

HIERARCHICAL ANALYSIS OF FOREST BIRD SPECIES–ENVIRONMENT RELATIONSHIPS IN THE OREGON COAST RANGE

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Abstract. Species in biological communities respond to environmental variation simultaneously across a range of organizational levels. Accordingly, it is important to quantify the effects of environmental factors at multiple levels on species distribution and abundance. Hierarchical methods that explicitly separate the independent and confounded influences of environmental variation across several levels of organization are powerful tools for this task. Our study used a hierarchical approach to partition explained variance in an Oregon Coast Range bird community among plot-, patch-, and landscape-level factors. We used a series of partial canonical ordinations to decompose species–environment relationships across these levels of organization to test four hypotheses about the importance of environmental control over community structure. We found that plot-level factors were better predictors of community structure than patch- or landscape-level factors. In addition, although landscape-level variables contributed substantial independent explanatory power, there was little evidence that patch-level environmental variability provided additional explanation of community structure beyond that provided by plot- and landscape-level factors. At higher levels of the hierarchical analysis, we found that, among plot-level factors, vegetation cover type was as powerful a predictor of community structure as detailed floristics, and more powerful than vegetation structure. At the landscape level, we found that landscape composition and configuration both provided substantial independent explanatory power, with landscape composition being the better overall predictor. Our results have a number of implications for sampling, analysis, and conservation. For example, misleading results could be obtained by studies conducted at a single organizational level. Also, the high degree of confounding among several levels of our analysis suggests that there is a lack of independence between the influences of environmental structure at different organizational levels. Due to this confounding, our results suggest that patch-based studies of forest–bird ecological relationships in the Oregon Coast Range may be equivocal. In addition, the power of mapped cover class as a plot-level predictor variable suggests that coarse-filter, multiscale approaches utilizing remote sensing and GIS may be nearly as effective at predicting local patterns as expensive field surveys of habitat conditions at the plot level, and more effective at predicting patterns continuously across large regions.

Key words: *bird communities; canonical correspondence analysis; community structure; forest birds; hierarchy; multiple-scale; Oregon Coast Range; species–habitat relationships; variance partitioning; vegetation cover type.*

INTRODUCTION

The environments in which organisms live are spatially structured at a number of scales. From the perspective of an organism, spatial discontinuities create variability in the distribution of suitable conditions, resources, competitors, and predators (e.g., Huffaker 1958, Levin 1974). Patchiness is fundamental to population dynamics (Levin 1974, Roughgarden 1976), community organization, and stability (Holt 1984, Holling 1986, Kareiva 1987, Tilman 1994) and strongly influences how organisms interact with their environments (Schoener 1971, Wiens 1976, Mangel and Clark

1986). Species composition reflects the joint effect of regional processes, such as dispersal, and local processes such as biotic interactions and behavior (Lande 1987, Ricklefs 1987). Subdivision and isolation of populations by habitat fragmentation can lead to reduced dispersal success and patch colonization rates that may result in a decline in the persistence of local populations and an enhanced probability of regional extinction for the entire population across the landscape (e.g., Lande 1987, With and King 1999a).

These population and community responses result from the details of how individual organisms experience and respond to environmental heterogeneity across a range of scales (Levin 1992). Species spatially subdivide the environment, focusing their activities within particular resource patches at characteristic scales of space and time (MacArthur et al. 1966, Levin and Paine 1974). Thus, there is no single “correct” scale for community analysis. The individualistic na-

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ture of species responses along multiscaled gradients of environmental heterogeneity implies that assessments of community-level species-environment relationships should consider a range of scales simultaneously.

Scale is an inherently continuous property and there is often no objective basis for researchers to determine which scales to include in their analysis. A heuristic solution is to bracket the range of scales that are expected to be important and to observe how patterns change across this range. However, due to the arbitrary selection of range and increment of measurement, this can lead to equivocal results that have no basis in theory. Analyzing species-environment relationships simultaneously across several levels of organization may provide more reliable inferences. Organizational levels are conceptually different than gradations of scale (Allen and Starr 1982). Scale refers to the range and increment used in the observation of a continuous phenomenon, and an organizational level is a tier of a hierarchically structured system, in which entities may be nested and are discretely defined. In this study, we employ a hierarchical conceptual model of system organization, wherein landscapes are composed of patches and patches, in turn, are composed of plots.

Many studies have been conducted on the relationships between bird communities and fine-scale local environmental variation (e.g., MacArthur 1958, James 1971), and until quite recently, fine-scale environmental variability has been the predominant focus of bird-environment research (Hildén 1965, Cody 1985). Other researchers have studied the interrelationships between habitat patch size and isolation and bird communities (MacArthur and Wilson 1967, Freemark and Merriam 1986, Blake and Karr 1987, van Dorp and Opdam 1987, Robbins et al. 1989, Opdam 1991). More recently, a strong interest has arisen in studying landscape-level influences on bird community structure (Beissinger and Osborne 1982, Askins et al. 1987, Andrén 1994, Blair 1996, Bolger et al. 1997, Drapeau et al. 2000, Howell et al. 2000). Some of these studies have separated different components of landscape-level influences (e.g., McGarigal and McComb 1995, Fahrig 1997, 1998, Trzcinski et al. 1999, Villard et al. 1999, Cushman and McGarigal 2003), but few studies have explicitly separated the effects of habitat factors across broad organizational levels, such as plot, patch, and landscape levels, on the distribution and abundance of organisms in biological communities (e.g., O'Neill et al. 1986, Kotliar and Wiens 1990, Schneider 1994).

Multilevel approaches that do not explicitly measure the interaction and confounding of explanatory power among organizational levels can misconstrue the nature of species-environment relationships (Borcard and Legendre 1994, Cushman and McGarigal 2002). Specifically, there is a need to explicitly separate relationships at each level and account for confounding among them. In this paper, we hierarchically partition species-

environment relationships in the forest bird community in the Oregon Coast Range across three levels of organization to test four research hypotheses.

Research hypotheses

First, we hypothesized that plot-level environmental variation would be more important in structuring the bird community than patch-level variation, which in turn would be more important than landscape-level variation. This hypothesis was motivated by the simple proposition that the scale over which a species most strongly interacts with its environment should correspond to the organizational level at which environmental variables affect the species most strongly. Most species interact most strongly with fine-scale habitat within the range of their immediate perception. This is the scale at which predation, competition, and other interspecific interactions occur, and is the context in which the organism experiences its environment. We predict that fine-scale vegetation structure and composition should be more strongly related to plot-level species abundance than coarse-scale variation in patch or landscape structure, because plot-level environmental factors influence the organisms directly, whereas coarser scale factors have a more dispersed and diffuse effect.

Second, at the plot level, we hypothesized that vegetation structure would be more important than floristics, which would be more important than mapped vegetation cover classes in influencing bird community structure. It is widely thought that birds select habitats more strongly on the basis of structural characteristics than of fine variations in vegetation composition (Cody 1985). In contrast, the percentage of a plot covered by mapped cover classes should be least related to bird community structure, because combining structural and floristic characteristics into categories eliminates variability that is related to species abundance at the plot level.

Third, we hypothesized that focal patch area would be substantially more important than focal patch isolation, shape, and edge contrast in influencing bird community structure. One of the cornerstones of conservation theory is that patch size and context are important correlates to species diversity in habitat patches (MacArthur and Wilson 1967). Here we test the hypothesis that patch size is substantially more important than patch isolation, shape, and edge contrast.

Fourth, we hypothesized that landscape composition would be substantially more important than landscape configuration (i.e., the spatial character and distribution of landscape elements) in influencing bird community structure. A number of theoretical studies have suggested that landscape composition is generally more important than configuration, and that configuration becomes significantly important only at low levels of habitat area (With and Crist 1995, Fahrig 1997, 1998, 2001, 2002, Hill and Caswell 1999, With and King 1999a,

b, Flather and Bevers 2001). Few empirical tests of this hypothesis have been conducted, although the results of some observational studies are consistent with these findings (Andr  n 1994, McGarigal and McComb 1995, Trczinski et al. 1999, Villard et al. 1999, Schmiegelow and Monkkonen 2002).

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 consisted of three major hydrological basins (Drift Creek, Lobster Creek, and Nestucca River basins) in the central Oregon Coast Range, USA. 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. The study area experienced a series of high-severity wildfires in the mid-1800s and regenerated naturally (Spies and Cline 1988). Over the past 40–50 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, at the time of the study the area exhibited a bimodal age distribution dominated by early-seral forests (<40 yr) and mature forests (100–150 yr). Mid-aged (40–100 yr) and old-growth (>150 yr) forest were poorly represented. Mature forest, as defined for the purpose of this study, consisted of coniferous, deciduous, and mixed stands with >20% overstory cover of trees with a mean dbh >53.3 cm, and often included remnant old-growth trees and patches with a mean dbh >81.3 cm and multistory canopy.

Landscape mapping

We used color infrared aerial photos to map 27 different cover classes (i.e., patch types) across each basin, including five nonforested cover classes and 22 forested classes; the latter varied on the basis of plant community, seral condition, and canopy closure (McGarigal and McComb 1995). We defined minimum patch size as 0.785 ha and >50 m wide in the narrowest dimension. This minimum 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 et al. 2002) to measure the area and fragmentation of mature forest in each landscape.

Study design

Our study design included six sub-basins each from Drift Creek and Nestucca River and seven sub-basins from Lobster Creek for which we measured environmental variables at all three levels of analysis. The landscapes ranged from 250 to 300 ha in size and cor-

responded to hydrologic sub-basins. Landscapes of this size reflected a compromise between landscape size and sample size. Because populations of the study species undoubtedly extend over larger geographic areas, it would have been desirable to sample larger landscapes. However, because of logistical constraints, we would not have been able to adequately replicate at the landscape level. In each of the three basins, our sample landscapes were selected to represent a broad range of mature forest area and fragmentation. Mature forest area ranged from 10% to 90%, and fragmentation was measured based on the length of high-contrast edge between mature forest and other patch types, as described in McGarigal and McComb (1995).

Data collection

Bird sampling.—We systematically located sample plots 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 plot corresponded to an effective sample plot area of 0.785 ha, and the grid provided a uniform sample of ~10% of the landscape area. This resulted in an average of 28 sample plots per landscape, for a total of 535 across all 19 landscapes.

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 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 each sampling period were included in the analysis. Only species occurring in at least three plots were retained for the analysis to minimize spurious relationships emerging from underrepresented species. This resulted in a database that included 53 species and a total of 15 774 detections.

Environment.—We collected environmental variables at three hierarchical levels: plot, patch, and landscape. Plot-level data were recorded for each of the 535 plots and included biotic and abiotic variables characterizing the physiographic and ecological conditions within each 0.785-ha plot. Patch-level data recorded structural aspects for each habitat patch in which a bird-sampling plot was located. Similarly, landscape-level data recorded composition and structural aspects of the 19 study landscapes.

1. Plot-level data.—We collected a total of 108 plot-level environmental variables. These variables were divided into four subgroups: abiotic, structure, cover, and floristics. The *abiotic* subgroup consisted of three variables: We recorded 44 vegetation *structure* variables

for each plot: aspects of the physical structure of the vegetation, such as abundance of snags of different sizes and decay classes, densities of conifer and hardwood trees of different sizes, basal area, and structure of understory vegetation. We recorded 34 floristics variables corresponding to the plot-level importance of 34 different plant species. Finally, we derived 27 plot cover variables from the cover class map. For each plot, we recorded the percentage of the plot area covered by each cover class.

2. *Patch-level data.*—We collected two sets of patch-level variables: one for the “patches” in which a sample plot was located and one for the “stands” that contained those patches. For the purposes of this study, a patch was defined as a contiguous area of the same cover class, as just defined. This represented the finest resolution of cover type mapping. In contrast, we defined stands as contiguous areas in the same seral condition for forested communities, regardless of cover class. The rationale for mapping patches in two ways and deriving patch-level data for both patches and stands is that we did not know, a priori, if the community as a whole or individual species within it would be more associated with the size and distribution of seral stage patches, or whether they would be more responsive to the size and distribution of more narrowly defined patches based also on floristics and canopy closure. We extracted six patch-level variables for each patch and each stand in which a sampling plot was located, using the spatial analysis program FRAGSTATS. These variables measure the size, spatial character, and context of the patches and stands. They include patch area, shape index, fractal dimension, core area index, similarity index (a measure of patch isolation), and edge contrast index (McGarigal et al. 2002).

3. *Landscape-level data.*—We also derived two sets of landscape-level data for each of the 19 study landscapes. The first of these measures landscape composition and the second measures landscape configuration. Landscape composition variables record the percentage of each landscape in each of the 27 mapped cover classes, as well as the density of roads and streams in each landscape. The landscape configuration variables included 18 FRAGSTATS landscape metrics for each landscape, for both a patch-based mapping and a stand-based mapping. These variables measure configurational attributes of the landscape mosaic overall (McGarigal et al. 2002). We derived landscape configuration variables for both patch-based and stand-based mapping because, as for the patch-level data, we did not know, a priori, if species would respond more to the configuration of seral stage patches or to more detailed mapping of cover classes.

Variable selection

Our variable selection approach was motivated by two overriding issues. First, we needed to greatly re-

duce the number of variables included in the analysis because of the danger of overfitting the models with spurious variables. This could lead to arbitrary inflation of the variance explained due to randomly covarying factors that are not ecologically related to the structure of the bird community. Thus, our first concern was to limit the inclusion to variables that significantly related to the structure of the bird community, and to exclude those that were not. Second, we required an approach that would ensure that included factors at each of the three organizational levels would accurately reflect the importance of the population of factors at each level. Our goal was to measure the relative importance of factors at the different organizational levels. This analysis assumes that the variables that we have measured at the three levels comprise an equally representative and unbiased measure of the importance of ecological factors that influence the community at each level. Although there is no way to explicitly test this assumption, we ensured that there was no systematic bias by subjecting variables at each organizational level to the same rigorous selection procedure. The steps of the variable pre-processing and selection procedure, which will be described in detail, are outlined in Fig. 1.

Plot-level variable selection.—There were two main components of the plot-level variable selection process. First, we used principal components analysis (PCA) to reduce the many intercorrelated floristics and structure variables to a few uncorrelated composite variables. The utility of this approach is threefold. First, it results in reduction in the number of variables under consideration. Second, it allows the inclusion of information from all variables in these subgroups weighted according to their importance in the overall plot-level set. Third, using composite variables eliminates collinearity, which can be a major problem in multivariate analyses in general, including canonical correspondence analysis (ter Braak 1986).

We conducted separate PCAs on floristic, structure, and cover variables. We extracted the first 10 components in each case and subjected them to varimax rotation to maximize interpretability (McGarigal et al. 2000). We retained only components with eigenvalues greater than 1 based on the latent root criterion (McGarigal et al. 2000). We also retained individual variables with final communalities of <50% (McGarigal et al. 2000). We included these in their raw form to ensure that the influence of these variables was not arbitrarily excluded. The PCA of the cover variables was not successful, with the variance being distributed broadly over the 10 components, and only three with eigenvalues over 1. This indicates that the composite variables derived from PCA do not successfully concentrate the variance in plot-level mapped cover classes into a few components. Thus, for ease of interpretation, we used the raw variables rather than principal components for the plot-level cover variable subset. In contrast, the PCAs for floristics and structure

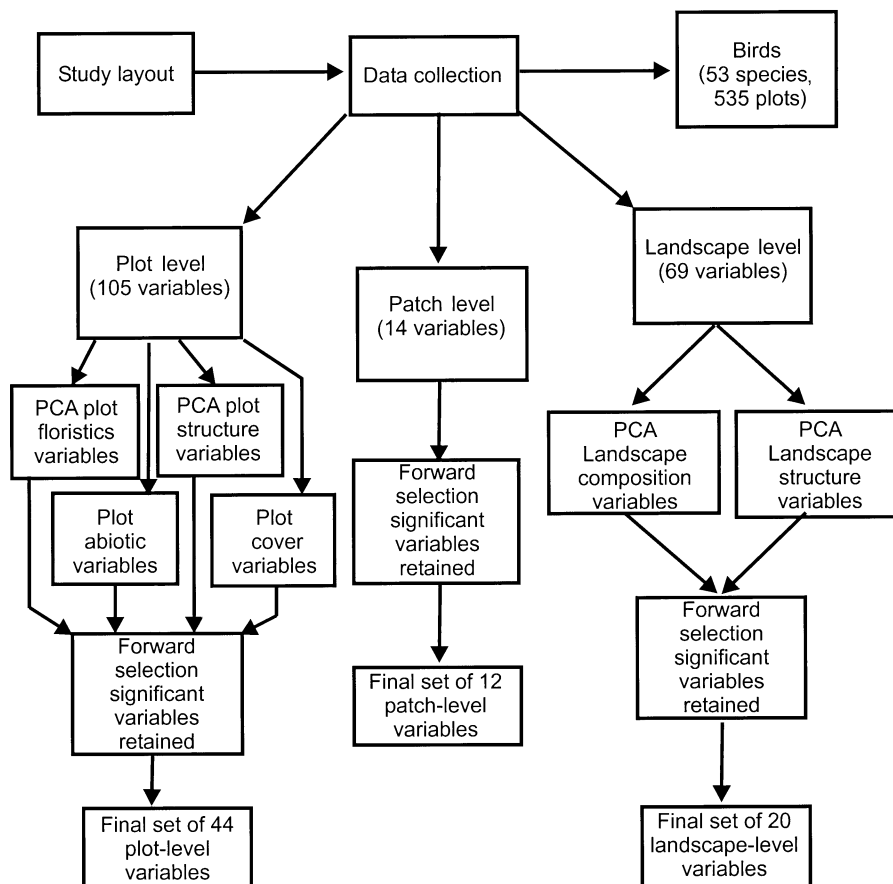


FIG. 1. Outline of the steps in the variable selection procedure.

were much more effective. For these, we retained the first 10 components and any raw variables with low final communalities.

The second main component of the variable selection process was to subject all plot-level variables to a single forward-selection routine in CCA using CANOCO 4 (ter Braak and Smilauer 1998). The forward-selection routine computed the statistical significance of the addition of each variable into the model. Some variables had little overall weight in the analysis and were discarded, whereas others that had strong relationships with community structure were also highly collinear with other more powerful predictor variables. Only variables that contributed significantly ($\alpha = 0.05$ significance level) to the overall plot-level model were retained. The forward selection retained 40 significant plot-level variables. These were divided among plot structure (12), floristics (14), cover (11), and abiotic (3); see Table 1.

Patch-level variable selection.—At the patch level, we did not use PCA because of the relatively small number of variables involved. PCA in this case would provide little improvement, given the small number of variables, and the raw variables have the advantage of

direct interpretability. All 12 patch-level variables were entered into the CCA forward-selection routine in CANOCO, and all were retained at the 5% significance level (Table 2). Interestingly, patch- and stand-based variables provided significantly different explanatory power; thus all six variables from both sets were retained.

Landscape-level variable selection.—We conducted separate PCA analyses on landscape composition and landscape configuration variables. We extracted principal components in each case with varimax rotation. The PCAs for landscape composition and configuration were quite effective. We retained all components with eigenvalues over 1, based on the latent root criterion. This resulted in 10 PC variables and two raw landscape composition variables, and four PC variables for each of patch-based and stand-based landscape configuration variables. All of these 20 landscape-level variables contributed significantly to the CCA model in forward selection and were retained for the analysis (Table 3). This is not surprising because the PCA ensures that they provide independent variance, and the latent root criterion ensures that they account for a non-negligible amount of variance.

TABLE 1. Acronyms and definitions for plot-level structure, floristic, cover, and abiotic variables selected for the analysis using a forward-selection routine in canonical correspondence analysis (CCA).

Variable	Definition
Plot-level structure	
Edgeden	density of edge within plot
Cwedge	contrast-weighted density of edge within plot
pae	binary patch edge variable
ste	binary stand edge variable
batotal	total basal area within plot
conhardba	ratio of conifer to hardwood basal area
struct1	gradient of increasing density of large, old snags
struct2	gradient of increasing density of small snags in second-growth conifer forest
struct4	gradient of increasing conifer saplings
struct7	gradient of increasing pole cover
struct8	gradient of increasing hardwood saplings with many small snags
struct9	gradient from high soil vegetation cover to bare soil
Plot-level floristics	
cacci	plot cover by vine maple
cacma	plot cover by bigleaf maple
copho	plot cover by devil's club
cruur	plot cover by trailing blackberry
csara	plot cover by red elderberry
flor1	gradient from conifer forest dominated by Douglas-fir to open habitats dominated by grass and forbs
flor2	gradient from hardwood to conifer forest
flor3	gradient of increasing understory hardwoods and bigleaf maple
flor4	gradient of increasing sword fern
flor5	gradient of increasing red huckleberry and salal
flor6	gradient of increasing salmonberry and currant
flor7	gradient of increasing western red-cedar and evergreen huckleberry
flor8	gradient of increasing Sitka spruce and false huckleberry
flor10	gradient of increasing thimbleberry, ocean spray and willow
Plot cover (all measured as percent cover)	
ccp	conifer closed-pole
cls	conifer large sawtimber
cop	conifer open-pole
cos	conifer open-sapling
csh	shrub-dominated open-canopy conifer
hls	hardwood large sawtimber
hop	hardwood open-pole
mgf	mixed grass-forb
mls	mixed large sawtimber
mos	mixed open-sapling
msh	shrub-dominated open-canopy mixed woods
Plot-level abiotic variables	
Slope	degrees of slope
Aspect	cosine of aspect
Elevation	meters

Note: All variables contribute significantly to the full plot-level CCA model at a 5% significance level.

Variance decomposition

Hierarchical partitioning.—A powerful approach for separating the effects of hierarchically structured variable sets uses canonical ordination techniques to partition the variation in multivariate data sets (Borcard et al. 1992, Cushman and McGarigal 2002). The method explicitly measures the variation in a community that is explainable independently and jointly by sets of explanatory variables. The variance decompositions that result provide a comprehensive picture of the relative importance, independent effects, and confounding of the explanatory variables in the analysis.

Our analysis used a three-tier decomposition of the variation in the bird community that is explainable by a series of habitat factors nested within three organi-

zational levels (plot, patch, and landscape). The decomposition can be visualized by a Venn diagram, commonly used in set theory (Fig. 2). Specifically, the first-tier decomposition extracts seven discrete components of explained community variation. The numbers in parentheses refer to the components depicted in Fig. 2: (1) pure plot-level effects; (2) pure patch-level effects; (3) pure landscape-level effects; (4) joint effects of plot- and landscape-level variables; (5) joint effects of plot- and patch-level variables; (6) joint effects of patch- and landscape-level variables; and (7) joint effects of plot-, patch-, and landscape-level variables.

This first-tier decomposition explicitly quantifies the relative importance and redundancy of each set of explanatory factors and allows us to test our first hy-

TABLE 2. Patch-level variables selected for the analysis following a forward-selection routine in canonical correspondence analysis.

Stand variable	Definition	Patch variable	Definition
SAREA	stand area	PAREA	patch area
SSHAPE	stand shape index	PSHAPE	patch shape index
SFRACT	stand fractal dimension	PFRACT	patch fractal dimension
SCAI	stand core area index	PCAI	patch core area index
SLSIM	stand landscape similarity index	PLSIM	patch landscape similarity index
SEGECON	stand edge contrast index	PEDGECON	patch edge contrast index

Note: All variables contribute significantly to the full patch-level model at a 5% significance level.

pothesis regarding the relative importance of plot-, patch-, and landscape-level factors.

Our remaining hypotheses are related to the second and third tiers of the hierarchical decompositions. At the second tier there are several choices as to what to partition. One can either partition the *marginal* effects of the corresponding first-tier variable set, or one can choose to partition only its *conditional* effects. We believe that important information is obtained by doing both second-tier partitions, and we did so in this analysis. For the second-tier decomposition of plot-level factors, we separated the influences of plot-level biotic factors from those of abiotic variables: (8)–(10) marginal and (11)–(13) conditional (Fig. 2). Similarly, the second-tier decomposition of patch-level factors separated patch area from overall patch structure: (14)–

(15) marginal and (16)–(17) conditional (Fig. 2; hypothesis 3). The second-tier partitioning of landscape-level factors separated the marginal and conditional landscape effects into components related to landscape composition, landscape configuration, and their joint effect: (16)–(19) marginal and (21)–(23) conditional (Fig. 2; hypothesis 4).

The third tier in our analysis consists of the decomposition of the conditional biotic component in both the marginal and conditional second-tier plot-level decompositions. Third-tier partitioning of the plot-level conditional effects allows us to quantify how much of the unique explanatory power provided by plot-level variables is due to floristics, vegetation cover, forest structure, and their confounded components (Fig. 2; hypothesis 2).

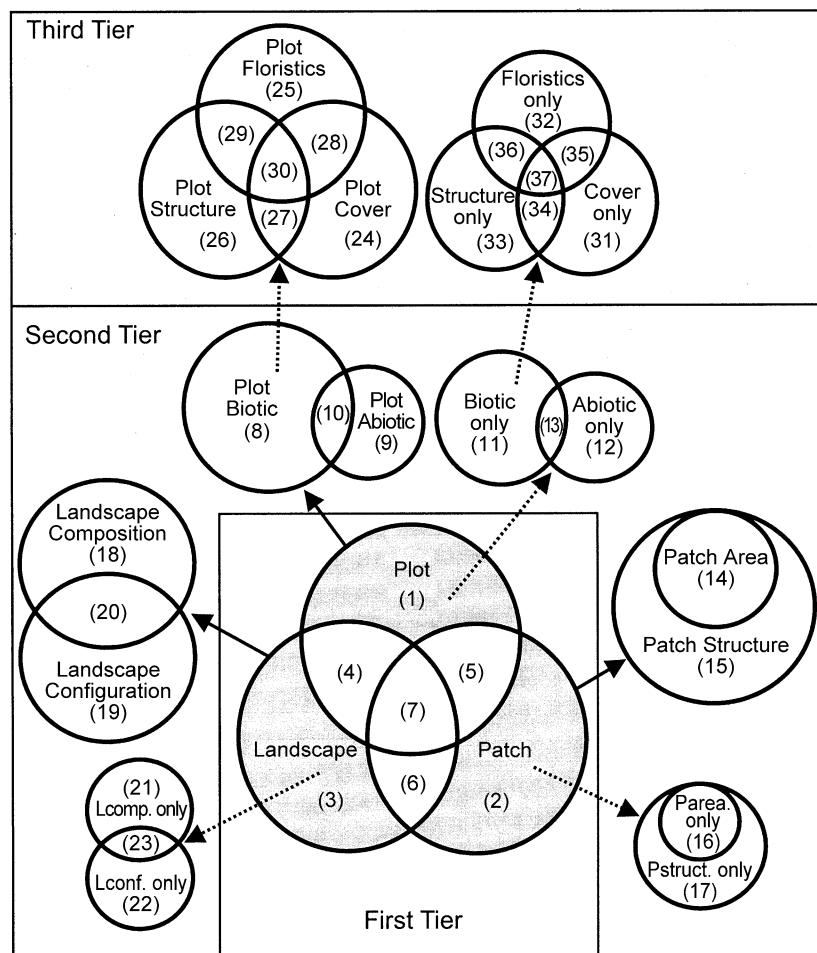
TABLE 3. Landscape-level variables selected for the analysis following a forward-selection routine in canonical correspondence analysis.

Variable	Definition
Landscape composition†	
Roadden	density of roads in the landscape (km/km ²)
Strmden	density of streams in the landscape (km/km ²)
lcomp1	gradient from landscapes dominated by pole-timber to those dominated by mature forest
lcomp2	gradient from landscapes dominated by mature hardwood to those dominated by mature conifer forest
lcomp3	gradient of increasing landscape cover by wetlands and open-pole timber
lcomp4	gradient of increasing landscape cover by shrubs and grass
lcomp5	gradient of increasing landscape cover by grass and forbs
lcomp6	gradient of increasing landscape cover by small sawtimber
lcomp7	gradient of increasing landscape cover by shrubby, open-canopy young conifer
lcomp8	gradient of increasing landscape cover by shrubby, open-canopy young mixed timber
lcomp9	gradient of increasing landscape cover by open-pole
lcomp10	gradient of increasing landscape cover by saplings
Landscape configuration‡	
lcp1	gradient from landscapes dominated by mosaic of many different kinds of small, clumped patches, to those dominated by few, large, complexly shaped patches
lcp2	gradient from landscapes with high density of small core areas to those dominated by large core areas
lcp3	gradient of increasing landscape dominance by the largest patch
lcp4	gradient of increasing mean patch fractal dimension
lcs1	gradient from landscapes dominated by many small stands of different types to those with very high total and mean core area
lcs2	gradient from landscapes dominated by large patches with large mean core area to landscapes with very high patch size variation
lcs3	gradient from landscapes with very high evenness and diversity to landscapes with very high perimeter-area fractal dimension
lcs4	gradient from landscapes with increasing mean shape index and mean patch fractal dimension

Note: All variables contribute significantly to the full patch-level model at a 5% significance level.

† Refers to the presence and amount of each land cover type within the landscape, but not the placement or location of land cover patches within the landscape mosaic.

‡ Refers to the spatial character and arrangement, position, orientation, and shape complexity of land cover patches in the landscape.

**First Tier**

- 1 Plot only
- 2 Patch only
- 3 Landscape only
- 4 Plot–Landscape
- 5 Plot–Patch
- 6 Patch–Landscape
- 7 Patch–Plot–Land.

Second Tier*Plot Marginal*

- 8 Biotic only
- 9 Abiotic only
- 10 Biotic–Abiotic

Plot Conditional

- 11 Biotic only
- 12 Abiotic only
- 13 Biotic–Abiotic

Patch Marginal

- 14 Area
- 15 Structure

Patch Conditional

- 16 Area
- 17 Structure

Landscape Marginal

- 18 Composition
- 19 Configuration
- 20 Comp.–Config.

Landscape Conditional

- 21 Composition
- 22 Configuration
- 23 Comp.–Config.

Third Tier*Plot-biotic Marginal*

- 24 Cover only
- 25 Floristics only
- 26 Structure only
- 27 Cover–Structure
- 28 Cover–Floristics
- 29 Structure–Floristics
- 30 Cover–Struct.–Flor.

Plot-biotic Conditional

- 31 Cover only
- 32 Floristics only
- 33 Structure only
- 34 Cover–Structure
- 35 Cover–Floristics
- 36 Structure–Floristics

FIG. 2. Venn diagram (modified from Cushman and McGarigal [2002]) showing the components of the hierarchical variance decomposition. This figure shows the relationships among the 37 different variance components of the decomposition as a conceptual guide. Results are presented in Fig. 4.

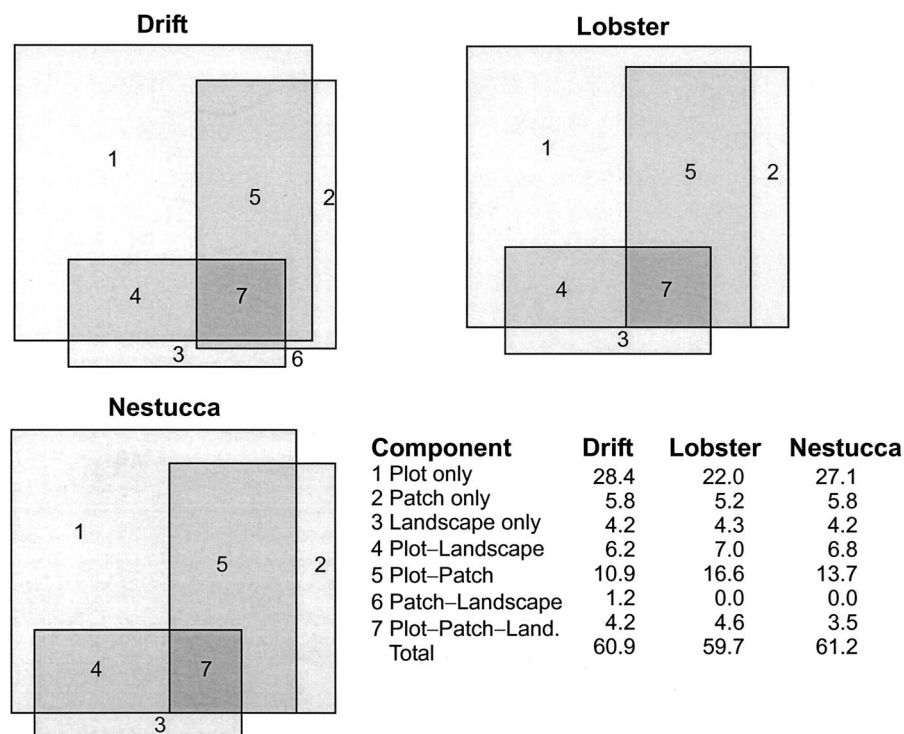


FIG. 3. Comparison of first-tier partitioning results across the three study basins. Numbers in the Venn diagram refer to variance components listed at right. The values associated with each component are the total variances in the bird data that were described by that component.

Partial canonical ordination approach.—The method employed in the decomposition is described in detail elsewhere (Cushman and McGarigal 2002). Briefly, we conducted a series of canonical correspondence analyses (CCA) and partial CCA analyses to isolate all of the variance “slices” needed for the partitioning process (Fig. 2). For each analysis, we recorded the trace, the percentage of total species variation explained by that analysis, and the significance of that analysis based on an unrestricted permutation test in CANOCO 4 (ter Braak 1992, ter Braak and Smilauer 1998). We then used basic algebra to compute the variance accounted for by each component in each tier of the decomposition (Cushman and McGarigal 2002).

RESULTS

Generality of partitioning results

We assessed the generality of the partitioning results by comparing the first-tier decomposition among the three basins. The variance accounted for overall, and by each individual component, was remarkably stable among basins. Among basins, total variance explained by plot-, patch-, and landscape-level variables differed by <4% (61.2% for Drift Creek, 59.7% for Lobster Creek, and 57.6% for Nestucca River) and the relative sizes of the different partitions varied less than 10% in all cases (Fig. 3).

The analyses in the different basins were not only similar in the variance accounted for, but also consistent in terms of the relationships between environmental variables and the partial ordination axes. The first two axes of analogous partial ordinations had the same qualitative interpretation in each basin. Furthermore, species scores were also consistent across basins for each partial ordination. Specifically, species scores for the conditional plot-, patch-, and landscape-level ordinations were all highly correlated among basins, with species scores on the first ordination axis having correlation coefficients between 0.65 and 0.93. The high similarity of results across basins suggests that the analysis successfully describes the dominant patterns between forest birds and environmental gradients that prevail at each of the three organizational levels, and legitimizes the combination of the basins into a single regional analysis.

Hypothesis 1: Plot > patch > landscape

We predicted that the structure of the bird community would be more related to local plot-level variation than to variation in patch size and configuration, and that patch-level variation, in turn, would be more important than landscape composition and configuration. As expected, plot-level factors were most important overall, accounting for 32.8% of the total variance in the bird

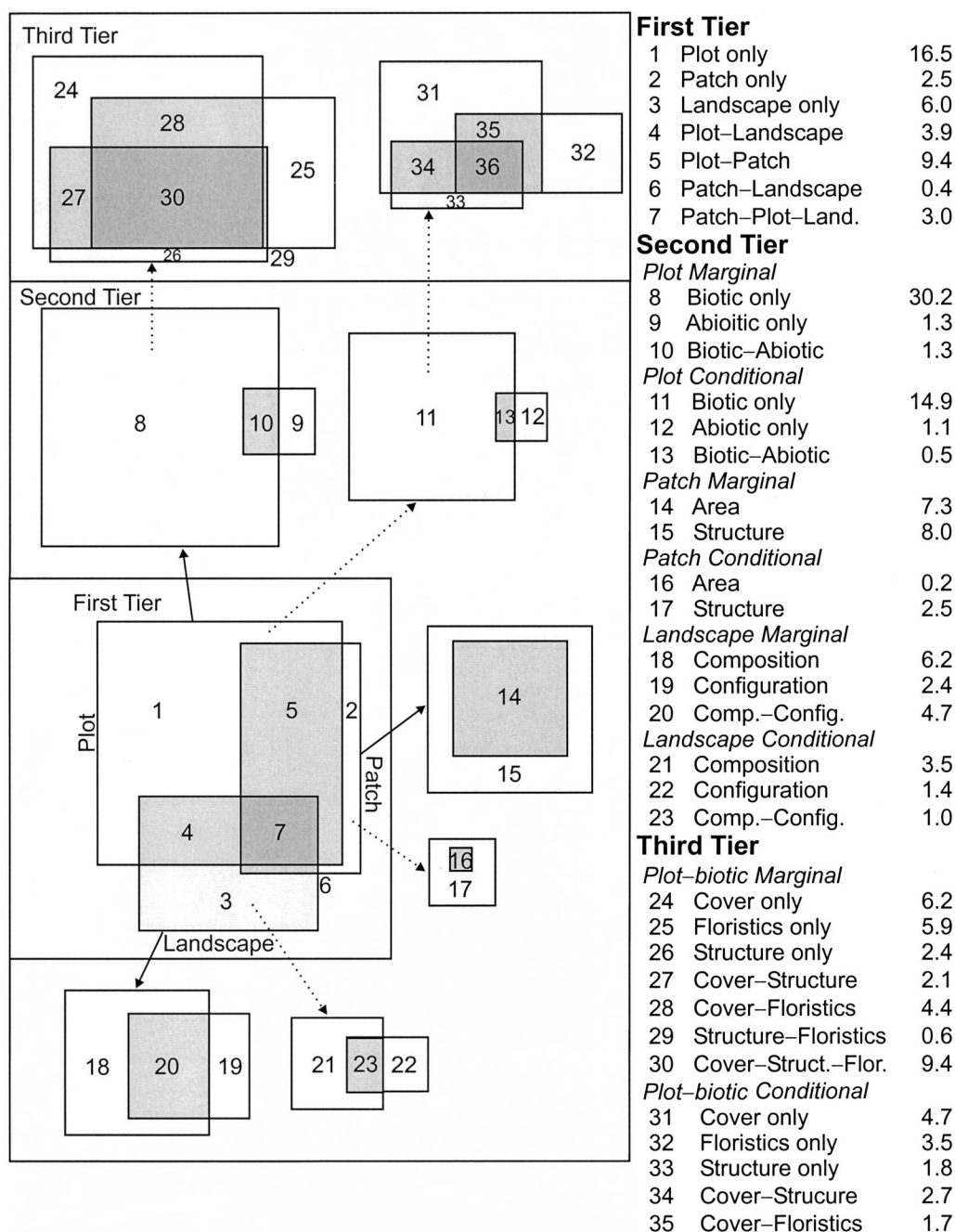


FIG. 4. Results of the full variance partitioning across all three levels of the hierarchy (modified from Cushman and McGarigal [2002]). The numbers in the Venn diagram refer to the specific variance components listed at right. Rectangle size is proportional to the total variance explained by each component, the exact values of which are listed on the right.

community (1 + 4 + 5 + 7; Fig. 4). However, patch- and landscape-level factors had virtually the same overall explanatory power, 15.3% and 13.3%, respectively (2 + 5 + 6 + 7 and 3 + 4 + 6 + 7; Fig. 4). These results suggest that plot-level variation was substantially more important than either patch- or landscape-level factors, but that the overall predictive power of patch- and landscape-level factors was approximately

equal. All three of the plot, patch, and landscape ordinations extracted significantly nonrandom patterns in community structure, as judged by Monte Carlo permutation tests (199 iterations, $P < 0.005$).

This comparison of total variance explained by plot-, patch-, and landscape-level factors is a useful first measure of relative importance, but it neglects the critical issue of confounding among hierarchical levels. In hi-

erarchically structured systems, portions of the variance in the response variables can be jointly and simultaneously explained by factors at different levels of the hierarchy. When this is the case, there is no way to determine to which level the effect is due, or whether there is an interaction of the two levels such that their joint action drives the observed patterns. It is essential to decompose the explained variance to quantify the independent and confounded effects of factors at the different hierarchical levels.

Accounting for the components of confounded variance in our analysis substantially altered the apparent relative importance of the three organizational levels. Two components of confounded variance were particularly important. The first was the confounding of plot- and patch-level variance (5 + 7 in Fig. 4). This component explained 12.4% of the species variance, which is 81% of the total patch-level explained variation. In other words, nearly all of the variance that was explained by patch-level variables was confounded with plot-level effects. It appears that, in the Oregon Coast Range, patch-level factors do not provide substantial additional explanation of the bird community after accounting for plot- and landscape-level factors.

The second important component of confounded explained variance was between landscape- and plot-level factors. Confounding between plot- and landscape-level factors was much less than that between plot- and patch-level factors. Specifically, less than half of the species variation explained by landscape-level factors was confounded with plot-level variables (4 + 7 in Fig. 4). In addition, there was little confounding between landscape- and patch-level factors. This indicates that patch structure varies largely independently of landscape configuration and composition. The independent landscape effect was highly significant, based on Monte Carlo permutation tests ($P < 0.005$), and accounted for 6.0% of the variance in the bird community (3 in Fig. 4). Thus, landscape-level factors provide substantial additional explanation of bird community structure, in addition to that provided by plot- and patch-level variables.

*Hypothesis 2: Plot-level vegetation structure
> floristics > cover type*

We used a two-step approach to address this hypothesis. First, we removed the confounding effects of abiotic plot-level factors, such as slope, elevation, and aspect, because they are not part of our hypothesis (Fig. 2). Then we conducted two partitionings of biotic plot-level variance. First, we partitioned the marginal, or total, biotic plot-level effects (24–30; Fig. 4). This describes the relative importance of floristics, structure, and composition at the plot level overall, ignoring confounding with patch- or landscape-level factors. Second, we partitioned the conditional, or unique, biotic plot-level effects (31–37; Fig. 4), which describe the relative importance of the three plot-level factors, after

removing the effects of patch- and landscape-level variation.

Contrary to our expectations, plot-level structural variables were least important overall for both the marginal and conditional third-tier decomposition. Specifically, in the marginal case, structural variables accounted for 14.5% of the variance in the species data (26 + 27 + 29 + 30; Fig. 4), compared to 22.1% for cover and 20.3% for floristics (24 + 27 + 28 + 30, 25 + 28 + 29 + 30; Fig. 4, respectively). Interestingly, the overall predictive power of mapped cover class was slightly higher than that of detailed floristic data, and much higher than that of the measured vegetation structure variables.

The conclusions are similar when confounding among the three biotic plot-level components is accounted for. The unconfounded effects of structure variables explained about one-third as much species variance as did the independent effects of either floristics or mapped cover type in both the marginal (24 and 25 vs. 26; Fig. 4) and conditional (31 and 32 vs. 33; Fig. 4) cases. Also, the independent effects of cover and floristics were approximately the same in both the marginal (24 vs. 25; Fig. 4) and conditional (31 vs. 32; Fig. 4) cases. These two partitioning analyses both show that the plot-level vegetation structure variables that we measured were much less effective predictors of community structure than either floristic variables or mapped cover type. In addition, simple mapped cover type was as successful at predicting community composition as detailed floristic data.

*Hypothesis 3: Patch area > patch isolation,
shape, and edge contrast*

Patch area alone was not the dominant source of patch-level predictive power. Patch isolation, shape, and edge contrast, independent of area, were better predictors of community structure than patch area for the both the marginal and conditional patch-level decompositions (15 and 17, respectively; Fig. 4). Specifically, in the marginal case, patch area accounted for 7.3% of the species variance, whereas patch isolation, shape, and edge contrast, after removing the area effect, accounted for >8.0%. Similarly, in the conditional case, patch area alone accounted for 0.2% of the species variance, whereas patch isolation, shape, and edge contrast, after removing the area effect, accounted for 2.5% (Fig. 4).

*Hypothesis 4: Landscape composition
> landscape configuration*

As we expected, for both the marginal and conditional landscape decompositions, landscape composition was a more important predictor of community structure than was landscape configuration. Specifically, in the landscape marginal decomposition, the independent effects of composition accounted for 6.2% of the species variance, compared to only 2.4% ex-

plained by configuration alone (Fig. 4). Confounding among landscape composition and configuration in the landscape marginal decomposition accounted for a total of 4.7% of the species variance. Similarly, in the partial landscape model, with plot- and patch-level effects removed, landscape composition accounted for 3.5% of the species variance, whereas landscape configuration accounted for only 1.4%. In this decomposition, 1.0% of the species variance was explained by the confounded composition–configuration component. Thus, consistent with our hypothesis, landscape composition appears to be a better predictor of community structure overall than does landscape configuration.

DISCUSSION

Hypothesis 1

The influences of processes and conditions in the immediate vicinity of individual organisms should be more strongly related to species presence and abundance than diffuse influences that act at coarser scales and are dispersed over larger areas. The presence and abundance of species at point locations should be more strongly related to the environmental conditions that the individual organisms directly experience at those sites than to the more diffuse influences of environmental structure at coarser scales. Further, we expect individual organisms and local populations to respond secondarily to environmental variation at the next coarser level of variation, the patch level, and to respond most weakly to the more diffuse influence of landscape composition and configuration.

This simple proximity–influence model is proposed as a null hypothesis, recognizing that a number of more complicated patterns of response could reflect differences in individual species' response to the scale of environmental variation. Alternatively, the relationship between proximity and influence could be incorrect, in general, for the bird community, and diffuse factors at coarser scales could be equally important or more important than fine-scale factors. This could reflect a hierarchical model of habitat selection (Hildén 1965, Rausher 1983, Wiens 1985). Species would select habitat based first on coarse-scale habitat characteristics, such as landscape configuration, then on meso-scale habitat characteristics, such as patch shape and edge contrast, and finally on microhabitat characteristics, such as vegetation structure and composition. Under this model, all three organizational levels of habitat variability play critical roles.

An alternative explanation recognizes the critical role of variation in how individual species scale the environment as a result of their different life-history strategies (Hansen and Urban 1992). Specifically, different species experience and respond to environmental variation in qualitatively different ways, depending on the grain of their perception (Wiens 1989a, b, Kotliar and Wiens 1990) and the relative fitness of different

behavioral responses to heterogeneity (MacArthur and Pianka 1966, Mangel and Clark 1986). Species may have evolved to maximize fitness by responding to environmental variation at scales in space and time that optimally benefit them and minimize competition with other species (Hutchinson 1957, 1959, Abrams 1983, Mangel and Clark 1986). This would result in communities in which all three levels of organization are important overall, because each is particularly important to certain subsets of species.

Our results provide an interesting perspective on these issues. Consistent with the proximity–influence hypothesis, plot-level environmental variation was much more strongly related to community structure than were factors at the patch and landscape levels. But our expectation of stronger patch-level than landscape-level effects was not seen. There was no substantial independent patch-level effect, and yet, there was a relatively strong independent landscape-level effect, although smaller than that of plot-level factors. The structure of the bird community in the Oregon Coast Range is consistent with the main component of the proximity–influence hypothesis; factors that vary at the scale of organisms' immediate experiences, the plot level, are substantially more important overall than factors that vary at coarser scales and whose influence on organisms is more diffuse. However, landscape-level factors also have a substantial influence, independent of fine-scale environmental variation at the plot level, which may reflect hierarchical habitat selection as well as species differences in the grain of their response to habitat structure.

Kotliar and Wiens (1990) postulate that adjacent levels in a hierarchy will have greater similarity in their effects than levels that are separated by other levels. This would be reflected in our analysis in higher confounding among plot- and patch-level factors and between patch- and landscape-level factors than would be seen between the plot and landscape levels. This was not true in all cases, with landscape- and plot-level factors being more highly confounded than were landscape- and patch-level factors. This indicates that, at least for the species–environment relationships of birds in the Oregon Coast Range, there is no support for the expectation that adjacent levels in a hierarchically organized system will have higher levels of confounding and redundancy.

Hypothesis 2

Plot-level results have several implications. First, for bird communities in the Oregon Coast Range, classic measures of vegetation structure are not as important as the overall floristic composition. This may indicate that bird species are keying into the distribution of individual plant types more strongly than has been thought previously, and are less strongly related to structural features (e.g., Cody 1985). In other words, it may indicate that gradients in floristic composition

better reflect the resources by which the community is organized than do gradients in dominant structure characteristics.

Second, it appears that mapped cover class captures patterns in community variation better than do more intensive measures of structure and floristics. It is surprising that a single, coarse-filter mapping of the community would capture the plot-level environmental variation that was most related to the bird community. This implies that the community may be organized at the plot-level largely by factors related to the three criteria that we used to develop the vegetation map, namely canopy closure, seral stage, and dominant vegetation type. The floristic and cover factors together explain well over 90% of the plot-level pattern in community structure, with structural variables explaining little additional variance. This indicates that nearly all of the plot-level explanation of species–environment relationships can be obtained without any reference to vegetation structure. In addition, because mapped cover type alone accounts for over half of the total variance explained by plot-level factors, coarse-scale studies need not leave out plot-level measures of habitat variation. There are not sufficient resources in most coarse-scale studies for exhaustive habitat sampling at the plot-level. These studies use GIS-derived data at the patch or landscape level to conduct their analyses and often neglect the plot level altogether. However, the success of mapped cover class as a plot-level predictor in our study suggests that GIS-produced cover maps have the potential to provide very powerful plot-level predictor variables that are also exhaustively sampled through space.

Hypothesis 3

A cornerstone of modern conservation biology theory is the idea that the area of habitat patches is related to the diversity of species in those patches (MacArthur and Wilson 1967). Any application of patch theory rests on several key assumptions. First, it assumes that the environment has been mapped at a scale that is meaningful to the organisms under study. Second, it assumes that the classes that define the patches are meaningful to the species. Finally, it assumes that the boundaries among patches reflect the boundaries that the organisms perceive. In our case, we are confident that the mapping is at a scale that matters to most species, but we are not sure it is the scale that matters most to any of them. We are also confident that the mapped classes are strongly related to the community, as the plot-level mapped cover class analysis shows. We hedged our assumption about the scale of measurement and detail of classification by analyzing both a patch- and a stand-based version of the patch-level mapping. This allowed us to represent patches as both general seral stages and more detailed community types. This gives us confidence that if there were to be strong relationships between patch size and configu-

ration and the bird community, then we would find them.

The small independent patch-level effect in our study indicates that patch size and configuration in the Oregon Coast Range provide little unique explanatory power beyond that provided by plot- and landscape-level factors. This does not imply that patch-level variation is not influential. Confounding with other levels was extensive, and it may be that patch-level patterns interact in important ways with environmental gradients at coarser and finer scales.

Contrary to our expectation, the second-tier patch-level partitioning showed that patch isolation, shape, and edge contrast, after removing the area effect, were more strongly related to community structure than was patch area alone. The details of patch isolation, shape, and patch context are often ignored in applications of patch theory in island biogeography and metapopulation dynamics studies (e.g., van Dorp and Opdam 1987). In most studies, patch area is the only factor considered. The patch-level decomposition indicates that patch isolation, shape, and patch context are more important to community structure than is patch area alone, and should not be ignored in patch-level studies of species–environment relationships.

Hypothesis 4

Much research has focused on separating the influences of landscape composition and landscape configuration on ecosystem and population processes (e.g., McGarigal and McComb 1995, With and Crist 1995, Fahrig 1997, 1998, Villard et al. 1999). If habitat area dominates species responses, and habitat configuration proves to be unimportant, habitat management and planning for species conservation could be greatly simplified (Fahrig 1997). If habitat configuration is important, then the problem is more complicated, and determining the important components of habitat pattern, and the existence of thresholds where the effect is magnified, would be key challenges. Our goal in testing the fourth hypothesis was to quantify the relative importance of landscape composition and configuration (and, implicitly, habitat area and configuration) to the community as a whole.

Several important conclusions arise from the landscape-level analyses. First, for both the marginal and conditional landscape-level partitioning, it appeared that the area of patch types in a landscape mosaic is more important to community structure than are the details of how those patch types are arranged in space. However, the configuration effect was not negligible, and landscape configuration provided substantial and highly significant additional explanation of bird community structure not provided by measures of landscape composition alone. This indicates that although landscape composition is most strongly related to community structure, it does not “dominate” the landscape-level response patterns. Landscape configuration

is also important, and our results suggest that landscape-level studies lose a great deal of explanatory power if they neglect to account for landscape configuration.

Synthesis

This study extends the original work by McGarigal and McComb (1995) to quantify the relationship between breeding bird abundance and the area and configuration of mature forest for several species strongly associated with mature forest in the Oregon Coast Range, and the subsequent work by Cushman and McGarigal (2003) to quantify the relative importance of mature forest area and fragmentation and differences among watersheds in influencing avian community diversity. Although these previous studies were able to confirm that landscape composition and configuration were important to several species and to community diversity, they were unable to separate the independent effects of landscape factors from factors operating at other levels of organization. By using a hierarchical approach to decompose species-environment relationships, following the procedure described in Cushman and McGarigal (2002), we were able to quantify the relative importance and confounding of environmental factors across three levels of system organization and to test several specific hypotheses about environmental control of community structure. The main conclusion to emerge from this study is that the bird community is structured by environmental factors acting simultaneously at all three levels of organization, and that the processes that structure the community at one level are not independent of those acting at other levels.

In the Oregon Coast Range, the bird community is structured by an interaction of plot-, patch-, and landscape-level factors. Fine-scale, plot-level factors appear to be predominantly important. Vegetation cover type is the most important plot-level habitat attribute, followed by details of site floristics. Vegetation structure appears to be less important. At the landscape level, both landscape-level habitat composition and configuration also have substantial influence on the bird community. These multilevel patterns of response may reflect either hierarchical habitat selection or differences in the level of primary response among the species in the community.

Implications for ecological surveys, management, and conservation

These results have several implications for ecological survey design, habitat management, and biological conservation. First, this study shows that different information about species-environment relationships is obtained from different organizational levels. This suggests that ecological surveys at the community or species levels should measure ecological parameters likely to be important to the species of interest across several levels of system organization. Specifically, fine-scale

local habitat characteristics, patch size, patch shape, landscape composition, and landscape configuration are all potentially important. Also, the strong performance of vegetation cover type at the plot level has implications for broad-scale analyses of habitat relationships. For example, plot-level cover type was an effective surrogate for much of the information provided by the more detailed, more expensive, and spatially constrained floristic and structural variables. Studies of broad-scale habitat relationships could greatly increase their explanatory power by including focal cover type in the analysis in addition to patch- or landscape-level factors. In addition, this study suggests that researchers should not neglect patch isolation, patch shape, patch context, or landscape configuration from patch- and landscape-level analyses. These factors accounted for substantial portions of the explanatory power at the respective organizational levels.

Second, the multiple-level patterns of species-environment relationships identified in this study have important implications for environmental management and biodiversity conservation. The predominant importance of plot-level factors, subordinate influence of landscape-level patterns, and relatively small, independent patch-level effect could imply that managers and conservationists should focus their attention on local habitat conditions within a landscape mosaic, with less concern about patch size and context. However, patch-level effects may be much more important in higher contrast systems. Our study area is a forested system consisting of a mosaic of forest patches at different stages of maturity. There might be strikingly different relationships in systems consisting of forest patches in a nonforest mosaic. Also, the large degree of confounding among the organizational levels suggests a more complicated story. Further work is needed to determine the nature and cause of this confounding. Specifically, it is important to determine whether species are responding to patterns at one level that are in turn correlated with patterns at another, or whether their response is to an interaction among patterns at multiple levels. If the former, then managers could select the operative level for management and conservation activities. If the latter, then the task is more complicated and would require a detailed understanding of the nature and causes of the across-level interactions.

Our analysis was conducted at the community level, and many management and conservation questions are centered at the level of species or guild. Although our community-level results may provide general guidance for some management questions, a detailed analysis of the relative importance of habitat factors at different organizational levels to individual species of concern or particular species groups would provide information of more direct management and conservation value. For example, it would be interesting to determine if species associated with old growth differed from species associated with closed canopy or open canopy, in terms

of the relative importance of factors at the different organizational levels, and the different variable subsets within each level. The analyses should be conducted for species divided by diet categories, body size, or migratory status.

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LITERATURE CITED

- Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* **14**:359–376.
- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, Illinois, USA.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355–366.
- Askins, R. A., M. J. Philbrick, and D. S. Sugeno. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* **39**:129–152.
- Beissinger, S. R., and D. R. Osborne. 1982. Effect of urbanization on avian community organization. *Condor* **84**:75–83.
- Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**:506–519.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* **68**:1724–1734.
- Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* **11**:406–421.
- Borcard, D., and P. Legendre. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (*Acari, Oribatei*). *Environmental and Ecological Statistics* **1**:37–53.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045–1055.
- Brown, E. R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 2: Appendices. U.S. Department of Agriculture Publication Number R6, Fish and Wildlife 192–1985.
- Cody, M. L. 1985. *Habitat selection in birds*. Academic Press, Orlando, Florida, USA.
- Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale analysis of species–environment relationships. *Landscape Ecology* **17**:637–646.
- Cushman, S. A., and K. McGarigal. 2003. Landscape-level patterns of avian diversity in the Oregon Coast Range. *Ecological Monographs* **73**:259–281.
- Drapeau, P., A. Leduc, J.-F. Giroux, J.-P. L. Savard, Y. Bergeron, and W. L. Vickery. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs* **70**:423–444.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modeling* **105**:273–292.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* **100**:65–74.
- Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* **12**:346–353.
- Flather, C. H., and M. Bevers. 2001. Patchy reaction–diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist* **159**:40–56.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape configuration by forest cutting: ecological consequences and principles. *Landscape Ecology* **1**:5–18.
- Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* **36**:115–141.
- Fuller, R. J., and D. R. Langslow. 1984. Estimating numbers of birds by point counts: how long should counts last? *Bird Study* **31**:195–202.
- Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: the role of species' life histories. *Landscape Ecology* **7**:163–180.
- Hildén, O. 1965. Habitat selection in birds. *Annales Zoologici Fennici* **2**:53–75.
- Hill, M. F., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* **2**:121–127.
- Holling, C. S. 1986. The resilience of terrestrial ecosystems: local surprise and global change. Pages 292–317 in W. C. Clark and R. E. Munn, editors. *Sustainable development of the biosphere*. Cambridge University Press, Cambridge, UK.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* **124**:377–406.
- Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecology* **15**:547–562.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia* **27**:343–383.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* **22**:415–427.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* **93**:145–159.
- James, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bulletin* **83**:215–236.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**:388–390.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624–635.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* **108**:207–228.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943–1967.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences (USA)* **71**:2744–2747.
- MacArthur, R. H. 1958. Population ecology of some warblers in Northeastern coniferous forests. *Ecology* **39**:599–619.

- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603–609.
- MacArthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. *American Naturalist* **100**:319–332.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. *Ecology* **67**:1127–1138.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. [Online: <www.umass.edu/landeco/research/fragstats/fragstats.html>.]
- McGarigal, K., S. A. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag, New York, New York, USA.
- McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* **65**:235–260.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology* **5**:93–106.
- Rausher, M. D. 1983. Ecology of host-selection behavior in phytophagous insects. Pages 223–257 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171.
- Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* **103**.
- Roughgarden, J. 1976. Influence of competition on patchiness in a random environment. *Theoretical Population Biology* **14**:185–203.
- Schmiegelow, F. K. A., and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* **12**:375–389.
- Schneider, D. C. 1994. *Quantitative ecology: spatial and temporal scaling*. Academic Press, San Diego, California, USA.
- Schoener, T. W. 1971. Theory of freeing strategies. *Annual Review of Ecology and Systematics* **2**:369–404.
- Spies, T. A., and S. P. Cline. 1988. Coarse woody debris in manipulated and unmanipulated coastal Oregon forests. Pages 5–24 in C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, editors. *From the forest to the ocean—a story of fallen trees*. USDA Forest Service General Technical Report **PNW-229**.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**:1167–1179.
- ter Braak, C. J. F. 1992. Permutation vs. bootstrap significance tests in multiple regression and ANOVA. Pages 79–85 in K. H. Jockel, G. Rothe, and W. Sendler, editors. *Bootstrapping and related techniques*. Springer-Verlag, Berlin, Germany.
- ter Braak, C. J. F., and P. Smilauer. 1998. *CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination*. Version 4. Microcomputer Power, Ithaca, New York, USA.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* **9**:586–593.
- van Dorp, D., and P. Opdam. 1987. Effects of patch size, isolation, and regional abundance on forest bird communities. *Landscape Ecology* **1**:59–73.
- Verner, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. USDA Forest Service Research Note **PSW-395**.
- Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13**:774–783.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**:81–210.
- Wiens, J. A. 1985. Habitat selection in variable environments: shrug-steppe birds. Pages 227–251 in M. L. Cody, editor. *Habitat selection in birds*. Academic Press, Orlando, Florida, USA.
- Wiens, J. A. 1989a. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wiens, J. A. 1989b. *The ecology of bird communities*. Volume 2. Processes and variations. Cambridge University Press, Cambridge, UK.
- Wiens, J. A. 1994. Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis* **137**:97–104.
- With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* **76**:2446–2459.
- With, K. A., and A. W. King. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* **14**:73–82.
- With, K. A., and A. W. King. 1999b. Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**:314–326.