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Hierarchical, Multi-scale decomposition of species-environment relationships

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Abstract

We present an adaptation of existing variance partitioning methods to decompose species-environment relationships in hierarchically-structured, multi-scaled data sets. The approach translates a hierarchical, multi-scale conceptual model into a statistical decomposition of variance. It uses a series of partial canonical ordinations to divide the explained variance in species-environment relationships into its independent and confounded components, facilitating tests of the relative importance of factors at different organizational levels in driving system behavior. We discuss the method in the context of an empirical example based on forest bird community responses to multiple habitat scales in the Oregon Coast Range, USA. The example presents a two-tiered decomposition of the variation in the bird community that is explainable by a series of habitat factors nested within three spatial scales (plot, patch, and landscape). This method is particularly suited for the problems of hierarchically structured landscape data. The explicit multi-scale approach is a major step forward from conducting separate analyses at different scale levels, as it allows comprehensive analysis of the interaction of factors across scales and facilitates ecological interpretation in theoretical terms.

Introduction

Ecological processes are often simultaneously influenced by factors acting across a range of scales, or at several organizational levels. Two of the major insights to emerge in ecology over the past fifteen years are that ecological processes are scale dependent, and that many ecological systems are hierarchically structured (Allen and Starr 1982; Wiens 1989; Kotliar and Wiens 1990). Hierarchical structure and scale dependence complicate ecological analyses. Drawing conclusions about a phenomenon based on one set of observations at one scale, or from one organizational level, may misconstrue the importance of factors thought to drive system behavior (Wiens 1989). It has been widely recognized that multi-scale, hierarchical approaches are required to rigorously describe the behavior of ecological processes and to identify the important causal mechanisms (O'Neill et al. 1986; Kotliar and Wiens 1990; Schneider 1994). Unfortunately, it has proven difficult to develop general approaches to quantify the relative influence and interactions of factors at different spatial scales and organizational levels. Such explicit separation of the effects of multiple sets of explanatory factors is essential if scientists wish to rigorously describe the interactions between patterns and processes in ecological systems.

A promising new approach uses canonical ordination techniques to partition the variation in hierarchically structured multivariate data sets (Borcard et al. 1992). The method is correlational, but differs from traditional correlation studies in that it explicitly measures both the independent explanatory power and confounding among several sets of explanatory variables. The variance decompositions that result provide a comprehensive picture of the relative importance, independent effects, and confounding of the factors included in the analysis. The canonical partitioning method was originally used to partition variation in community data sets among environmental and spatial components (Borcard et al. 1992; Borcard and Legendre 1994; Legendre and Borcard 1994). Liu and Brakenhielm (1995) used a related method to partition variance in a plant community into components explainable by geographical position, climate and pollutant deposition. More recently, Anderson and Gribble (1998) extended the technique to include the effects of temporal variation, such that variation in community data is partitioned into the components explainable by environmental, spatial, and temporal factors, and their overlap.

We propose an extension of this method to address the specific challenges of hierarchically structured landscape data. The hierarchical variance partitioning approach provides a framework to comprehensively address the complex questions of hierarchically structured system behavior and control. For example, the structure of a forest bird community is influenced by local-scale microhabitat structure and composition, as well as by the size and structure of the patch the site resides in, and the composition and configuration of the landscape mosaic containing the patch. Thus, a research project studying the factors influencing the structure of the bird community might include hypotheses about the influence of plot-, patch- and landscape-level factors and their interactions. There are many such organizational hierarchies that may be of interest, such as organism-population-species, species-guild-community, channel unit-reach-river, and gap-stand-forest, as well as scale hierarchies in time and space, such as day-week-season-year, and local-regional-global.

Many ecological phenomena are driven by multiple factors acting at multiple organizational levels, and across multiple spatial and temporal scales. The approach described here is a general method for decomposing multi-scale, multi-level influences in ecological systems. It allows the researcher to comprehensively address complex patterns of independent and confounded effects among multiple causal factors at multiple organizational levels. The advantage of the canonical partitioning approach is its simultaneous treatment of nested factors across organizational and scale levels, with statistical decomposition of variance enabling the quantitative assessment of conceptual models of system organization and control. This allows ecologists to explicitly test hypotheses about the existence and nature of hierarchical structure, and about the relative importance and confounding of factors across hierarchical levels.

The goal of this paper is to present the hierarchical canonical variance partitioning method and demonstrate how it can be applied to the types of analyses which interest landscape ecologists. We illustrate the method using an example from our bird community work in the Oregon Coast Range. In the example, we hierarchically decompose the explained variance in the bird community among plot-, patch- and landscape-level factors. Our purpose is not to present a full analysis of this data set, but rather to illustrate the use of the method as clearly as possible. As a result, we have abbreviated much of the discussion of the creation of the data set and the ecological interpretation of the results, focusing instead on the reasoning behind the hierarchical approach and the mechanics of its execution.

Methods

Example data set: bird and environmental data

Vegetation and birds were sampled in 30 landscapes (250–300 ha) distributed equally among three basins in the Oregon Coast Range (on the US north-west coast) in the breeding seasons of 1990–1992 (McGarigal and McComb 1995). In each landscape, we established a uniform grid of sample plots, on which we recorded detailed vegetation and forest structure data. We surveyed breeding birds using standard methods and computed the abundance of each observed bird species. Species detected at three or fewer plots were omitted from the analysis, resulting in a total of 69 species retained in the analysis.

The environmental data were collected in a hierarchical design, which forms the basis of our two-tiered partitioning. The three main levels of this design are plot, patch and landscape. At the plot level, defined as a 50 -m radius circular area (0.785 ha) centered on the sampling point, we recorded a number of variables from three sub-groups: floristics, vegetation cover, and forest structure. Briefly, the floristics subgroup was composed of the plot percent cover of 58 species of plants divided among herbs, shrubs and trees. We used principal component analysis (PCA) and the latent root criterion to reduce the floristics data set to 10 uncorrelated components that accounted for most of the total floristics variance (McGarigal et al. 2000). The plot vegetation cover sub-group was composed of the percent of each plot covered by each of 32 cover types defined largely on the basis of plant community and stand condition (seral stage), such as conifer large sawtimber, mixed grass-forb, hardwood closed pole, etc. (see McGarigal and McComb (1995) for a complete description). The vegetation structure sub-group was composed of variables related to stand age and structure, such as basal area of conifers, tree density by diameter class, snag density by size and decay class, etc. Again, we used PCA to reduce the structure sub-group to 10 uncorrelated components that were significant based on the latent root criterion. We then subjected the entire plot-level data set to forward selection in CANOCO (ter Braak and Smilauer 1998) and dropped all variables that were not significant at p = 0.05 to reduce collinearity among explanatory variables. The resulting plot data set was composed of 7 floristics variables, 24 cover variables and 5 structure variables.

The patch-level environmental data consisted of FRAGSTATS (McGarigal and Marks 1995) 'patch-level' metrics for the patches in which each plot resided. Patches were defined on the basis on cover type, as above, and then delineated and mapped on aerial photographs (1988–1989 color infrared, 1:20000) based on a minimum patch size of 0.785 ha and $\geqslant$ 50 m wide in the narrowest dimension, and then transformed into planimetrically-corrected digital coverages. On *a priori* grounds, we identified 16 patch metrics for inclusion that comprehensively measured the spatial character and context of each patch. We extracted these metrics for each plot and subjected them to forward selection in CANOCO, and eliminated all that were not significant at p = 0.05, yielding a final set of 10 patch structure variables.

The landscape-level environmental data consisted of FRAGSTATS 'class-level' composition metrics for 32 cover types and 37 'landscape-level' configuration metrics for the landscapes in which each plot resided, based on the digital cover type maps described above. The class-level composition metrics record the percent of the landscape in each cover-type, and reflect landscape composition, not landscape configuration. In contrast, the landscape-level metrics record various configurational attributes of the landscape, such as patch density, contrast-weighted edge density, mean core area, contagion etc., rather than its composition. Using the latent root criterion in PCA, we reduced the landscape-level variable set to six uncorrelated configuration variables, and 10 uncorrelated composition variables for each plot. All 16 landscape-level variables were significant at p = 0.05 using forward selection in CANOCO, and all were included in the partitioning analysis. In summary, the data set consists of 535 observations for which there are measures of relative abundance for each of 69 breeding bird species (response variable set) and a vector of 62 environmental variables (explanatory variable set) subdivided into several nested sub-groups.

Conceptual model of the partitioning design

The decomposition can be visualized by a Venn diagram, such as commonly used in set theory (Figure 1). The first tier of the decomposition separates the influences of plot-, patch- and landscape-level factors on community structure (i.e., multi-scale decomposition). The second tier decomposes community variation explained by specific first-tier partitions into their constituent components (i.e., hierarchical decomposition of habitat factors).

In our example, the first-tier decomposition extracts seven discrete components of explained community variation (Figure. 1, 1A). The numbers in parenthesis below refer to the components depicted in Figure 1. These components are as follows:

- Pure plot-level effects (i.e., variation in bird community structure explained by plot-level variables which is **not** also explained by patch- or landscape- level variables).
- Pure patch-level effects;
- Pure landscape-level effects;
- Joint effects of plot- and landscape-level variables (i.e., community variation that is jointly explained by plot- and landscape-level factors, but is independent of measured patch-level variables).
- Joint effects of plot- and patch-level variables;
- Joint effects of patch- and landscape-level variables;
- Joint effects of plot-, patch- and landscape-level variables (i.e., community variation that is simultaneously explained by plot-, patch- and landscape-level variables).

This first-tier decomposition explicitly quantifies the relative importance and redundancy of each set of explanatory factors. Traditional community analyses have focused on the marginal effects of factors at a single scale, usually at the plot-level. However, the marginal effects of a single set of factors from a given scale provide only a single slice through a much more complicated story. The independent effects of plot (1),

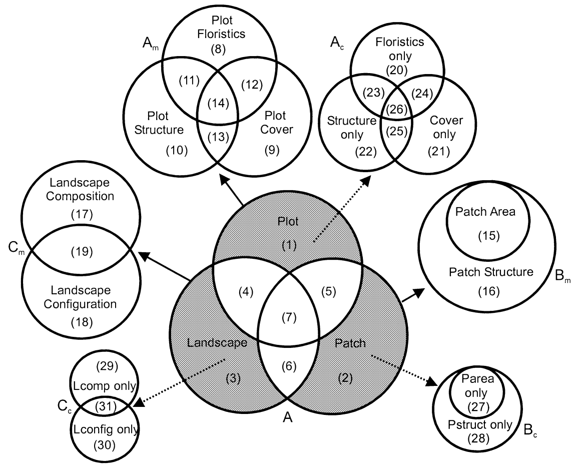

Figure 1. Conceptual model showing the first- and second-tier decompositions. Circles correspond to the total species variance accounted for by each individual variable subset. The numbered areas correspond to the individual variance components. In this two-tiered partitioning, we derive a total of 31 separate variance components, 7 at the first tier (depicted by the inner three overlapping circles), and 24 at the second tier associated with six different partitionings (depicted by the six sets of overlapping circles on the periphery). In the figure, the solid arrows are from first-tier circles to second-tier marginal decompositions, while dotted arrows are from first-tier independent effects, to second-tier conditional decompositions. The seven different decompositions are labeled as follows: A. first-tier decomposition of plot-, patch-, and landscape-level factors; B_1. Second-tier decomposition of marginal patch-level factors; B_2. Second-tier decomposition of conditional patch-level factors; C_1. Second-tier decomposition of marginal landscape-level factors; C_2. Second-tier decomposition of conditional landscape-level factors; D_1. Second-tier decomposition of marginal plot-level factors; D_2. Second-tier decomposition of conditional plot-level factors.

patch (2), and landscape (3) factors provide essential measures of the unique contributions of factors from these different scales. Similarly, the confounded components {(4), (5), (6), and (7)} quantify the level of redundancy among variables measured at different scales. The size of the independent effects and the extent and nature of scale confounding have major implications for how rigorously we can ascribe patterns in community responses to ecological factors acting at a particular scale. In previous studies that considered only a single scale, or that considered several scales but did not partition effects, the sizes of these independent and confounded components are not known. Thus, first-tier decomposition of plot-, patch- and landscape-level influences on community structure is essential if scientists wish to quantify the relative importance and separation of the effects of ecological factors acting at these alternate scales.

Extending the variance partitioning to a second tier provides rich information about the relative importance of subsets of factors that compose the first tier (Figure 1). In our example, we present three different types of second-tier partitions to demonstrate the versatility of the method (note, many other meaningful partitions are possible). First, plot factors were divided into three sets: floristics, vegetation cover, and forest structure. Thus, the second-tier decomposition of plot-level factors results in seven variance components {(8)–(14)} which are analogous to those of the first tier. In contrast, there may be occasions when a researcher is interested in comparing the explanatory power of a sub-set of variables to that of the entire set, rather than explicitly partitioning the set into predefined groups. In our example, at the patch-level, we are interested in comparing the relative importance of patch area with that of total patch structure, in which patch area is nested. Thus, in the second-tier decomposition of patch-level factors, there are two components: (15) variance explained by patch area, and (16) variance explained by patch structure independent of area. Third, at the landscape level, we define two variable sub-sets, corresponding to landscape composition and landscape configuration. Unlike patch area, the effects of landscape composition and configuration are not nested; therefore, the decomposition of these allows us to compare their relative importance and the extent of their redundancy. Accordingly, the second-tier decomposition of landscape-level factors produces three variance components, corresponding to the effects of landscape composition independent of configuration (17), the effects of landscape configuration independent of composition (18), and the variation in the community that is simultaneously explained by both (19).

At the second tier the ecologist has several choices as to what to partition. One can either partition the *marginal* effects of the corresponding first-tier variable set, or its *conditional* effects. We believe important information is obtained by doing both second-tier partitions, and we do so in our example. For example, partitioning the marginal effect of plot-level variables allows us to quantify the total explanatory power of floristics, vegetation cover, and forest structure, and their overlap. In Figure 1 this is equivalent to decomposing the variance associated with the entire plot circle in the first-tier partition {(1)+(4)+(5)+(7)}. In contrast, partitioning 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 overlap. In Figure 1 this is equivalent to decomposing the variance associated with the shaded portion of the plot circle in the first-tier partition (1). Both of these partitionings are important. In Figure 1, the marginal decomposition of plot is labeled D_m, while the conditional partitioning is labeled D_c. Similarly, the marginal and conditional patch-level, and landscape-level decompositions are labeled B_m, B_c, C_m, and C_c, respectively.

Data analysis

In our example, we use canonical correspondence analysis (CCA) in the computer program CANOCO (ter Braak and Smilauer 1998). We used CCA with biplot scaling and focus on inter-site distances for all analyses (ter Braak and Smilauer 1998). We selected this technique because it is based on unimodal models of species abundance along environmental gradients, and preliminary analyses indicated that many of the species in the community showed strong unimodal patterns (ter Braak (1986, 1987)). However, it is important to note that the partitioning method is versatile and can be used in a variety of univariate and multivariate contexts, with linear or unimodal response models, and total abundance, relative abundance, or presence-absence data.

In CCA analysis of community 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 (ter Braak 1986). When the analysis includes covariables, the effect of these variables on community response is partialed out, and the sum of canonical eigenvalues represents the variance in the community explained by the environmental variables after accounting for the covariables (ter Braak 1988). The trace, or sum of all eigenvalues, of the unconstrained correspondence analysis (CA) of the community data is a measure of the total variation in the species data (also known as the total inertia). Thus, 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 (Borcard et al. 1992).

Using this principle, we conducted a series of CCA and partial CCA analyses to isolate all of the variance components needed for the partitioning process (Table 1). For each analysis, we recorded the sum of canonical eigenvalues, the percentage of total species variation explained, and the significance of that analysis based on 199 permutations under the null model in CANOCO (ter Braak 1992; ter Braak and Smilauer 1998; Anderson and Legendre 1999). The permutations test the significance of the unimodal relationship between the constraining environmental variables and the species variables, after removing the effects of any covariables.

After running the necessary CCA and partial CCA models, we calculated the percentage of total species variation associated with each partition listed in Figure 1. The method of calculation for the first tier is exactly the same as that used by Anderson and Gribble (1998). The general theory of these types of calculations is given in Whittaker (1984). In our terminology, numbers in square brackets refer to the percentage of total species variance explained by the individual CCA analyses (Table 1), and numbers in parentheses refer to final variance partitions, as shown in Figure 1 and Table 2. We first will give the calculations for each type of component in the first-tier decomposition (Table 2) and then describe the second tier.

The percentage of total species variation explained by plot-, patch- and landscape-level factors together equals [1]+[7]+[12] or [2]+[4]+[12] or [3]+[8]+[6]. The pure *plot*-level component is equal to [6]. This is the percentage of total species variance explained by plot-level factors, but not also explained by patch- or landscape-level variables. The pure *patch*-level component equals [9] and the pure *landscape*-level component equals [12]. The calculation of the remaining four components requires some intermediary steps.

The key to the calculation of the remaining components of the first tier is (7), the three-way overlap among plot-, patch- and landscape-level factors (Table 2). Note that the overlap between plot and patch factors, {(5)+(7)}, is calculated as [1]−[4] or [2]-[7]. Similarly, note that the overlap between plot and landscape factors {(4)+(7)} is [1]−[5] or [3]−[10]. Once we have calculated these two overlap regions we can isolate (7) as follows. We already know independent effect of plot-level factors, (1), from analysis [6]. In addition, we know the marginal effect of plot-level factors, {(1)+(4)+(5)+(7)}, from analysis [1]. We also know the overlap between plot and patch, {(5)+(7)}, and plot and landscape, {(4)+(7)}, from above. Using simple algebra, we can solve for (7) by noting that the independent effects of plot factors plus the two overlap components of plot with patch, and plot with

Table 1. Description of the first 18 canonical and partial canonical ordinations needed for the partitioning process for 69 species of birds sampled across 535 plots, distributed across three basins in the Oregon Coast Range, between 1990 and 1992. Analyses 19–48, corresponding to the second-tier plot, plot-only, patch-only, and landscape-only decompositions, are not shown to save space; they are computationally the same as those shown, except for different explanatory variables and covariables. The analyses listed are sufficient to demonstrate the technique. Letters in parentheses correspond to the variance in species data explained by the sum of canonical eigenvalues of the corresponding analysis, and are the same as those in Figure 1. Total inertia = 2.035. Sum of canonical eigenvalues from CCA reflects the total variance explained by the analysis. Total explained variation is the proportion of the total species variation (total inertia) explained by that analysis. All listed analyses were significant ($P < 0.005$) based on Monte Carlo permutation.

Analysis Number	Explantory Set	Covariable set	Explained Variation (%)
First Tier Decomposition (A)			
[1]	Plot	None	32.9
[2]	Patch	None	14.1
[3]	Landscape	None	16.0
[4]	Plot	Patch	21.7
[5]	Plot	Landscape	24.6
[6]	Plot	Patch and Landscape	16.1
[7]	Patch	Plot	2.8
[8]	Patch	Landscape	10.8
[9]	Patch	Plot and Landscape	2.2
[10]	Landscape	Plot	7.8
[11]	Landscape	Patch	12.7
[12]	Landscape	Plot and Patch	7.0
Second Tier Decomposition (B_m)			
[13]	Patch area	None	7.6
[14]	Patch full	Patch area	6.5
Second Tier Decomposition (C_m)			
[15]	Landscape composition	None	13.3
[16]	Landscape configuration	None	6.9
[17]	Landscape composition	Landscape configuration	9.1
[18]	Landscape configuration	Landscape composition	2.7
[19–48] Not Shown			

landscape, equal the marginal effects of plot-level factors plus (7). There are three alternative formulas for calculating (7) (Table 2). Once the value of (7) is known, the remaining three components {(4),(5),(6)} are easily derived:

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

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

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

Now we proceed to the second tier. Recall that at the second tier we are doing two sets of analyses, the first of marginal effects, and the second of conditional effects. The second-tier partitioning of *plot*-level effects is computationally the same as the first-tier partitioning, as we are partitioning variation among three overlapping variable sets in both cases. The marginal plot-level partitioning is exactly the same as the first tier, except that in all CCA analyses, plot-, patch- and landscape-level variables and covariables are replaced by plot-floristics, plot-cover and plot-structure variable sets, respectively. Accordingly, the CCA runs and calculations are omitted here and from Table 1 to save space. The conditional partitioning is very similar to marginal partitioning, except that in all analyses the patch- and landscape-level variable sets are added as covariables. This removes the patch- and landscape-level influences from all CCA analyses, with the result that the partitioning is only for the independent plot-level effects [(1) in Figure 1]) among floristics, cover and structure.

The second-tier partitioning of *patch*-level effects is very simple in our case. Recall that we wish only to separate the influence of patch area from that of total patch structure. Thus, for the marginal decomposition, we need to calculate three variance components, corresponding to the variation explained by to-

Table 2. Calculations to decompose the variance in the bird community into the components explained by plot-, patch- and landscape-level factors {(1) to (7)}, patch area, and patch structure {(15) to (16)}, and Landscape composition and structure{(17) to (19)}. Numbers in parentheses refer to the variance components in Figure 1. Numbers in square brackets refer to the analyses listed in Table 1. Calculations for components {(2) to (3)}, {(5) to (6)}, {(8) to (14)}, (18) and {(20) to (28)} are omitted to save space, but are derived the same way as those shown and are described in the text. Note, not all alternative calculations are shown.

Number	Component Description	Component Calculation
First Tier Decomposition (A)		
(1)	Variation due to plot factors alone	[6]
(4)	Variation jointly explained by plot and landscape factors, independent of patch factors	[1]–[5]–(7) or [3]–[10]–(7)
(7)	Variation jointly explained by plot, patch and landscape factors	[6]+([1]–[4])+([1]–[5])–[1] or [9]+([2]–[8])+([2]–[7])–[2] or [12]+([3]–[10])+([3]–[11])–[3]
	and landscape factors	
	Total explained by patch, plot and landscape factors	[1]+[7]+[12] or [2]+[4]+[12] or [3]+[8]+[6] or (1)+(2)+(3)+(4)+(5)+(6)+(7)
	factors	
Second Tier Decomposition (B_m)		
(15)	Variation explained by patch area	[13]
(16)	Variation explained by patch structure, independent of area	[14] or [2]–[13]
	Total explained by patch factors	[13]+[14] or [2]
Second Tier Decomposition (C_m)		
(17)	Variation explained by landscape composition, independent of landscape structure	[17]
(19)	Variation explained jointly by landscape composition and landscape structure	[15]–[17] or [16]–[18]
	Total explained by landscape factors	[17]+[18]+([15]–[17]) or [3]

tal patch structure, patch area, and patch structure independent of patch area [Figure 1; (15)+(16), (15), and (16) respectively]. For this marginal patch-level partitioning, two additional analyses are needed (Table 1; [13] and [14]). The total patch-level explanatory power is [2], the variation explained by patch area is [13] and that explained by patch structure, independent of patch area is [14] (Table 2). The conditional patch-level partitioning is easily obtained by adding the plot- and landscape-level variable sets as covariables to analyses [13] and [14], with [9] as the conditional patch-level effect that is being partitioned.

The second-tier *landscape*-level decomposition is also quite simple. In our case, we a priori divided the landscape variables into two sets, corresponding to measurements of landscape composition and measurements of landscape configuration. We wish to know the relative importance and degree of overlap of these two variable sets in their relationships with patterns in the bird community. Three additional CCA analyses are required for the marginal decomposition of the variation explained by landscape-level factors into the components due to composition (17), configuration (18), and the overlap between composition and configuration (19) (Figure 1). The total landscape-level explanatory power is [3]; the variation explained by composition, independent of configuration, is [17]; the variation explained by configuration independent of composition is [18]; and the variation jointly explained by landscape composition and configuration is [15]–[17] (Table 2; note the alternate computations). The conditional landscape-level partitioning is the same as the marginal partitioning, with the addition of plot- and patch-level variable sets as covariables to CCA analyses [15]–[18], and with [12] as the conditional landscape-level effect that is being decomposed.

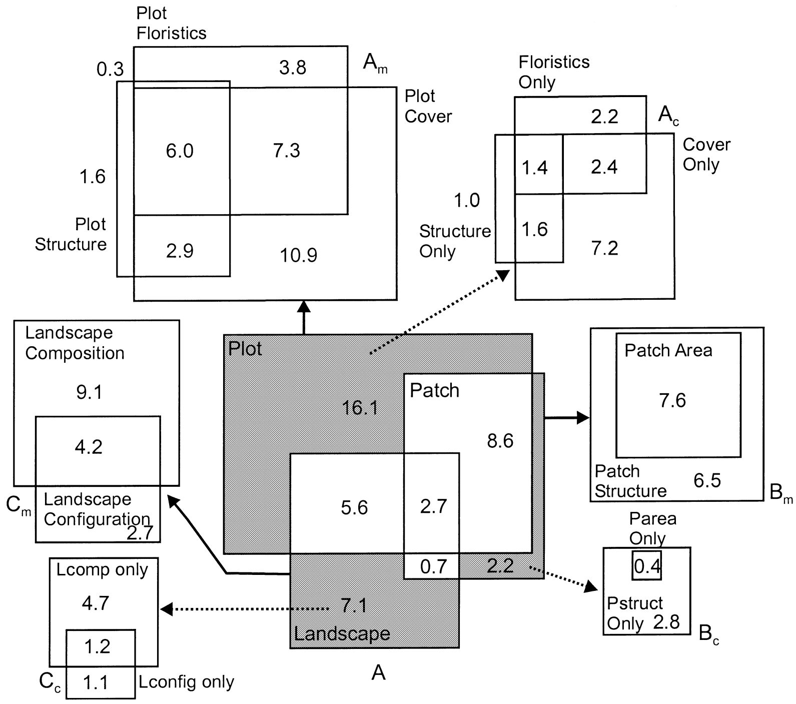

Figure 2. Results of first- and second-tier decompositions of the influence of plot-, patch- and landscape-level factors on bird community structure in the Oregon Coast Range. The area of each rectangular cell is proportional to the variance accounted for by that component. The numbers in the components list the percent explained variance accounted for by each component.

Results

The total variation in the bird community data set was 2.035 (sum of all eigenvalues in the CA). Over 42% of this total variation was explained by plot-, patch- and landscape-level factors. For each CCA analysis, the sum of canonical eigenvalues and variance explained are recorded in Table 1. The results of the full decomposition are depicted in Figure 2. In Figure 2, the areas of the individual rectangles are proportional to the variation explained by each component. At the first tier, plot-level factors had both the largest marginal effect (32.9%), and the largest independent effect (16.1%). Patch- and landscape-level factors were similar in their marginal effects, explaining 14.1% and 16.0% of the species variance, respectively. However, they differed substantially in their independent effects, with patch-level factors explaining only an additional 2.5%, while landscape-level variables explained 7.1% beyond what was explained by plot- and patch-level factors. Both patch- and landscape-level factors were heavily confounded with the influences of plot-level variables. For example, approximately 80% of the explanatory power of patch-level, and 52% of the explanatory power of landscape-level variables was confounded with the effects of plot-level variables.

At the second tier, plot-level vegetation cover had greater explanatory power than either floristics or vegetation structure, followed in importance by floristics (Figure 2). At the patch-level, patch area alone explained roughly half of the variation that was explained by total patch structure, indicating that while area was important, other patch-level structural measurements contributed substantial additional explanatory power. At the landscape-level, the marginal and independent effects of landscape composition were both larger than those of landscape configuration. Interestingly, the independent effects of landscape composition were more than three times larger than those of landscape configuration. The sizes of these marginal, independent and confounded effects could have interesting implications for interpreting the influences of habitat patterns at multiple scales on the structure of forest bird communities in the Oregon Coast range.

Discussion

Whenever ecologists adopt a multi-scale or hierarchical perspective in their research, variance partitioning can be a powerful tool to explicitly account for hierarchical structure in a comprehensive statistical analysis. Multi-scaled, multi-level research problems have emerged as a dominant research theme in landscape ecology (O'Neill et al. 1986; Wiens 1989; Kotliar and Wiens 1990; Schneider 1994). The hierarchical variance partitioning approach translates a multi-scaled, hierarchical conceptual model of system organization and control into a statistical decomposition of variance, allowing the ecologist to explicitly test hypotheses about the nature of system organization, and the relative importance and confounding among processes acting at different levels and at different scales. The approach can be readily tailored to fit nearly any hierarchical conceptual model, giving the researcher great flexibility in the hypotheses that can be tested. Our example was based on partitioning explained variance across levels of a hypothesized organizational hierarchy. We could have chosen a different conceptual model, had we different hypotheses. The hierarchical partitioning approach provides a comprehensive and flexible framework for analyzing ecological questions at multiple organizational levels and across spatial and temporal scales.

We demonstrated the approach using CCA because of the unimodal nature of our community data. However, hierarchical partitioning is a generalized approach that can be used with a number of analytical methods. For example, had we found that our community data were linearly related to environmental gradients at the different organizational levels, we could have used redundancy analysis (ter Braak and Prentice 1988; Liu and Brakenhielm 1995) instead of CCA. Similarly, had we believed that the assumptions of the underlying regression models were seriously violated, we could have conducted an equivalent non-metric decomposition using partial mantel tests (Legendre and Legendre 1998; Borcard and Legendre 1994). In addition, the partitioning approach is equally suited to univariate response data, in which case multiple linear or non-linear regression can be used analogously to conduct the decomposition (Legendre and Legendre 1998).

The hierarchical approach provides some critical advantages over the traditional method of comparing results of separate analyses from different organizational levels. The first advantage is the partialization of effects. In traditional multi-scale landscape analysis, researchers usually compare the magnitudes of the marginal effects of factors at the different levels. While this gives a measure of the total statistical relationship between factors at each scale and the response variables, it does not give any measure of their independent effects. The hierarchical model explicitly quantifies the independent and confounded components of explained variation due to each set of factors in the conceptual model. This allows the researcher to explictly compare the importance of factors, based on both their marginal and their independent effects, and explicitly quantifies the extent of confounding among the different levels of the conceptual model. This gives the researcher a much richer view of how the system is structured and of the relative importance of different factors across scales and levels in driving system behavior.

The second great advantage of the partitioning approach is its ability to test specific hypotheses about the organization and control of multi-scale, multi-level ecological systems. Researchers can propose conceptual models of system organization and control which suggest specific hypotheses about the size and confounding of different variance components. The hierarchical decomposition method is a flexible tool that can be used to decompose relationships in nearly any hierarchical conceptual model, and test any number of hypotheses about the nature of system organization and control.

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