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Patterns in the species–environment relationship depend on both scale and choice of response variables

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Multi-scale investigations of species–environment relationships are an important tool in ecological research. The scale at which independent and dependent variables are measured, and how they are coded for analysis, can strongly influence the relationships that are discovered. However, little is known about how the coding of the dependent variable set influences community-level analyses. In this study, we used canonical correspondence analysis to quantify species–environment relationships between environmental factors collected at three spatial scales and the structure of a forest bird community in the Oregon coast range. The main question in our analysis was how coding the bird data as abundance versus presence/absence affected the nature and strength of observed relationships. As we expected, the structure of the bird community was better described overall using abundance data than it was using presence/absence data. However, individual species and life-history groups appeared to exhibit different species–environment relationships in abundance versus presence/absence data. In particular, common species with a high frequency of occurrence among sample points exhibited a stronger 'abundance' signature, whereas uncommon species with a low frequency of occurrence exhibited a stronger 'presence/absence' signature. In addition, the apparent importance of plot-level factors in explaining the variation in the bird community was greater for abundance data, whereas patch and landscape factors were more important in the presence/absence data. Thus, conclusions about the relative importance of factors at different scales is largely contingent on the way in which the species-response data are coded for analysis. For communities as a whole, and for individual species within them, the strength and nature of species–environment relationships can differ dramatically between analyses using presence/absence versus abundance data.

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Apparent species–habitat relationships are strongly dependent on the scale at which the dependent and independent variables are measured. Recently, there has been much research exploring the scale dependence of species–environment relationships (Allen and Starr 1982, Wiens 1989, Kotliar and Wiens 1990, Allen and Hoekstra 1991, Schooley and Wiens 2001, Cushman and McGarigal 2003). These studies suggest that drawing conclusions about a phenomenon based on one set of observations at a single scale may misconstrue the importance of habitat factors thought to drive system behavior. Other studies have focused on how transformation of independent variables at a given scale influences observed patterns (Jackson 1993, Peres-Neto and Jackson 2001). These two areas of research have convincingly shown that the scale of measurement and

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data transformations of independent variables can have profound impacts on the strength and nature of observed species–environment relationships.

Somewhat less attention has been paid to the question of how the scaling of dependent variables influences analyses of species–habitat relationships. Bart and Klosiewski (1989) compared the efficacy of using raw abundance or presence/absence coded data to measure changes in avian density. They found very high correlations between the two approaches, indicating high similarity among their predictions. In contrast, Strayer (1999) found that presence/absence models generally have low power to detect population declines of less than 50%, and that detection power is dependent upon the spatial pattern of the population decline. Manuel et al. (2001) compared the efficacy of abundance and presence/absence models to predict species distributions. They discovered that predictive accuracy is affected by frequency of occurrence of the target organism in the database, and argue that many evaluations of presence/absence models are misleading.

In this paper we extend this line of investigation. We compared community-level analyses of species–environment relationships using both presence/absence and abundance data. The goal was to quantify how differences in the resolution of the response variable influence measurements of the structure of the bird community as a whole, the ecological relationships of individual species, and inferences about the relative strength of species–environment relationships at different spatial scales. We expected that abundance and presence/absence data may provide markedly different pictures of the ecological relationships among species. In addition, we expected that the relative strength of the relationships among scales (e.g. the relative importance of landscape-level relationships) may differ for presence/absence and abundance data. If this is true, then researches should more carefully consider the resolution of the response variables when designing a study, and be aware of how these choices may influence their results.

We had several specific hypotheses that motivated our investigations. First, we hypothesized that abundance coded data would provide a better explanation of species–environment relationships at the community level than presence/absence coded data, as recoding from abundance to presence/absence eliminates much information about the relationships between species abundance patterns and environmental gradients. However, we believed that this overall community-level pattern would not hold for all species. Specifically, we expected that species and functional groups that were relatively infrequently sampled in the database would be more successfully modeled using presence/absence data. This was expected because the dominant component of the variance of rarely recorded species is related to the pattern of presence and absence among sites rather than abundance within sites. Third, based on previous work that showed that forest bird species which are strongly associated with patch- or landscape-level factors tend to be relatively large-bodied and rare (Cushman and McGarigal 2003), we hypothesized that landscape- and patch-level environmental attributes would be stronger predictors of species composition in presence/absence analyses than in abundance coded analyses.

Methods

The data-set is taken from McGarigal (1993) and has been described in detail elsewhere (McGarigal and McComb 1995, 1999, Cushman and McGarigal 2003). Briefly, it consists of 535 50-m radius plots for which a total of 69 species of birds and 66 environmental variables were recorded. We used two forms of the species data-set in this analysis. In the first, the species data were converted to number of individuals detected per visit. In the second, we recoded this abundance data set into a presence/absence data-set. We derived environmental variables for each of three spatial scales: plot, patch, and landscape. Forty-three ‘plot’ scale variables were extracted from 50-m radius circular plots around each sample point, and included geomorphic, floristic and stand structure variables. Variables at the ‘patch’ scale described structural attributes of the two-dimensional polygon, or patch, containing the sample point. We used FRAGSTATS (McGarigal et al. 2002) to compute twelve metrics describing the spatial character of each patch, such as patch size and shape complexity. Patches were defined and delineated on the basis of similarity in overstory vegetation composition and structure and were of variable size, with a minimum mapping unit of 0.10 hectare. The ‘landscape’ scale consisted of 30, 300-ha sub-basins (i.e. second- or third-order watershed) containing the sample points. We used FRAGSTATS to compute twenty landscape metrics describing the composition and configuration of the entire patch mosaic.

Next, we hierarchically partitioned the variance in the species data that was explainable by the environmental variables (Anderson and Gribble 1998, Cushman and McGarigal 2003) using canonical correspondence analysis (ter Braak and Smilauer 1998) to quantify the strength of species–environment relationships for the community as a whole, and for individual species, for both the abundance and presence/absence data-sets. The hierarchical variance partitioning approach explicitly separated the effects of plot-, patch-, and landscape-level factors on the structure of the bird community. The details of the approach are given elsewhere (Cushman and McGarigal 2003).

The main result of the partitioning is a quantitative division of the variance in the bird community that is

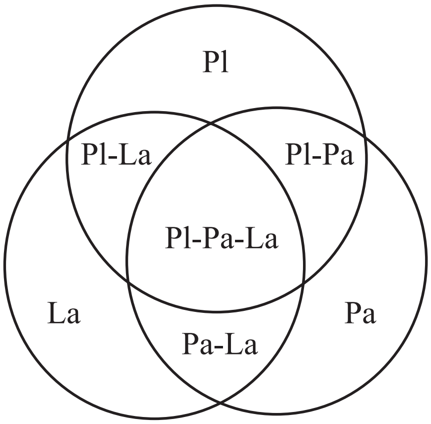


Fig. 1. Conceptual model showing the decomposition of the variance in the bird community data set explainable by seven different components representing the independent and confounded effects of three sub-sets (plot, patch, and landscape) of environmental variables. Circles correspond to the total species variance accounted for by each individual variable sub-set. The numbered areas correspond to the individual variance components. Pl = plot-level variables measured for each of 535 50-m radius circular plots. Pa = patch-level variables measured for the patch surrounding each sample point. La = landscape-level variables measured for the landscape (i.e. 300-ha sub-basin) containing each sample point. The areas of overlap among circles (e.g. Pl-Pa) represent the variance in the bird community that is jointly explainable by the associated sets of environmental variables; that is, confounded variation that cannot be exclusively associated with a single variable sub-set.

explainable by the measured environmental variables into seven components representing the independent and confounded effects of plot-, patch-, and landscape-level factors (Fig. 1). This community-level variance partitioning quantifies the relative strength and interaction of the three levels of explanatory variables in explaining the variation in the bird community as a whole. In addition to comparing community differences between presence/absence and abundance data, we were interested in the ecological relationships of individual species. Canonical correspondence analysis provides a measure of the variance in each species accounted for by the community models, called CFit (ter Braak and Smilauer 1998). CFit measures how much of the variation in a given species is accounted for by the particular CCA model.

We evaluated the stability of the results between presence/absence and abundance data by comparing the sizes of the community-level variance partitions and the species-level CFit statistics. Specifically, we computed the 'absolute' and 'relative' deviations among all seven components of the community partitioning (Fig. 1) and six different CFit statistics for the individual species (Table 1). The six CFit statistics provide measures of the 'marginal' and 'conditional' variance explained in each species by plot-, patch-, and landscape-level factors. 'Marginal' variance explained is the total variation explained by a given set of factors (plot, patch, or landscape), while 'conditional' variance explained is the variance explained by a given set of factors after removing the variance that is jointly explainable by the one or both of the other two sets. 'Deviation' refers to the difference in variance explained between presence/absence and abundance models. 'Absolute deviation' refers to the difference in the absolute variance. 'Relative deviation' refers to the difference in relative strength of a component between models.

We associated the magnitude of the relative and absolute deviations for the six different CFit components for each species with several life history factors, including frequency of occurrence in the database, body size, and territory density. Body size was measured in centimeters from toe to beak (Peterson 1990). The remaining life-history variables were taken from Hansen and Urban (1992). We used Pearson correlation to associate the magnitudes of the absolute and relative deviations with the continuous life history variables (e.g. frequency of occurrence).

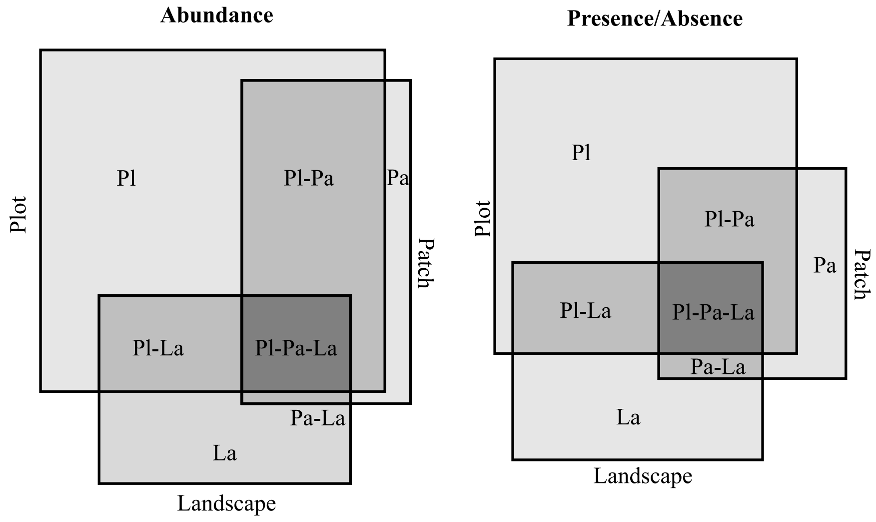
Results and discussion

Community partitioning differences

Overall, the percentage of community variation explained by environmental variables was approximately

Table 1. Description of the CFit variance components used in comparing differences across species between presence/absence and abundance data. CFit measures how much of the variation in a given species is accounted for by a particular canonical correspondence analysis model (ter Braak and Smilaeur 1998); that is, the percentage of a species' variance explained by a particular set of environmental variables.

Variance component	Description
Total explained	Variance explained by all factors combined (i.e. full model)
Plot marginal	Variance explained by plot-level factors in total
Patch marginal	Variance explained by patch-level factors in total
Landscape marginal	Variance explained by landscape-level factors in total
Plot conditional	Variance explained by plot-level factors, after removing variance jointly explained by patch- or landscape-level factors
Patch conditional	Variance explained by patch-level factors, after removing variance jointly explained by plot- or landscape-level factors
Landscape conditional	Variance explained by landscape-level factors, after removing variance jointly explained by patch- or plot-level factors



Abundance

Presence/Absence

	Variation explained (%)			
	Abundance		Presence/Absence	
Component	Absolute	Relative	Absolute	Relative
Pl	16.5	40.0	13.2	40.0
Pa	2.5	6.0	2.6	7.9
La	6.0	14.4	6.3	19.0
Pl-Pa	9.4	22.5	4.3	13.0
Pl-La	3.9	9.4	3.4	10.3
Pa-La	0.4	1.0	0.8	2.4
Pl-Pa-La	3.0	7.2	2.5	7.6
Total	41.7	100.0	33.1	100.0

Fig. 2. Results of the decomposition 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 labeling is the same as in Fig. 1. The numbers at the bottom of the figure report the exact absolute and relative variance in the bird community accounted for by each component based on abundance and presence/absence species data. Absolute variance represents the actual percentage of variance in the bird data accounted for by a given component. Relative variance represents percentage of the total explained variance accounted for by a given component.

9% higher for abundance than presence/absence data (Fig. 2). As expected, this shows that abundance data provides a 'better' overall measure of species–environment relationships for the community than does presence/absence data. Consistent with our second hypothesis, however, the relative importance of the conditional patch- and landscape-level factors were higher for the presence/absence data (Fig. 2). In addition, the size of the plot-patch confounding was much smaller for the presence/absence data than for the abundance data (Fig. 2). Thus, while the total variation explained decreased in the presence/absence analyses, the relative sizes of the patch and landscape partitions increased. This implies that analysis with presence/absence or abundance response data give different measures of the relative importance of environmental factors measured at plot-, patch-, and landscape-levels in structuring the bird community. In particular, landscape- and patch-level factors appear relatively more important when data are analyzed in presence/absence form.

Species differences

The explained variance in individual species often differed much more dramatically than the overall community, both in total variation explained, and in the relative importance of the three scales of measured environmental variables. The maximum positive deviations (i.e. presence/absence greater than abundance) and negative deviations (i.e. abundance greater than presence/absence) for each CFit variance component provide a useful description of the range of differences across species (Table 2). The maximum positive and negative deviations among species in total variance explained between presence/absence and abundance were 33.3% and −36.1%, respectively. This large range of deviation in total explained variance indicates major differences among species in how well their ecological relationships are described using abundance vs presence/absence data.

It is informative to compare the average relative deviations for each of the six CFit variance components

Table 2. Maximum and average deviations across species between presence/absence and abundance data for each variance component (Table 1) associated with the variance decomposition of a bird community in the Oregon coast range. Maximum positive deviation is the largest increase in the relative variance explained by presence/absence data over abundance data for a single species; conversely, maximum negative deviation is the largest increase in the relative variance explained by abundance data over presence/absence data for a single species. Average absolute deviation is the average difference in the actual variance explained between presence/absence and abundance data across all species. Average relative deviation is the average difference in the relative variance explained across all species, where relative variance refers to the relative strength of a component measured as a percentage of the total variance explained.

Variance component	Maximum positive deviation (%)	Maximum negative deviation (%)	Average absolute deviation (%)	Average relative deviation (%)
Total explained	33.3	− 36.1	− 3.33	− 5.4
Plot marginal	11.2	− 19	− 3.61	− 1.86
Plot conditional	19.2	− 26.8	− 2.26	− 2.52
Patch marginal	24.6	− 14.1	− 0.52	2.33
Patch conditional	6.4	− 7.7	0.04	0.42
Land marginal	19.9	− 36.7	0.41	3.17
Land conditional	13.2	− 10.1	− 0.06	0.58

across species (Table 2). First, average total explained variance among species was less for presence/absence than for abundance data. Second, average plot-level effects were smaller for the presence/absence results than for the abundance results. In contrast, the average patch- and landscape-level effects were greater for presence/absence analyses. Thus, the patterns in explained variation among species are consistent with the patterns observed at the community level; namely, that in presence/absence data, plot-level effects appear relatively less important, and patch- and landscape-level effects relatively more important than they do in abundance data.

It is also instructive to investigate the frequencies of deviations of different magnitudes among species for the different CFit variance components. First, nearly twice as many species (43 vs 27) were better explained overall in abundance analyses than in presence/absence analyses (Table 3). Furthermore, over twice as many species that differed by at least 10% between presence/absence and abundance were better explained in abundance data. However, a substantial number of species (10) were much better explained by analyses of presence/absence data, implying that researchers could reach drastically different conclusions about the strength of particular species–environment relationships using abundance data vs presence/absence data, and that the 'direction' of these differences varies among species.

Inspection of the frequencies of different sized deviations for plot, patch and landscape effects further demonstrates the asymmetry of the plot response from that of patch and landscape factors. Nearly twice as many species have larger amounts of variance explained by plot effects in abundance data than in presence/absence data. This pattern continues for the species with the largest deviations, with nine out of eleven, and nine out of ten species, respectively, having greater relative plot-level variation explained in abundance than presence/absence. Patch and landscape factors have the opposite trend, with the largest relative variation explained by the presence/absence models for most species. For example, for marginal patch- and landscape-level effects, six of seven and 14 of 16 species, respectively, with greater than 10% deviation were better explained by the presence/absence model (Table 3). These patterns demonstrate that plot factors tend to be relatively more

Table 3. Tally of number of species showing positive and negative deviations in relative percent variance explained between presence/absence and abundance data for each variance component (Table 1) associated with the variance decomposition of a bird community in the Oregon coast range. Positive deviations include species in which presence/absence data was explained better than abundance data by the given environmental variable set. Conversely, negative deviations include species in which abundance data was better explained than presence/absence data. Thus, +10% records the number of species whose relative explained variation was at least 10% greater in that variance component in presence/absence than in abundance data.

Variance component	Positive deviation	Negative deviation	+5%	− 5%	+10%	− 10%
Total explained	27	43	19	34	10	22
Plot marginal	28	42	8	21	2	9
Plot conditional	22	48	9	20	1	9
Patch marginal	48	22	17	5	6	1
Patch conditional	41	39	3	2	0	0
Land marginal	43	27	24	4	14	2
Land conditional	39	31	11	8	1	2

Table 4. Results of correlation analyses for differences in the relative variance explained between presence/absence and abundance data for each of the variance components (Table 1) associated with the variance decomposition of a bird community in the Oregon coast range. Numbers in parentheses represent the number of species with suitable life history data and used in the corresponding analysis. Frequency = frequency of occurrence of the species across 535 sample plots. Size = body length of the species in cm. Territory density = average territory density (No. ha^{-1}). The first line records the Pearson's correlation coefficient (r); the second line records the probability of that r given no relationship. Correlations significant at a 0.05 alpha level are in bold.

Variance component	Frequency (69)	Size(69)	Territory density (40)
Total explained	**−0.241**	**0.267**	**−0.483**
	0.046	0.027	0.002
Plot marginal	−0.19	0.081	−0.17
	0.118	0.509	0.293
Plot conditional	**−0.339**	0.17	−0.02
	0.004	0.163	0.904
Patch marginal	**0.438**	−0.128	0.121
	0.001	0.296	0.457
Patch conditional	**0.244**	−0.036	0.198
	0.043	0.769	0.22
Landscape marginal	0.196	−0.18	0.211
	0.107	0.139	0.191
Landscape conditional	0.121	−0.105	−0.035
	0.322	0.392	0.829

1 – Hansen and Urban (1992).

important when using abundance data, and that patch and landscape factors appear to be more important when assessing species–environment relationships using presence/absence data.

Life history correlates

Correlations between the sizes of relative deviations and life history characteristics revealed several important patterns (Table 4). First, the frequency of occurrence of the species in the data base was significantly correlated with differences in total explained variance and with differences in three of the six CFit variance components. Specifically, frequency of occurrence was negatively related to differences between presence/absence and abundance data in total variance explained. This shows, consistent with our hypothesis, that species that were rare in the data base tended to be better explained in the presence/absence data base, whereas species that were very frequent tended to be better explained by abundance data. The correlation for the plot conditional variance component was also negative, showing that rare species tended to have larger portions of their variance accounted for by the conditional plot-level factors in the presence/absence data. In contrast, both the marginal and conditional patch-level components were positively correlated with frequency, indicating that species that were rare tended to have larger portions of their variance explained by patch factors in presence/absence data than abundance data.

The cause of the relationship between total variance explained and frequency may be relatively simple. Nearly all the variance in species that are present in most sites is related to differences in abundance, rather than presence/absence. Thus, abundance data should better explain these species. In contrast, variance in species that are present in relatively few sites is dominated by whether the species is present or absent at a site. In other words, frequently recorded species provide an 'abundance' signature, while rare species provide a 'presence/absence' signature. Super abundant, and very rare species, tended to express large differences in variance explained between presence/absence and abundance data overall, and for patch- and plot-level variance components in particular. Thus, ecologists should consider how the frequency of detection of species in their data base is likely to affect the apparent strength of the species–environment relationships, and keep in mind that rare species are often better described in presence/absence data and frequent species in abundance data.

There were two interesting correlations among other two continuous life-history attributes (Table 4). Body size and territory density were significantly correlated with differences in total variance explained. Large species, with low density, tended to be better explained by presence/absence data than abundance data overall.

Conclusions

Scientists may reach markedly different conclusions about the importance of factors structuring communities and the species–environment relationships of individual species simply by using abundance or presence/absence data. In the case of forest birds in the Oregon coast range, abundance data provides a better overall description of community structure, as measured by total variance explained. However, among species, there is great variability in variance accounted for in abundance or presence/absence forms of the data. In general, infrequently recorded species tend to be better explained by presence/absence data than abundance data, while the opposite is true for common species. Generally, patch and landscape factors appear more important in presence/absence and plot factors appear more important in analyses of abundance data. This may follow from the trend of large-bodied, rare species to be more strongly related with patch- and landscape-level variation (Cushman and McGarigal 2003), Thus, conclusions about the relative importance of factors at these different scales is largely contingent on the 'scale' at which the species-response data are analyzed. In addition, there were a number of significant relationships between life-history attributes and differences between presence/absence and abundance models. This indicates that researchers may be able to anticipate whether abundance or presence/absence coding will reveal the strongest species–environment relationships based on the biological and ecological characteristics of the study species, such as commonness and body size.

While other researchers have studied the influence of coding dependent variables as presence/absence or abundance on estimates of regional species abundance (Bart and Klosiewski 1989), population declines (Strayer 1999), and strength of individual species–environment relationships (Manuel et al. 2001), there has been little work done on the question of how the scale of dependent variable coding influences community-level analyses, and in particular, how it influences the apparent importance of factors at different spatial scales in structuring the community. Our results show that there can be substantial differences between the strength and nature of community-level species–environment relationships for presence/absence and abundance based analyses, and that there can be very large apparent differences in the relative importance of environmental factors measured at different spatial scales.

These findings could have serious implications for management and conservation decisions, which, in an effort to maximize efficiency and minimize cost, are often based on synthetic, community-level analyses. Clearly, for communities as a whole, and for individual specie within them, the strength and nature of species–environment relationships can differ dramatically between analyses of presence/absence or abundance data. Conclusions about the relative importance of environmental factors at different scales in structuring the community as a whole, and conclusions about strength of species–environmental relationships of individual species could be substantially different if researchers analyze the same data set in an abundance or a presence/absence form. This suggests that community-level analyses can run the risk of misconstruing the species–habitat relationships of individual species that exhibit strongly different relationships than average. Accordingly, researchers should take great care in deciding at what resolution to record the species response variables, and be aware that their conclusions may differ if their data are analyzed in a different form. Further work is needed to determine if the deviation patterns we observed related to scale of observation, frequency of detection, and life-history attributes between presence/absence and abundance data are widespread ecological patterns, or if they are specific to our data set.

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