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Do forest community types provide a sufficient basis to evaluate biological diversity?

Samuel A Cushman^{1*}, Kevin S McKelvey¹, Curtis H Flather², and Kevin McGarigal³

Forest communities, defined by the size and configuration of cover types and stand ages, have commonly been used as proxies for the abundance or viability of wildlife populations. However, for community types to succeed as proxies for species abundance, several assumptions must be met. We tested these assumptions for birds in an Oregon forest environment. Measured habitat was a weak proxy for species abundance and vegetation cover type was a weak proxy for habitat, explaining only 4% of the variance in species abundance. The adequacy of forest community types as habitat proxies was highly dependent on classification rules and the spatial scales at which communities were defined. Habitat was perceived differently by species guilds and a single, generalized characterization of habitat is therefore unlikely to provide a reliable basis for multi-species conservation efforts. Given the weak relations between forest vegetation and species abundance, evaluation of landscape pattern is unlikely to be an effective replacement for the direct monitoring of species population size and distribution.

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The idea that easily measured characteristics of the vegetation community can be used as surrogates for biological diversity has a long history in conservation biology. In 1982, The Nature Conservancy proposed a two-stage approach to biodiversity conservation. The first stage, the coarse filter, was based on conservation of representative vegetation communities, while the second stage, the fine filter, focused on individual species not sufficiently protected by the coarse filter (Noss 1987; Hunter *et al.* 1988). This concept was originally linked to reserve design (Hunter *et al.* 1988), but more recently, particularly in the silvicultural literature, the concept of a coarse filter has been linked to natural disturbance regimes (Haufler *et al.* 1996; Bergeron *et al.* 2002) and applied to actively managed landscapes (Bergeron *et al.* 2002). In this context, the characterization of landscapes in terms of broad vegetation characteristics has been assumed to provide an effective surrogate for biological diversity at all levels of organization (Lemelin and Darveau 2006).

These concepts have frequently been adopted as the central basis for efforts to conserve biological diversity (Schulte *et al.* 2006). For example, maintenance of forest cover types and ages that lie within a range of “desired conditions” has recently been institutionalized as the primary conservation standard for the US Forest Service, a public agency with stewardship responsibility for 78 million ha of land. The agency asserts that maintaining a diversity of vegetation types will maintain the health of

ecological systems, including viable populations of plant and animal species (Federal Register 70:3:1023). Due to the expected efficacy of this approach, the agency is no longer required to directly monitor species or maintain viable populations (Federal Register 70:3:1023).

For the diversity of vegetation types to serve as an effective proxy for species viability, several conditions must be met simultaneously (Noon *et al.* 2003). The most crucial are: (1) habitat is a proxy for population abundance and (2) mapped vegetation types provide a proxy for the habitat of multiple species. The first assumption requires that species population sizes be strongly associated with environmental conditions, so that environmental conditions alone are a sufficient proxy for population status and trends. The second assumption states that broadly defined vegetation types provide an effective surrogate for these environmental conditions. Neither of these premises has been rigorously assessed (Brooks *et al.* 2004; Wilcove and Master 2005; Rohr *et al.* in press). Habitats encompass a broad suite of environmental conditions that influence a species, including abiotic conditions and the occurrence of other species. In this paper, we define habitat at two levels: first as floristic and structural elements measured at the scale of forest plots and second as forest community types representing stands of homogenous cover type and successional stage. Here, we use the relative abundance of birds co-located with floristic and structural data in a forested landscape in the Oregon Coast Range to address the following questions:

- (1) Is habitat a proxy for species abundance?
- (2) Are mapped vegetation-community types a proxy for habitat?
- (3) Does the effectiveness of habitat as a proxy for species abundance vary among guilds?

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■ Methods

Species data consisted of the relative abundance of 53 species of breeding birds at 535 plots located within three major hydrological basins in forested regions of western Oregon, USA (McGarigal and McComb 1995; Cushman and McGarigal 2004; WebPanel 1). To test for guild associations, we divided these species into open-canopy, closed-canopy, and generalist habitat guilds (Hansen and Urban 1992; WebTable 1).

The habitat dataset contained variables from two sources (McGarigal and McComb 1995): detailed measurements of vegetation composition and structure at the level of the sample plot and a map of forest community types derived from aerial photography (WebTables 2–4). To test the effects of classification scheme on the strength of observed relationships between community type and species abundance, we mapped community types in three ways, delineating vegetation patches based on cover type, successional stage, and cover types across successional stages. In addition, because species respond to habitat conditions at multiple scales (Lichstein *et al.* 2002; Steffan-Dewenter *et al.* 2002; Cushman and McGarigal 2004), we compared the effectiveness of two scales of community type as a proxy for habitat: plot-level community type, defined as the percentage of the 50-m radius survey plot covered by each mapped community type, and landscape-level community composition, defined as the percentage of the landscape surrounding each plot covered by each mapped community type. Landscapes were defined as hydrological sub-basins and ranged in size from 250–300 ha (McGarigal and McComb 1995).

We used hierarchical variance partitioning (Cushman and McGarigal 2002) to answer the first two research questions: do habitats provide a proxy for bird abundance and do community types provide a proxy for habitat? Hierarchical variance partitioning uses a series of partial canonical ordinations to partition explained variance into its components (WebPanel 1; WebTable 5). The method translates a hierarchical conceptual model into a statistical decomposition of variance. In this context, the analysis decomposes the variance in species abundances that is explainable by habitat variables. In this way, it allows a comparison of the relative explanatory power of habitat factors in total (question 1) to the subset of factors comprising mapped forest community types (question 2).

Results of canonical analyses can be sensitive to both the statistical method employed and the number of explanatory variables included (Oksanen and Minchin 1997; Legendre and Gallagher 2001). Accordingly, we evaluated concordance of results across a factorial of two ordination methods (canonical correspondence analysis [CCA] and row normalized redundancy analysis [RDA]) and two sets of variables (all environmental variables and a reduced set). In the reduced set, we retained the best four or five environmental variables in each set (WebTable 6) through forward variable selection using

Akaike's information criterion (AIC; Venables and Ripley 2002). Concordance of results across these different methods and variable sets would indicate that the results were insensitive to the methods used. For each method, partitioning variance in bird relative abundance resulted in eight variance components (Table 1; WebFigure 1). We used factorial ANOVA to determine if the classification scheme used to delineate forest community types influenced the effectiveness of community type as a habitat proxy.

We evaluated whether the effectiveness of habitat as a proxy for species abundance varied among guilds (question 3) using canonical variates analysis (ter Braak and Smilauer 1998; WebPanel 1). The analysis provides a test for significant differences among the three habitat guilds (open canopy, closed canopy, generalist), based on the amount of variance in species abundance that can be explained by the three scales of habitat data (plot-level field measurements, plot-level community type, and landscape composition of community types), across the three classification schemes (cover type, successional stage, and cover type by successional stage). Thus, the analysis distinguishes between guilds, based on the strength of their association with plot-level vegetation versus mapped community types, while simultaneously assessing differences among guilds in their sensitivity to how forest community types were defined.

■ Results

The results from each variance partitioning approach were in agreement in all qualitative aspects across the

Table 1. Description of the eight variance components resulting from the decomposition of species variance among plot-level (50-m radius survey plots) vegetation characteristics, plot-level community type, and landscape-level community type

Component acronym	Species variance explained by
FP	Fine-scale vegetation composition and structure only
CP	Plot-level community type only
CL	Landscape composition of community type only
FP–CP	The combination of fine-scale vegetation and plot-level community type
FP–CL	The combination of fine-scale vegetation and landscape-level community type
CL–CP	The combination of plot-level and landscape-level community type
FP–CL–CP	The combination of fine-scale vegetation, plot-level, and landscape-level community type
UNEXP	Unexplained by fine-scale vegetation, plot-level, or landscape-level coarse filter

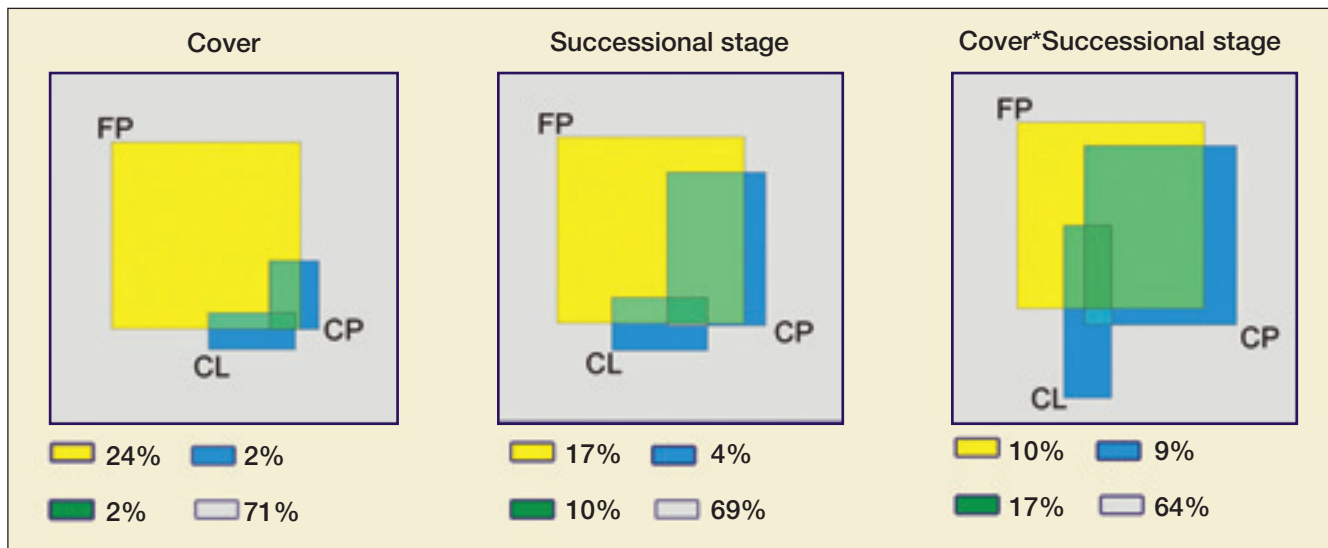


Figure 1. Variance partitioning plots showing variance in bird abundance explained by fine-scale vegetation and mapped community type across the three community-type definitions. The three intersecting rectangles correspond to each of the three levels of independent variables: FP = plot vegetation, CP = plot community type, and CL = landscape community type. The four focal components of variance are variance explained exclusively by plot vegetation (yellow) or community type (blue), jointly by plot vegetation and community type (green), and unexplained (gray). Habitat accounts for less than 40% of the variance in species abundance in all three representations of community type. The relative strength of vegetation communities as predictors of species abundance is low when defined by cover type alone, and is substantially greater when defined by a combination of cover type and successional stage.

four combinations of analytical method and variable sets (WebTable 7). Here, we report only the CCA results obtained using the full variable set. The majority of variance in the relative abundances of the 53 bird species could not be explained by measured habitat variables (Figure 1). In addition, the total amount of variance was sensitive to community-type classification rules. The proportion of species variance explained by all habitat variables (including plot-level vegetation and mapped community types) was 36% when communities were defined as the combination of cover type and successional stage, and declined to 31% when communities were based on successional stage only, and to 29% when community types were based on cover type only.

Little of the variance in species' relative abundances (4%) and only a small fraction of the variance that was explained by measured habitat variables (14%) was explained by community types when they were defined by cover type (Figure 1). When community types were defined by successional stage, they explained 14% of total variance in species abundances, accounting for 45% of the variance explainable by habitat variables. When community types were defined as a combination of cover type and successional stage, they explained 26% of the total variance and 72% of the variance explainable by habitat variables.

Total variance explained differed among guilds (Table 2). Open-canopy species had significantly higher (mean = 35%) variance than either closed-canopy (mean = 29%) or generalist (mean = 25%) species (Duncan multiple range test, $P = 0.0014$). There were no significant interactions between habitat guild and map

classification and no significant differences among the three community classifications in terms of average explained variance.

The canonical variates model significantly discriminated among guilds across the three community classifications (Monte Carlo, $P < 0.005$). The canonical variates plot (Figure 2) confirms that larger amounts of variance are explained by community types when defined as a combination of cover type and successional stage. The plot also illustrates marked differences among guilds in the scales at which they are most strongly related to environmental variation. Open-canopy species showed weaker relationships to landscape composition and stronger relationships to plot-level characteristics than did closed-canopy or generalist species. In contrast, closed-canopy and generalist species were similar in their relationships to habitat elements across scale, with the relative explanatory power of landscape composition increasing greatly when community types were defined as the combination of cover type and successional stage.

Table 2. Differences in total variance explained by habitat variables for three habitat guilds (open canopy, closed canopy, generalist) across three definitions of community type (cover type, successional stage, cover–successional combination)

Source	df	Type III SS	F	P
Guild	2	2725.28	6.84	0.0014
Community definition	2	658.76	1.65	0.1948
Guild*definition	4	325.14	0.41	0.8026

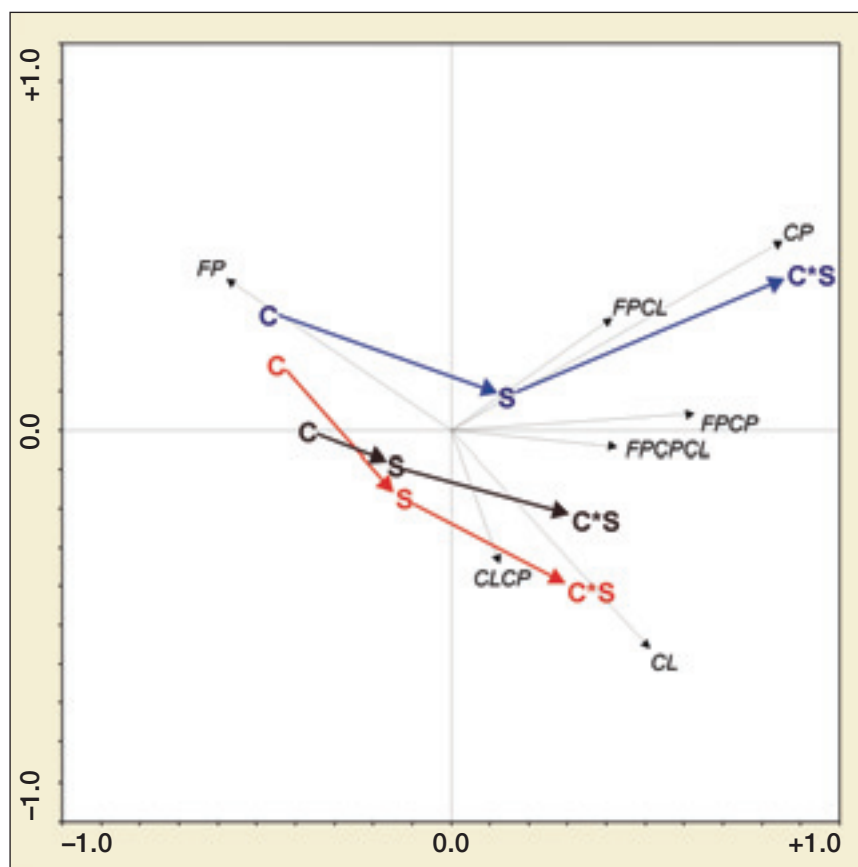


Figure 2. Canonical variates plot showing differences in the relative amounts of species variance explained by fine-scale vegetation characteristics (FP), plot-level community type (CP), percentage of the landscape covered by each community type (CL), and their interactions (CL-CP, FP-CP, FP-CL, FP-CP-CL; Table 1) across the three classifications of natural communities (C = cover type, S = successional stage, C*S = cover type by successional stage). The two axes represent the two orthogonal combinations of variance components that maximally discriminated guilds across community classifications, and the arrows point in the direction of maximum increase of each variance component in the canonical space. The first axis can be interpreted as a gradient from high relative explanatory power of plot-level vegetation characteristics on the left, to high relative explanatory power of community type on the right. Axis 2 can be interpreted as high relative explanatory power of landscape composition at the bottom, to high relative explanatory power of plot-level characteristics (both vegetation and community type) at the top. Blue line = open-canopy associated species, red line = closed-canopy associated species, brown line = generalist species.

Discussion

Is habitat a proxy for species abundance?

Habitat variables explained less than 40% of the total variance in the species abundances in all cases (Figure 1). Thus, in this example, measured habitat was a weak proxy for species abundance. The low explanatory power of habitat variables was not due either to a paucity of measured variables (52 plot and 12 landscape variables; WebTables 2,3) or small sample size (535 plots; over 40 000 bird detections). This dataset was derived from one of the most intensive species-environment studies ever conducted for birds.

Are mapped vegetation community types a proxy for habitat?

For broadly defined community types to serve as effective proxies for habitat, most of the important habitat relationships must occur at the broadest levels, with fine-scale patterns being relatively unimportant. The performance of community types as habitat proxies was sensitive to classification rules (Figure 1). The most detailed community mapping in our analysis explained almost seven times as much variance as the least. That the effectiveness of community type is highly sensitive to classification rules has important implications: the efficacy of any particular cover-type map as a habitat proxy cannot be assumed and vegetation community-type maps lacking proper classification resolution may utterly fail as proxies for habitat quality.

Does the effectiveness of habitat as a proxy for species abundance vary among guilds?

The efficacy of habitat as a proxy for species abundance differed significantly among guilds (Table 2). Open-canopy species had greater amounts of variance explained by habitat than either closed-canopy or generalist species, and these differences were consistent across all community-type definitions. Furthermore, guilds responded to different habitat variables at different scales. This suggests that any single characterization of habitat will not be optimal for all species, and that development of separate habitat relationships for individual species may often be necessary.

For these species and this locale, we conclude that coarsely defined plant community types, particularly those

based on cover types, do not provide strong surrogates for species abundance. This does not imply that there are not important habitat relationships among these species. The canonical ordinations relating species to environmental gradients were all highly significant ($P < 0.005$), with high species-environment correlations, indicating strong statistical relationships between species and habitat characteristics. Discovering such relationships is essential for identifying potential habitat, evaluating the effects of land management on habitat quality, and projecting future potential habitat. However, because the majority of variance was unexplained, these statistical habitat relationships cannot be used as a reliable index for the abun-

dance patterns of these 53 avian species. Thus, while habitat–relationship models are a necessary guide for management and conservation, they do not provide an effective surrogate for populations themselves.

Total variance in species abundance explainable by habitat variables will likely vary among taxonomic groups and study areas. However, the results presented here probably provide a best-case scenario. Breeding birds are known to be closely tied to specific habitats (Cody 1985) and the environmental data used in these analyses were more detailed and accurate than that typically available to managers, with fine-scale and accurate mapping of cover types and successional stages from low-elevation aerial photography (McGarigal and McComb 1995). Forest managers typically use coarse-grained land-cover maps, often limited to a few major cover types with poor discrimination between successional stages, and containing significant classification error rates. In our analyses, cover type could only explain about 4% of the total variance in bird abundance; the cover-type maps available to most managers would probably have even weaker relationships to species abundance than indicated here.

■ Conclusions

The proposal that mapped vegetation types can be an effective proxy for species abundance is untested for most taxa in most ecological systems. In this analysis, it does not appear that habitat is a strong proxy for breeding-bird relative abundance. Furthermore, sufficiency of vegetation community types as proxies for habitat was highly dependent on the classification attributes and spatial scales at which communities were defined and the species to which these attributes were correlated. While this analysis is limited to breeding birds in one region and does not provide a general test, unless other taxa respond very differently to cover-type data, satellite-derived vegetation mosaics will be of little practical use for inferring abundance. Given these uncertainties, it is critical to repeat this evaluation on other taxa in different ecological systems. However, based on this test, the assumption that maps of cover type and successional stage can serve as effective proxies for species abundance or viability cannot be generally accepted. It is therefore premature to presume that measuring the extent and diversity of vegetation communities can supplant the need to monitor species in actively managed landscapes.

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WebPanel 1. Study area and statistical methods

The study area consisted of three major hydrological basins (Drift Creek, Lobster Creek, and Nestucca River basins) in the central Oregon Coast Range, where elevation ranges from sea level to 968 m and climate is maritime, with mild, wet winters and cool, dry summers. The study area was characterized by steep slopes and deeply cut drainages and lay almost entirely within the western hemlock (*Tsuga heterophylla*) vegetation zone. The natural forest overstory was dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and red alder (*Alnus rubra*). Western redcedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyllum*) were also common. Understory vegetation was variable in composition and distribution. Common species included salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), Oregon grapes (*Berberis* spp), huckleberries (*Vaccinium* sp), and swordfern (*Polystichum munitum*).

Over 70% of the study area consisted of public lands administered by the USDA Forest Service and USDI Bureau of Land Management. In portions under public ownership, the landscape consisted of a matrix of late-successional, unmanaged forest dominated by Douglas-fir and red alder interspersed with many small (8–25 ha), young, even-aged Douglas-fir plantations. On private land, the landscape consisted largely of extensive, young (0–40-year-old), even-aged Douglas-fir plantations, with isolated patches of late-successional forest. Consequently, a wide range of landscape structural conditions existed in the study area, particularly with respect to the extent and fragmentation of late-successional forest.

Bird abundance dataset

The details of the bird abundance dataset are presented by McGarigal and McComb (1995). Briefly, the data were extracted from the larger bird dataset used by McGarigal and McComb (1995) and Cushman and McGarigal (2003). 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% of the area of each landscape. We acquired between 32 and 38 sample points per landscape, for a total of 1046 points. In the analysis reported here, we sub-sampled this dataset, using the 535 points for which detailed vegetation and abiotic data were collected at the plot level.

We sampled diurnal breeding birds in Drift Creek in 1990, Lobster Creek in 1991, and Nestucca River in 1992. Confounding of year and basin was not significant (McGarigal and McComb 1995). Each year, we sampled birds four times in each landscape at regular intervals between May 1 and July 12. Surveys began 15–20 minutes before sunrise and ended within 4 h after sunrise. On each visit, observers waited 2 minutes to allow birds to resume normal activity and then recorded all birds detected within 50 m during an 8-minute 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. In our analysis, we excluded species with three or fewer detections in the dataset, resulting in a final dataset consisting of the relative abundance of 53 species across 535 plots.

Variance partitioning methods

The method of using a series of canonical ordinations to decompose species variance is described in detail in Cushman and McGarigal (2002). Here, we provide a brief synopsis of the method. In the analyses in this paper, we completed 12 different decompositions, corresponding to the combinations of the factorial of the four different ordination methods (CCA all variables, CCA reduced variables, RDA all variables, RDA reduced variables) across three different classification schemes for forest community types (cover type, successional stage, cover*successional; WebTable 7).

The decomposition separates the effects of plot vegetation, plot-level community type, and landscape community type composition. The decomposition can be visualized by a Venn diagram, such as those commonly used in set theory (WebFigure 1). This decomposition extracts seven discrete components of explained community variation, and one component of unexplained variation:

- (1) Pure plot vegetation effects (FP; ie variation in bird community structure explained by plot-level variables, which is not also explained by plot-level community type of landscape community type composition);
- (2) Pure plot-level community type effects (CP);
- (3) Pure landscape community type composition effects (CL);
- (4) Joint effects of plot vegetation and landscape community type composition variables (FPCL; ie community variation that is jointly explained by plot- and landscape-level factors, but is independent of measured patch-level variables);
- (5) Joint effects of plot vegetation and plot-level community type variables (FPCP);
- (6) Joint effects of plot-level community type and landscape community type composition (CLCP);
- (7) Joint effects of plot vegetation, plot-level community type, and landscape community type composition (FPCLCP).

The variance decomposition explicitly quantifies the relative importance and redundancy of each set of explanatory factors. The independent effects of plot vegetation (1), plot-level community type (2), and landscape community type (3) provide measures of the unique contributions of factors from these different scales. Similarly, the confounded components ([4], [5],

WebPanel 1. Studyarea and statistical methods (continued)

[6], and [7]) quantify the level of redundancy among variables measured at different scales.

In CCA or RDA analysis of species abundance data, the sum of canonical eigenvalues is a measure of the amount of variation in the species data that is explained by the variables in the constraining environmental variable set. The sum of all eigenvalues of the unconstrained correspondence analysis (CA) of the species data is a measure of the total variation in the species data. The ratio of the sum of canonical eigenvalues and the sum of unconstrained CA eigenvalues is the proportion of the total variance in the community that is explained by the environmental variables, after removing the effect of any covariables.

Using this principle, we conducted a series of CCA and RDA analyses to isolate all of the variance components needed for the partitioning process (WebTable 5). After running the necessary CCA and RDA models, we calculated the percentage of total species variation associated with each partition listed in WebFigure 1. In our terminology, numbers in square brackets in WebTable 5 refer to the percentage of total species variance explained by the individual analyses, and numbers in parentheses refer to final variance partitions, as shown in the list above.

The percentage of total species variation explained by plot vegetation, plot-level community type, and landscape community composition together equals $[1]+[7]+[12]$ or $[2]+[4]+[12]$ or $[3]+[8]+[6]$. The pure plot vegetation component is equal to [6]. The pure plot community type component equals [9] and the pure landscape community composition component equals [12]. The key to the calculation of the remaining components is (7), the three-way overlap among plot vegetation, plot-level community type, and landscape community type composition. Note that the overlap between plot vegetation and plot-level community type factors, $\{(5)+(7)\}$, is calculated as $[1]-[4]$ or $[2]-[7]$. Similarly, note that the overlap between plot vegetation and landscape community composition factors $\{(4)+(7)\}$ is $[1]-[5]$ or $[3]-[10]$. Once we have calculated these two overlap regions we can isolate (7). We know the independent effect of plot vegetation factors, (1), from analysis [6]. In addition, we know the marginal effect of plot vegetation factors, $\{(1)+(4)+(5)+(7)\}$, from analysis [1]. We also know the overlap between plot vegetation and plot-level community type, $\{(5)+(7)\}$, and plot vegetation and landscape community type composition, $\{(4)+(7)\}$,

from above. Using simple algebra, we can solve for (7) by noting that the independent effects of plot vegetation factors plus the two overlap components of plot vegetation with plot-level community type, and plot vegetation with landscape community type composition, equal the marginal effects of plot vegetation plus (7). Once the value of (7) is known, the remaining three components $\{(4),(5),(6)\}$ are easily derived:

$$(4) = [1] - [5] - (7) \text{ or } [3] - [10] - (7)$$

$$(5) = [1] - [4] - (7) \text{ or } [2] - [7] - (7)$$

$$(6) = [2] - [8] - (7) \text{ or } [3] - [11] - (7)$$

Canonical variates method

Canonical variates analysis is a multivariate technique in which orthogonal linear combinations of independent variables are constructed that maximize the between-group differences among several predefined groups. In this example, the independent variables are the seven components of explained variance. The groups are the three guilds across the three different forest community-type classification schemes. The observations in this analysis consist of the 53 bird species, grouped by guild. The seven variance components obtained through the decomposition make up the set of descriptors which are then combined in linear combinations to maximize discrimination among guilds across community-type classification schemes. In a nutshell, the analysis provides a means to simultaneously compare differences among guilds and community type classifications in terms of the relative explanatory power of fine-scale plot vegetation, plot-level community type, and landscape community-type composition. It is analogous and statistically similar to a factorial multivariate analysis of variance, with the advantage of Monte-Carlo permutation testing of significance and the production of a visually interpretable plot showing the pattern of discrimination along the first two canonical axes (Cushman 2003; Figure 2).

Additional references

Cushman SA. 2003. Hierarchical analysis of forest bird species–environment relationships in the Oregon Coast Range (PhD dissertation). Amherst, MA: University of Massachusetts, Amherst.

WebTable 1. List of the 53 bird species included in the analysis. Guilds include open canopy (OC), generalist (G), and closed canopy (CC) associated species (from Hansen and Urban [1992])

Common name	Taxonomic name	Guild	Common name	Taxonomic name	Guild	Common name	Taxonomic name	Guild
American goldfinch	<i>Carduelis tristis</i>	OC	House wren	<i>Troglodytes aedon</i>	G	Townsend's solitaire	<i>Myadestes townsendi</i>	G
American robin	<i>Turdus migratorius</i>	OC	Hutton's vireo	<i>Vireo huttoni</i>	G	Varied thrush	<i>Ixoreus naevius</i>	CC
Black-capped chickadee	<i>Poecile atricapilla</i>	G	MacGillivray's warbler	<i>Oporornis tolmiei</i>	OC	Violet-green swallow	<i>Tachycineta thalassina</i>	OC
Bewick's wren	<i>Thryomanes bewickii</i>	G	Northern flicker	<i>Colaptes auratus</i>	OC	Warbling vireo	<i>Vireo gilvus</i>	OC
Black-throated gray warbler	<i>Dendroica nigrescens</i>	G	Orange-crowned warbler	<i>Vermivora celata</i>	OC	White-crowned sparrow	<i>Zonotrichia leucophrys</i>	OC
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	OC	Olive-sided flycatcher	<i>Contopus cooperi</i>	CC	Western bluebird	<i>Sialia mexicana</i>	OC
Brown creeper	<i>Certhia americana</i>	CC	Pine siskin	<i>Carduelis pinus</i>	G	Western tanager	<i>Piranga ludoviciana</i>	G
Band-tailed pigeon	<i>Columba fasciata</i>	OC	Pileated woodpecker	<i>Dryocopus pileatus</i>	CC	Willow flycatcher	<i>Empidonax traillii</i>	OC
Bushtit	<i>Psaltriparus minimus</i>	G	Pacific-slope flycatcher	<i>Empidonax difficilis</i>	CC	Wilson's warbler	<i>Wilsonia pusilla</i>	G
Chestnut-backed chickadee	<i>Poecile rufescens</i>	CC	Purple finch	<i>Carpodacus purpureus</i>	G	Winter wren	<i>Troglodytes troglodytes</i>	CC
Cedar waxwing	<i>Bombycilla cedrorum</i>	OC	Red-breasted nuthatch	<i>Sitta canadensis</i>	CC	Wrentit	<i>Chamaea fasciata</i>	G
Common raven	<i>Corvus corax</i>	G	Red-breasted sapsucker	<i>Phrycapicus ruber</i>	CC	Western wood-peewee	<i>Contopus sordidulus</i>	CC
Dark-eyed junco	<i>Junco hyemalis</i>	G	Red crossbill	<i>Loxia curvirostra</i>	CC	Yellow-rumped warbler	<i>Dendroica coronata</i>	G
Evening grosbeak	<i>Coccothraustes vespertinus</i>	G	Eastern towhee	<i>Pipilo erythrophthalmus</i>	OC			
Golden-crowned kinglet	<i>Regulus satrapa</i>	CC	Red-tailed hawk	<i>Buteo jamaicensis</i>	G			
Gray jay	<i>Perisoreus canadensis</i>	CC	Ruffed grouse	<i>Bonasa umbellus</i>	OC			
Hammonds flycatcher	<i>Empidonax hammondi</i>	CC	Rufous hummingbird	<i>Selasphorus rufus</i>	G			
Hairy woodpecker	<i>Picoides villosus</i>	CC	Song sparrow	<i>Melospiza melodia</i>	OC			
Hermit thrush	<i>Catharus guttatus</i>	G	Steller's jay	<i>Cyanocitta stelleri</i>	G			
Hermit warbler	<i>Dendroica occidentalis</i>	CC	Swainson's thrush	<i>Catharus ustulatus</i>	G			

WebTable 2. Description of fine-scale variables (FP) measuring vegetation and abiotic conditions at the sample plot

<i>Plot field variables</i>	<i>Definition</i>
edgeden	density of edge within the plot
cwedge	contrast-weighted density of edge within the plot
pae	binary patch edge variable
ste	binary stand edge variable
batotal	total basal area within the 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
cacci	plot cover by vine maple
cacma	plot cover by <i>Acer macrophyllum</i> (big-leaf maple)
cbeaq	plot cover by <i>Berberis aquifolium</i> (Oregon grape)
cbene	plot cover by <i>Berberis nervosa</i> (dwarf Oregon grape)
cconu	plot cover by <i>Cornus nuttallii</i> (common dogwood)
chodi	plot cover by <i>Holodiscus discolor</i> (ocean spray)
cmefe	plot cover by <i>Menziesia ferruginea</i> (fool's huckleberry)
copho	plot cover by <i>Oplopanax horridus</i> (devil's club)
crhma	plot cover by <i>Rhododendron macrophyllum</i> (rhododendron)
crhpu	plot cover by <i>Rhamnus purshiana</i> (cascara)
cribr	plot cover by <i>Ribes bracteosum</i> (stink currant)
cruur	plot cover by <i>Rubus ursinus</i> (trailing blackberry)
csara	plot cover by <i>Sambucus racemosa</i> (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 swordfern
flor5	gradient of increasing red huckleberry and salal
flor6	gradient of increasing salmonberry and current
flor7	gradient of increasing western red cedar and evergreen huckleberry
flor8	gradient of increasing sitka spruce and fool's huckleberry
flor10	gradient of increasing thimbleberry, ocean spray, and willow

WebTable 3a. Plot community type (CP) variables included in the analysis when community type was defined by cover type (CT)

<i>Plot composition</i>	<i>Definition</i>
mixedP	Percentage of plot covered by mixed forest
hardwoodP	Percentage of plot covered by hardwood forest
coniferP	Percentage of plot covered by conifer forest
bareP	Percentage of plot covered by bare ground

WebTable 3b. Plot community type (CP) variables included in the analysis when community type was defined by successional stage (SS)

<i>Plot composition</i>	<i>Definition</i>
LS	Percentage of plot covered by large sawtimber
SS	Percentage of plot covered by small sawtimber
CP	Percentage of plot covered by closed pole
OP	Percentage of plot covered by open pole
S	Percentage of plot covered by saplings

WebTable 3c. Plot community type (CP) variables included in the analysis when community type was defined by a combination of cover type and successional stage (CTSS)

<i>Plot composition</i>	<i>Definition</i>
b	Percentage of plot covered by bare soil
ccp	Percentage of plot covered by conifer closed pole
cls	Percentage of plot covered by conifer large sawtimber
cop	Percentage of plot covered by conifer open pole
cos	Percentage of plot covered by conifer opens sapling
csH	Percentage of plot covered by conifer shrub
hcp	Percentage of plot covered by hardwood closed pole
hls	Percentage of plot covered by hardwood large sawtimber
hop	Percentage of plot covered by hardwood open pole
hsh	Percentage of plot covered by hardwood shrub
hss	Percentage of plot covered by hardwood small sawtimber
mcp	Percentage of plot covered by mixed closed pole
mgf	Percentage of plot covered by mixed grass–forb
mls	Percentage of plot covered by mixed large saw
mop	Percentage of plot covered by mixed open pole
mos	Percentage of plot covered by mixed open sapling
msh	Percentage of plot covered by mixed shrub

WebTable 4a. Landscape composition (CL) variables included in the analysis when community type was defined by cover type (CT)

<i>Landscape composition</i>	<i>Definition</i>
mixedL	Percentage of landscape covered by mixed forest
hardwoodL	Percentage of landscape covered by hardwood forest
coniferL	Percentage of landscape covered by conifer forest
bareL	Percentage of landscape covered by bare ground

WebTable 4b. Landscape composition (CL) variables included in the analysis when community type was defined by successional stage (SS)

<i>Landscape composition</i>	<i>Definition</i>
GL	Percentage of landscape covered by grass
GFL	Percentage of landscape covered by grass–forb
LSL	Percentage of landscape covered by large sawtimber
POL	Percentage of landscape covered by pole timber
SAL	Percentage of landscape covered by sapling
SHL	Percentage of landscape covered by shrub
SSL	Percentage of landscape covered by small sawtimber

WebTable 4c. Landscape composition (CL) variables included in the analysis when community type was defined by a combination of cover type and successional stage (SS)

<i>Landscape composition</i>	<i>Definition</i>
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

WebTable 5. Description of the 12 canonical analyses conducted to partition species variance into the eight components depicted in WebFigure 1.

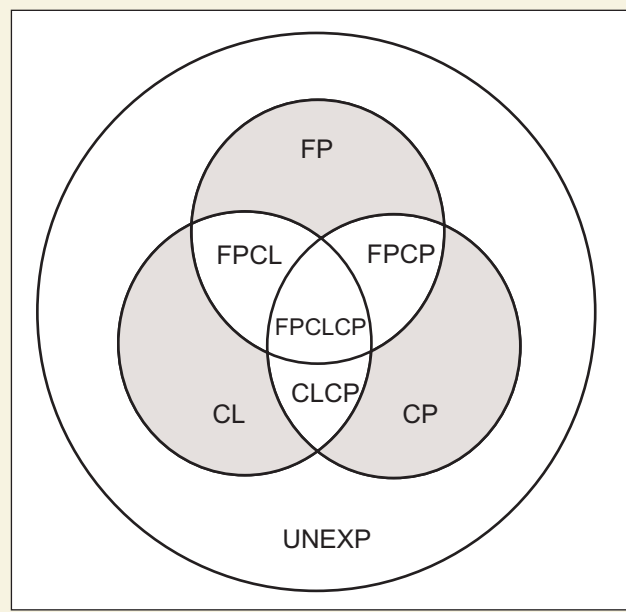
<i>Analysis number</i>	<i>Predictor dataset</i>	<i>Covariate dataset</i>
[1]	Plot vegetation (FP)	None
[2]	Plot community type (CP)	None
[3]	Landscape community-type composition (CL)	None
[4]	FP	CP
[5]	FP	CL
[6]	FP	CP, CL
[7]	CP	FP
[8]	CP	CL
[9]	CP	FP, CL
[10]	CL	FP
[11]	CL	CP
[12]	CL	FP, CP

Notes: This was done for each of three definitions of community type (cover type, successional stage, cover type*successional stage), with each of four methods (CCA all variables, CCA reduced variable set, RDA all variables, RDA reduced variable set). This resulted in 12 different partitionings, each producing eight components of variance (WebTable 7).

WebTable 6. The “best” five environmental variables from each set containing more than five variables. The three variable sets are fine-scale vegetation characteristics (FP), plot-level community type (CP), and percentage of the landscape covered by each community type (CL). Variable selection was based on forward selection using Akaike’s information criterion (AIC) as the selection criterion. All variables were significant at $P < 0.05$. Variables in italics were common to both CCA and RDA models

Variable set	RDA reduced set	CCA reduced set
FP	<i>Batotal</i> <i>flor1</i> <i>flor2</i> <i>flor4</i> <i>struct2</i>	<i>batotal</i> <i>flor1</i> <i>flor2</i> <i>conhardba</i> <i>struct4</i>
CL successional	<i>xls</i> <i>xpo</i> <i>xss</i> <i>xsh</i> <i>xg</i>	<i>xls</i> <i>xpo</i> <i>xss</i> <i>xsa</i> <i>xgf</i>
CP cover–successional	<i>cls</i> <i>mls</i> <i>mgf</i> <i>ccp</i> <i>hls</i>	<i>cls</i> <i>mls</i> <i>mgf</i> <i>cos</i> <i>mos</i>
CL cover–successional	<i>lcomp1</i> <i>lcomp2</i> <i>lcomp5</i> <i>lcomp7</i> <i>strmden</i>	<i>lcomp1</i> <i>lcomp2</i> <i>lcomp5</i> <i>lcomp3</i> <i>roadden</i>

WebFigure 1. Conceptual diagram showing the eight components of species variance. Table 1 describes each component. By decomposing variance with hierarchical variance partitioning it is possible to comprehensively describe the relative importance and interaction of fine-scale plot vegetation, plot-level vegetation communities, and the composition of the landscape by vegetation communities.



WebTable 7. Variance explained among the eight components in each of four analytical approaches. The analytical approaches include canonical correspondence analysis on the full variable set (CCA full), canonical correspondence analysis on the reduced variable set (CCA reduced), redundancy analysis on the full variable set (RDA full), and redundancy analysis on the reduced variable set (RDA reduced). %tot = the percentage of the total inertia (variance) explained by each partition; %exp = the percentage of the total explained inertia (variance) attributable to each partition, where total explained inertia (variance) equals the sum of the constrained eigenvalues. The variable sets are composed of fine-scale vegetation characteristics (FP), plot-level community type (CP), percentage of the landscape covered by each community type (CL), and factorial combinations of these characteristics.

Component	CCA full		CCA reduced		RDA full		RDA reduced	
	%tot	%exp	%tot	%exp	%tot	%exp	%tot	%exp
<i>Cover</i>								
FP	24.4	83.8	12.9	73.2	32.8	82.8	17.6	72.0
CP	1.0	3.4	1.3	7.4	0.6	1.6	0.8	3.5
CL	1.4	4.9	2.2	12.6	1.4	3.6	2.7	11.1
FP-CP	1.3	4.4	1.0	5.6	2.5	6.3	2.3	9.4
FP-CL	0.8	2.6	0.0	0.0	1.5	3.7	0.2	0.7
CP-CL	0.0	0	0.0	0.0	0.0	0.0	0.1	0.4
FP-CP-CL	0.3	1.0	0.2	1.2	0.8	2.0	0.7	2.9
Total	29.2	100	17.6	100	39.6	100	24.4	100
Residual	70.9		82.4		60.3		75.6	
<i>Successional</i>								
FP	17.2	55.6	7.6	37.0	20.8	50.1	9.7	32.8
CP	2.2	7.1	4.2	20.4	1.9	4.5	5.6	19.1
CL	2.0	6.4	2.0	9.7	2.1	5.0	2.7	9.0
FP-CP	7.6	24.7	5.6	27.3	12.5	30.1	8.8	29.7
FP-CL	1.2	3.9	0.4	2.1	2.4	5.8	0.9	3.0
CP-CL	0.0	0.1	0.3	1.7	0.0	0.0	0.4	1.4
FP-CP-CL	0.7	2.2	0.4	1.9	1.9	4.5	1.5	5.0
Total	30.9	100	20.5	100	41.6	100	29.6	100
Residual	69.1		79.4		58.4		70.5	
<i>Cover-successional</i>								
FP	10.3	28.8	3.6	16.3	12.4	27.3	4.7	15.5
CP	5.7	15.8	5.4	24.8	4.5	10.0	6.3	20.7
CL	3.0	8.5	2.1	9.7	3.0	6.7	2.9	9.7
FP-CP	13.5	37.8	9.3	42.3	18.5	40.8	12.9	42.7
FP-CL	1.3	3.6	0.2	1.1	3.0	6.7	0.9	3.0
CP-CL	0.3	0.9	0.3	1.5	0.2	0.4	0.2	0.7
FP-CP-CL	1.7	4.6	1.0	4.4	3.7	8.2	2.3	7.7
Total	35.8	100	21.9	100	45.3	100	30.2	100
Residual	64.2		78.1		54.6		69.8	