area, fragmentation, and basin interacted substantially in their effects on species diversity at the landscape level. Basin-level differences were effectively “noise” that diminished the discrimination among area and fragmentation levels on the basis of the diversity variables. When the basin effect was statistically removed through partial CVA, both the area and fragmentation discriminant models improved substantially in terms of variance explained, classification accuracy, and statistical significance. This indicates that there is substantial variability among basins in bird diversity, but this variability, which is almost entirely due to differences in total bird density rather than species richness, density, or evenness, is not related to differences among levels of area or fragmentation. Note, therefore, that from the perspective of the study design, basins served well as blocks for investigating mature forest area and fragmentation effects on species diversity patterns.

Second, the effects of mature forest area and mature forest fragmentation on bird community diversity are partly covarying and confounded. As a result of this confounding of effects, when the area effect was removed from the diversity variables, discrimination between levels of fragmentation decreased. Likewise, discrimination among levels of area decreased after the fragmentation effect was removed from the diversity variables. These decreases in variance explained are measures of the degree of confounding in the effects

of mature forest area and fragmentation on bird diversity in the Oregon Coast Range. This emphasizes the importance of accounting for interactions and confounding among habitat area and fragmentation. If we had studied the relationship of area alone, or fragmentation alone, without considering their interactions, we would have arrived at substantially different conclusions. For example, the relative importance of habitat fragmentation would have appeared much greater had we not accounted for its interactions with habitat area.

Third, our results suggest that differences among levels of mature forest area have a larger overall impact on bird community diversity at the landscape level than do differences in mature forest fragmentation. The independent effects of area on overall community diversity are substantially greater than those of fragmentation, as measured by classification accuracy and Monte Carlo permutation tests in the CVA models. We predicted that all four diversity variables would be more related to mature forest area than to fragmentation. This was true for species richness and density, but not for evenness. These results together provide strong evidence that, in the Oregon Coast Range, although mature forest area has a somewhat stronger overall influence on bird community diversity than does fragmentation, these two factors effect community structure in different ways: mature forest area primarily affects species richness density, whereas mature forest fragmentation primarily affects species evenness.

#### *Fragmentation thresholds*

A major unresolved issue is determining when habitat loss and fragmentation become important. Much of the debate has centered on identifying and describing threshold behavior in organism responses to habitat loss and fragmentation (Gardner and O'Neil 1991, With and Crist 1995, Fahrig 1997, 1998, 2001, 2002, Hill and Caswell 1999, With and King 1999a, b, Flather and Bevers 2001). The point at which habitat becomes functionally disconnected (or fragmented) depends not only on the pattern of habitat distribution but also on characteristics (e.g., life history) of the target organisms or ecological process under consideration (With and Crist 1995, With et al. 1997). However, both theoretical and empirical work have suggested that habitat fragmentation is not likely to be important when habitat is extensive and highly connected, but is likely to become important when habitat area is relatively low (e.g., Andr n 1994, With and Crist 1995, Jansson and Angelstam 1999). The focus of all these studies has been on the response of individual species (e.g., occurrence, dispersal success, population persistence) to gradients of increasing habitat loss and fragmentation, yet we were interested in testing whether there would be a similar effect on community diversity patterns.

Our results suggest a threshold-like response in species richness to decreasing late-seral forest area. Specifically, species richness increased dramatically as

late-seral forest area decreased from 100% to 80% of the landscape, indicating the addition of a rather large suite of early-seral species with the addition of a relatively small amount of early-seral forest (Fig. 6). Interestingly, we did not observe a similar threshold-like decline in species richness when the late-seral forest area declined from 20% to 0% of the landscape, because late-seral species were able to persist in the mid-seral forest stands present in these landscapes.

Our results do not support the hypothesis that the effect of habitat fragmentation will be minimal at high levels of habitat area and will increase in importance as habitat area decreases. There was significant discrimination between fragmented and unfragmented landscapes with respect to species evenness, and the degree of discrimination did not vary in relation to mature forest area. Thus, there appears to be no strong relationship between the effect of fragmentation of mature forest on bird diversity and the area of mature forest at the landscape level in the Oregon Coast Range. However, why fragmentation of mature forest has a relatively strong and consistent effect across the gradient of mature forest cover is worthy of further investigation.

#### CONCLUSIONS

The diversity of the bird community in the Oregon Coast Range is influenced by both the extent and fragmentation of mature forest at the landscape level. Species richness and species density respond more strongly to mature forest area than to fragmentation, and are significantly lower in landscapes that are completely dominated by mature forest than in landscapes containing a mixture of seral stages. This reflects the selective loss of a number of early-seral species when mature forest completely blankets the landscape. In contrast, species evenness is more strongly related to fragmentation than to area of mature forest at the landscape level. In fragmented landscapes, the most dominant species, which in this region are associated with mature forest, decrease in abundance, whereas most of the moderately abundant species increase in relative abundance. This results in communities that are more even in fragmented landscapes.

The effects of mature forest area and fragmentation on community diversity are partly confounded and co-varying. This can result in an inaccurate representation of the importance of area or fragmentation if care is not taken in the experimental design and analysis to separate their confounding effects. In this study, we found that when area effects were not removed from the diversity variables, fragmentation appeared to explain species diversity as well or better (depending on the measure of success used) than mature forest area. In contrast, when area effects were removed, the effects of fragmentation level on species diversity overall were no longer significant. Overall, mature forest area generally was more important than fragmentation in its

influence on species diversity. A notable exception was for species evenness, which was more strongly related to mature forest fragmentation. However, we did not find that the relative strength of fragmentation effects increase as habitat area decreases. Although the influences of mature forest area overall are stronger than those of fragmentation, these two factors influence community evenness and richness in opposite ways. Thus, it may be inaccurate to talk about landscape-level effects on community diversity overall. Instead, researchers should investigate the behavior of the individual components of diversity, including richness, density, and evenness in their independent responses to both habitat area and fragmentation.

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