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

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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.

Front Ecol Environ 2008; 6(1): 13–17, doi:10.1890/070039

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? Hierarchal 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

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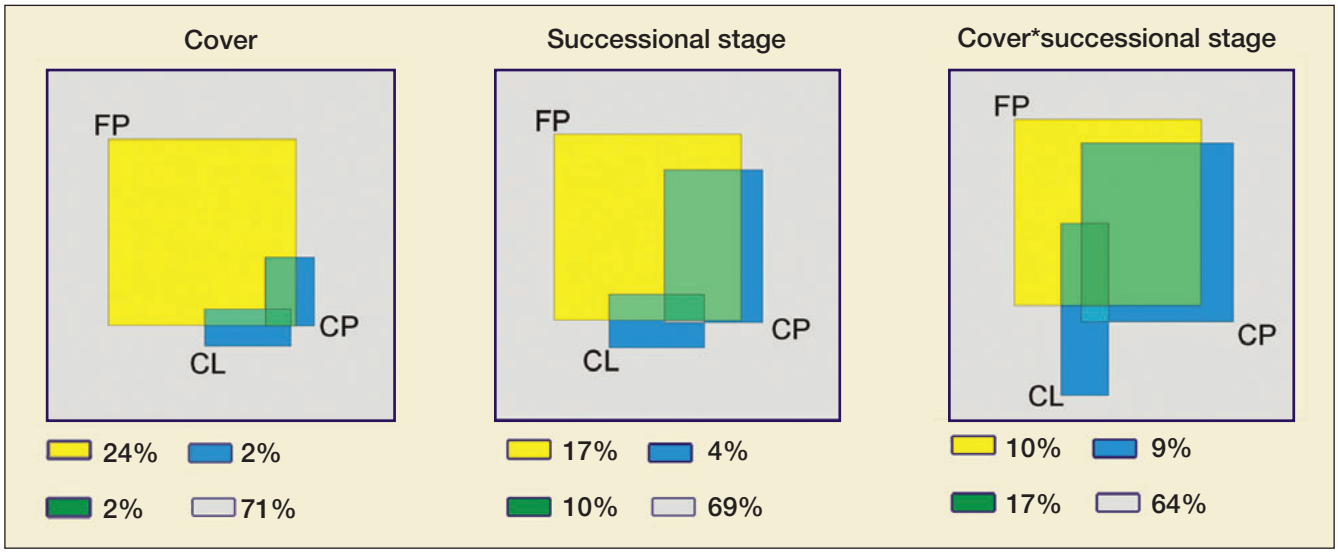

Figure 1. *Variance partitioning plots showing variance in bird abundance explained by fine-scale vegetation and mapped community type across the three community-type definitions. The three intersecting rectangles correspond to each of the three levels of independent variables: FP = plot vegetation, 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

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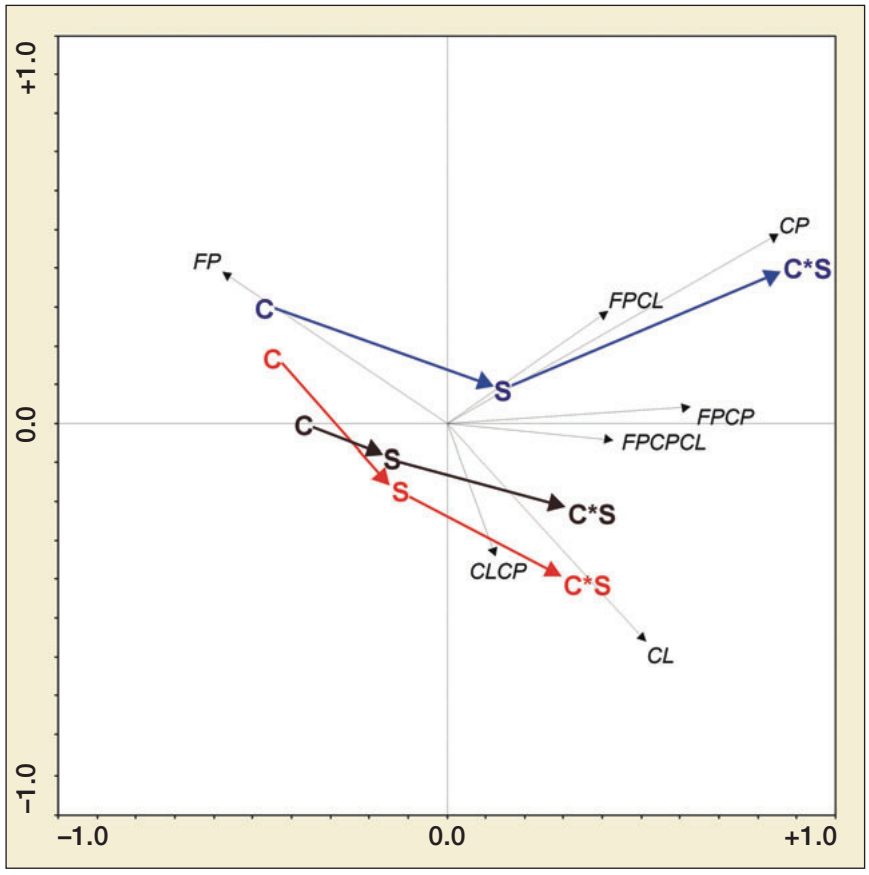

*Figure 2. Canonical variates plot showing differences in the relative amounts of species variance explained by fine-scale vegetation characteristics (FP), plot-level community type (CP), percentage of the landscape covered by each community type (CL), and their interactions (CL–CP, FP–CP, FP–CL, FP–CP–CL; 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 and 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-

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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.

Acknowledgements

Funding for this work was provided by the USDA Forest Service, Rocky Mountain Research Station, US Department of Education GAANN program, Cooperative State Research, Extension, and Education Service, US Department of Agriculture, and the Department of Natural Resources Conservation at the University of Massachusetts.

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