

Use of Abundance of One Species as a Surrogate for Abundance of Others

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Abstract: *Indicator species concepts have a long history in conservation biology. Arguments in favor of these approaches generally stress expediency and assume efficacy. We tested the premise that the abundance patterns of one species can be used to infer those of other species. Our data consisted of 72,495 bird observations on 55 species across 1046 plots distributed across 30 sub basins. We analyzed abundance patterns at two spatial scales (plot and sub basin) and for empirical and a priori grouping. There were few significant indicator relationships at either scale or under either grouping rule, and those few we found did not explain a substantial portion of the abundance of other species. Coupled with the lack of proven efficacy for species surrogacy in the literature, our results indicate the utility of indicators and similar types of surrogate approaches must be demonstrated rather than assumed.*

Keywords: bird communities, biodiversity monitoring, indicator species, surrogate species

Uso de la Abundancia de una Especie como Sustituta de la Abundancia de Otras

Resumen: *Los conceptos de especies indicadoras tienen una larga historia en la biología de la conservación. Los argumentos a favor de estos generalmente enfatizan la viabilidad y asumen eficacia. Probamos la premisa de que los patrones de abundancia de una especie pueden ser usados para inferir los de otras especies. Nuestros datos consistieron de 72,495 observaciones de aves de 55 especies en 1,046 parcelas distribuidas en 30 subcuencas. Analizamos los patrones de abundancia a dos escalas espaciales (parcela y subcuenca) para agrupación empírica y a priori. Hay escasas relaciones indicadoras significativas en ambas escalas y bajo ambas reglas de agrupamiento, y las pocas que encontramos no explicaron una porción sustancial de la abundancia de otras especies. Asociado con la falta de eficacia probada de las especies sustitutas en la literatura, nuestros resultados señalan que la utilidad de los indicadores y de enfoques similares debe demostrarse y no asumirse.*

Palabras Clave: comunidades de aves, especies indicadoras, especies sustitutas, monitoreo de biodiversidad

Introduction

Species surrogacy is a core concept in the field of conservation biology (Landres et al. 1988; Lambeck 1997; Wiens et al. 2008). Its appeal lies in the hope of gaining effective and efficient means to evaluate status and trends of multiple species from monitoring a few surrogate species. There are many variants of this concept and different uses. Variants include ideas associated with shared habitat or functional requirements (guild mem-

bership), trophic dependencies (keystone species), area requirements (umbrella species), ecological function (engineer species), and ecological associations (focal species as defined by Lambeck 1997). (See Noon et al. [2008] for a more complete list of surrogate types.) Uses include assessing the efficacy of reserve design or the status and trends of unmeasured species. Wiens et al. (2008) proposed that species can be grouped through the use of multivariate clustering and that a surrogate can be chosen from each of the resulting groups to represent the group

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for purposes of monitoring. From a historical standpoint, this concept is most similar to the guild-indicator concept (Block et al. 1987).

Monitoring a single species or habitat element, although often technically challenging, is conceptually simple. Monitoring an ecosystem, however, is not. The primary driver behind using surrogacy to monitor ecosystems is expediency. As Wiens et al. (2008) state: "...surrogate species or groups of species can be used as proxies for broader sets of species when the number of species of concern is too great to allow each to be considered individually." Implicit in this statement, and in all surrogate approaches and implementations, is the assumption that the surrogacy concept has merit. Tests have been few, but when done, their results are seldom encouraging (Verner 1984; Landres et al. 1988; Simberloff 1998; Andelman & Fagan 2000; Lindenmayer et al. 2002; Roberge & Angelstam 2004). Monitoring an indicator species is much less onerous than monitoring all species, but the risk of bias is large if the chosen indicator does not sufficiently represent the abundances of the other species.

We evaluated the surrogate-species concept for forest birds at two spatial scales and under two species-grouping approaches. The overarching question is whether the abundance of one species across a large sample of locations provides a surrogate for the abundance of other species. We based our evaluation of this question on an a priori grouping of species into life-history categories (Hansen & Urban 1992), an approach most similar to guild surrogacy (Block et al. 1987). There are, of course, many other approaches for choosing surrogate groups. To test whether there was an alternative and more efficacious grouping approach, we used cluster analysis to generate empirical groups on the basis of observed similarity of abundances. In the first case, we tested whether there were strong surrogate relationships among species within objectively defined groups formed on the basis of ecological characteristics. In the latter case, the test was whether species in empirically formed groups derived from cluster analysis provide substantial surrogacy for the abundances of other group members. This empirical clustering approach should produce the best within-group surrogacy relationships possible given these data and therefore should indicate the maximum amount of variation in abundance explainable by any grouping strategy.

We also evaluated the scale dependency of surrogacy relationships. Most ecological processes are scale dependent (Wiens 1989; Levin 1992), and the ability of one species' abundance patterns to predict those of another is likely to be highly scale dependent (Grenyer et al. 2006). For example, one might find weak surrogate relationships between two species at the scale of patterns of co-occurrence at individual point-count plots, but find stronger relationships for co-occurrence at a watershed

scale. We evaluated the strength of surrogate species relationships for both grouping criteria at two spatial scales, corresponding to patterns of co-occurrence at the point-count plot and sub basin levels. If the abundances of species within ecological groups are highly correlated, then the abundance patterns of a member of the group should explain a large proportion of variability in the abundances of remaining species in the group. Our central objective was to identify individual bird species that effectively indicated the abundance of other species or groups of species and to determine if species grouping strategy and spatial scale of analysis influenced the apparent strength and number of surrogate relationships.

Methods

Bird Data Set

We based our analyses on a breeding-bird data set collected in the Oregon Coast Range (McGarigal & McComb 1995; Cushman & McGarigal 2004; Cushman et al. 2008). The data consist of the relative abundances of 55 species of birds in 1046 point-count plots distributed among 30 sub basins. Sub basins ranged in size from 250 to 300 ha and were selected to provide a replicated factorial of area and fragmentation of late seral forest (McGarigal & McComb 1995). This design ensures a representative sample of a broad range of landscape composition and configuration, which is necessary for generalizable conclusions regarding species surrogacy (McGarigal & Cushman 2002).

Point-count plots were distributed in a 200 × 400 m grid with between 32 and 38 point counts per sub basin. On each of four visits, observers waited 2 minutes to allow birds to resume normal activity and then recorded all birds detected within 50 m during an 8-min sampling period (Fuller & Langslow 1984; Verner 1988). Only new detections during the 8-min sample period were included in the analysis. Mean number of individuals of each species was calculated for each point-count plot (McGarigal & McComb 1995). The resulting database includes 82 bird species and an average of 2693 individual bird detections per replicate sub basin, for a total of 80,794 bird detections. We removed species with fewer than four occurrences among plots, reducing the species number to 55 and the total number of observations to 72,495 (Supporting Information). The bird data therefore reflect patterns of abundance in space and not over time. Thus they enable evaluation of the effectiveness of species surrogacy among many locations at a single time and do not allow exploration of effectiveness of surrogates across time.

We performed identical analyses on four forms of this data set. First, we analyzed the data in relative abundance and presence-absence from among plots. Results of previous analyses show some differences in the relative strength of species-environment relationships in

forest birds when the data are coded as abundance versus presence or absence (Cushman & McGarigal 2004b). Second, we performed all analyses on two sets of point-count plots. The first included all 1046 plots sampled in McGarigal and McComb (1995), and the second included all plots that were not on an edge between two different patches. This was done to avoid including stations that detected birds simultaneously in different habitat types. We calculated relative abundance as number of individuals detected per unit area per visit.

Species Grouping Rules and Spatial Scales

We used all data in both grouping and analysis. We produced two groupings of the species sampled across the 1046 plots and summarized species' abundance of the species at two spatial scales.

GROUPING RULES

The most objective evaluation of the strength of surrogacy relationships uses a priori species groupings that are defined independently from the test data set. For this analysis, we used categories and grouping defined by Hansen and Urban (1992). This provided grouping on the basis of migratory status, microhabitat association, seral-stage association, and functional group (Supporting Information).

In the second grouping approach, we based hierarchical agglomerative clustering (McGarigal et al. 2000) of species on abundance patterns to identify species groups empirically. This allowed identification of groups of species in the data set that are most similar in their abundance profiles among sample locations.

SPATIAL SCALES

To determine whether species surrogate relationships were scale dependent, we evaluated patterns of co-occurrence and abundance among species at two spatial scales. First, we evaluated patterns among species across the 1046 sample plots. This plot-scale analysis evaluated patterns of co-occurrence and abundance at the finest spatial scale, that of individual plots. Strong surrogate relationships between two species at the plot scale would mean that observing one species at a location in a landscape would indicate a high probability that the paired species would also be found at that location.

There may be cases in which species are relatively weakly associated at the fine spatial scale of individual locations, but are highly associated at coarser scales, such as sub basins, because of shared habitat requirements at the landscape scale. To investigate this possibility, we evaluated a second scale of co-occurrence on the basis of similarity of abundances within each of the 30 sub basins. This was produced by calculating a matrix containing the

average abundance of each species across all point-count plots in each sub basin. Strong surrogate relationships between two species at the sub basin scale would mean that observing one species in a sub basin would indicate a high probability that the paired species would also be found within that sub basin.

Cluster Analysis to Empirically Group Species

For the two analyses we based on empirical grouping, we conducted an initial polythetic agglomerative hierarchical clustering to identify empirical species groups (McGarigal et al. 2000). It is possible that strong associations among species' abundances could exist that are not consistent with the a priori species groups defined by Hansen and Urban (1992). For example, the groups defined by Hansen and Urban (1992) are trophically horizontal in that they define groups of species that are similar in a major life history characteristic. It may be that indicator relationships are stronger if they are trophically vertical; for example, a raptor may indicate the abundance of its prey. To test for this kind of structure, we used polythetic-agglomerative hierarchical clustering of species on the basis of their similarity in abundance among plots (McGarigal et al. 2000). We used a Spearman correlation distance of species' abundances as the dissimilarity measure and Wards minimum-variance linkage as the fusion strategy. The correlation distance ranged from zero for two species that are perfectly positively correlated to one for two species that are perfectly but inversely correlated. In addition, the use of Spearman's correlation distance allows for monotonic, but nonlinear relationships between species' abundances, and because it is based on rank abundances it is invariant to differences in relative abundances among species.

We interpreted the cluster dendrogram, scree plot of fusion distance across cluster number, and agglomerative coefficient (coef.hclust, Cluster library, R-project.org) to determine the effectiveness of the cluster analysis and the number of meaningful clusters. The goal was to measure the ability of species to indicate others; therefore, we were interested in measuring the amount of clustering due to nonrandom patterns of co-occurrence. We accomplished this by comparing the cluster solution for the original data with cluster solutions for 1000 randomizations of the data set in which each species' observed abundances were randomly assigned to plots (i.e., column randomization in the sample-by-species data set). This randomization eliminated all nonrandom patterns of co-occurrence and preserved the species' abundance profiles. Comparing cluster membership and fusion distances for the randomizations with those produced by the nonrandomized data allowed formal comparison of clustering associated with nonrandom co-occurrence from clustering due to chance.

Within-Group Mantel Analysis

Strong within-group correlation is a necessary condition for successful surrogacy. We used within-group Mantel analysis to evaluate the strength of within-group correlation of abundance. The species groups were based on Hansen and Urban (1992; Supporting Information) in the a priori case and the results of the polythetic-agglomerative hierarchical clustering in the empirical-grouping case. We computed a matrix of Spearman's correlation distances among abundances of all species pairs (as described above) and built a series of model matrices in which species pairs within the same group were assigned a value of zero, while those in separate groups were assigned a value of one (Legendre & Legendre 1998). We then used Mantel tests (Mantel 1967) to determine whether species within the same group had higher correlations of abundance than species in different groups. The existence of high within-group similarity in abundance patterns would result in significant correlation between the abundance and model matrices and a substantial proportion of the variance in pairwise species correlations would be explained by the grouping assignments. We used Monte Carlo permutations with 1000 randomizations to test for significance (mantel, Vegan library, R-project.org).

Within-Group Canonical Ordination Analysis

The existence of significant within-group correlation (above) is not a sufficient measure of the strength of any particular indicator species; a key attribute of a successful indicator species is its ability to indicate the abundance patterns of many other species. Therefore, in addition to the Mantel analysis, we used redundancy analysis (Legendre & Legendre 1998) to evaluate the ability of each species within a group to explain the abundances of the remaining species in that group. The analysis proceeded by removing one species and using it as the independent variable to predict the abundance of the remaining species and repeating this process with replacement for all species in each group. For this analysis, the species data set (i.e., y-variable set) was standardized by column (species) totals to remove the effect of differences in relative abundances among species. The analysis computes the proportion of variance in abundance of all species in the group that can be explained by the species that is removed and hence that species' utility as an indicator.

We evaluated the statistical significance of relationships between each potential indicator species and its respective species group with a one-tailed paired *t* test. A separate paired *t* test was conducted for each species group. The paired observations consisted of the variance explained by the indicator species within its group and the variance explained by that species across the entire species pool. If there were effective indicators, we expected the average within-group variance explained to

be higher than that explained for the full assemblage. Because the average variance explained within groups may not reveal whether any single species is an effective indicator, we also evaluated the utility of the best indicator species for each group (i.e., the species with the greatest within-group explanatory power).

Results

Results of analyses based on presence-absence or relative abundance across all plots or only plots located in patch interiors produced were extremely similar and provided identical interpretation of the number, strength, and nature of surrogate relationships. We present results for analysis of relative abundance across all plots. Full results for all combinations of edge and interior \times presence and absence are in Supporting Information.

A Priori Grouping and Plot-Level Analyses

Open-canopy and closed-canopy bird groups had positive and statistically significant within-group Mantel correlations (Table 1). Group membership explained 15.4% of the correlation of abundance for closed-canopy species and 4% of the correlation of abundance for open-canopy species (r^2 in Table 1). There were no statistically significant relationships between migratory status, microhabitat association, or functional group and the correlation of abundance in within-group species pairs. Nevertheless, four of the six functional groups had negative Mantel correlations.

For the a priori groups, canonical ordination between each species and the rest of the group accounted for very little variance in species' abundance on average. Variance explained by species within groups was significantly greater than variance explained in the full species pool for only one of the 13 a priori groups (species associated with open canopy; Table 2). Species associated with open-canopy habitat on average explained 7.8% of the variance in the abundances of other species associated with open canopy, which is 6.5% more than the variance explained on average by these species in the full species pool. For 6 of the 13 groups, canonical analysis explained less within-group variance in species' abundance than the full species pool (Table 2). The ability of the single best species to explain variance in abundance of other in-group species varied markedly among a priori species groups (Table 3). Across groups, the single best species explained on average 8.8% (range 0.6–35.6%) of variance in abundance of other in-group species. The Western Bluebird (*Sialia mexicana*) was the best overall indicator species because it explained the most in-group variance of any species within its seral-stage group (29.4%), microhabitat group (14.1%), and functional group (35.6%).

Table 1. Mantel tests for significant correlation of abundance profiles among bird species belonging to specific groups at the plot and sub basin scale.

	Group ^b	Plot scale ^a		Sub basin scale ^a	
		r	p	r	p
A priori groups migratory status	NT	0.015	0.260	-0.004	0.472
Migratory status	R	0.036	0.084	0.020	0.165
Migratory status	S	-0.037	0.888	-0.066	0.800
Seral stage	CC	0.392*	<0.001*	0.331*	<0.001*
Seral stage	G	0.011	0.251	0.032	0.154
Seral stage	OC	0.2*	<0.001*	0.032	0.221
Microhabitat	G	0.042	0.092	0.013	0.318
Microhabitat	L	0.016	0.250	-0.021	0.587
Microhabitat	S	0.031	0.143	0.012	0.348
Functional group	A	-0.011	0.554	-0.033	0.706
Functional group	GB	0.036	0.146	0.060	0.159
Functional group	GF	-0.023	0.809	-0.042	0.872
Functional group	GL	0.052	0.053	0.015	0.241
Functional group	R	-0.003	0.476	-0.003	0.436
Functional group	W	-0.008	0.570	-0.069	0.872
Empirical groups					
Cluster 1	1	0.234*	<0.001*	0.240*	<0.001*
Cluster 2	2	0.062*	0.030*	0.248*	<0.001*
Cluster 3	3	0.458*	<0.001*	0.438*	<0.001*

^aSignificant Mantel tests are indicated with an asterisk (*).

^bKey: NT, Neotropical migrant; R, resident; S, short-distance migrant; CC, closed-canopy-associated species; G, seral-stage generalist; OC, open-canopy-associated species; L, log-associated species; S, snag-associated species; A, air-feeding species; GB, game birds; GF, ground-feeding species; GL, gleaners; R, raptors; W, woodpeckers.

Table 2. Canonical ordination analysis of variance in abundance explained by bird species within each group compared with variance explained by those species in the full bird assemblage^a.

Grouping factor	Group ^c	Plot data ^b					Sub basin data ^b				
		var. expl. group	var. expl. full	difference	df	p	var. expl. group	var. expl. full	difference	df	p
Migratory status	NT	0.006	0.009	-0.002	16	0.979	0.074	0.082	-0.008	16	0.799
Migratory status	R	0.003	0.007	-0.005	28	1.000	0.065	0.066	-0.001	28	0.592
Migratory status	S	0.040	0.012	0.029	8	0.051	0.102	0.083	0.020	8	0.166
Seral stage	CC	0.004	0.008	-0.004	19	0.996	0.096	0.070	0.026	19	0.012*
Seral stage	G	0.002	0.006	-0.004	20	1.000	0.064	0.065	-0.002	20	0.623
Seral stage	OC	0.078	0.013	0.065	13	0.016*	0.182	0.092	0.090	13	<0.001*
Microhabitat	S	0.026	0.008	0.018	37	1.000	0.068	0.067	0.001	37	0.445
Microhabitat	G	0.005	0.008	-0.003	4	0.209	0.074	0.073	0.001	4	0.778
Microhabitat	L	0.018	0.012	0.005	11	0.096	0.078	0.093	-0.014	11	0.450
Functional group	A	0.105	0.011	0.094	6	0.081	0.189	0.083	0.106	6	0.038*
Functional group	GF	0.014	0.011	0.004	16	0.071	0.086	0.078	0.007	16	0.155
Functional group	GL	0.005	0.008	-0.003	21	1.000	0.062	0.072	-0.010	21	0.987
Functional group	W	0.020	0.005	0.015	4	0.097	0.049	0.072	-0.023	4	0.915
Cluster	1	0.106	0.015	0.091	12	0.010*	0.167	0.090	0.077	21	<0.001*
Cluster	2	0.002	0.005	-0.003	29	1.000	0.077	0.060	0.016	17	0.011*
Cluster	3	0.013	0.010	0.003	11	0.049*	0.062	0.066	-0.004	14	0.735

^aVar. expl. group, average variance in abundances of the group explained by each group in canonical ordination; Var. expl. full, average variance in abundances of the full species assemblage explained by each group member.

^bThe p value reported is for a one-tailed paired t test testing whether species within each group explain significantly larger amounts of the variance of the group than that of the full species pool. Significant one-tailed t tests are marked with an asterisk (*).

^cKey: NT, neotropical migrant; R, resident; S, short-distance migrant; CC, closed-canopy-associated species; G, seral-stage generalists; OC, open-canopy-associated species; L, log-associated species; S, snag-associated species; A, air-feeding species; GB, game birds; GF, ground-feeding species; GL, gleaners; R, raptors; W, woodpeckers.

Table 3. Variance explained by bird species with the greatest explanatory ability for each group compared with the variance explained in the full species pool by that species on the basis of canonical ordination analyses.^a

Grouping factor	Group ^b	Plot analysis			Sub basin analysis		
		species ^c	var.expl. group	var.expl. full	species ^c	var.expl. group	var.expl. full
Migratory status	NT	MGWA	0.016	0.012	MGWA	0.213	0.147
Migratory status	R	WIWR	0.006	0.020	PUFI	0.142	0.082
Migratory status	S	AMGO	0.137	0.022	WEBL	0.258	0.115
Seral stage	CC	RBSA	0.010	0.005	WETA	0.216	0.078
Seral stage	G	BGWA	0.007	0.010	TOSO	0.154	0.094
Seral stage	OC	WEBL	0.294	0.020	HOWR	0.298	0.090
Microhabitat	S	WEBL	0.141	0.020	RBSA	0.117	0.066
Microhabitat	G	AMGO	0.019	0.022	MGWA	0.181	0.147
Microhabitat	L	RSTO	0.037	0.010	RSTO	0.148	0.129
Functional group	A	WEBL	0.356	0.020	VGSW	0.315	0.067
Functional group	GF	WCSP	0.054	0.025	RSTO	0.196	0.129
Functional group	GL	OCWA	0.017	0.014	MGWA	0.121	0.147
Functional group	W	DOWO	0.046	0.003	HAWO	0.082	0.080
Groups	1	WEBL	0.349	0.020	WEBL	0.315	0.115
Groups	2	BGWA	0.005	0.010	BEWR	0.143	0.066
Groups	3	EVGR	0.024	0.006	VATH	0.127	0.130

^aVar.expl.group, average variance in abundances of the group explained by each group in canonical ordination; var.expl.full, average variance in abundances of the full species assemblage explained by each group member.

^bKey: NT, Neotropical migrant; R, resident; S, short-distance migrant; CC, closed-canopy-associated species; G, seral-stage generalists; OC, open-canopy-associated species; G, microhabitat generalists; L, log-associated species; S, snag-associated species; A, air-feeding species; GB, game birds; GF, ground-feeding species; GL, gleaners; R, raptors; W, woodpeckers.

^cFull list of species, including common, scientific, and definitions of abbreviated names are provided in Appendix 1.

A Priori Grouping and Sub Basin Analyses

At the sub basin level, the closed-canopy bird group had statistically significant positive within-group correlations (Table 1). The grouping variable accounted for 9.7% of variance in the correlation of abundances of closed-canopy species at the sub basin level. As in the plot-level case, there were no statistically significant relationships between migratory, microhabitat association, or functional group and the correlation of abundance in within-group species pairs.

For the a priori groups, canonical ordination between each species and the rest of the group accounted for very little variance in species' abundance on average. The paired *t* test of differences in variance explained by species within groups to variance explained in the full species pool on average was significant for just 3 of the 13 a priori groups (closed-canopy, open-canopy, and aerial-feeding species; Table 2). Species associated with closed-canopy habitat on average explained 9.6% of variance in abundances of other closed-canopy associated species, 2.6% more than the variance explained on average by these species in the full species pool. Likewise, species associated with open-canopy habitat explained 18.2% of variance in abundances of other open-canopy species, 9.0% more than for the full species pool. Finally, aerial-feeding species on average explained 18.9% of variance in abundance of other aerial-feeding species, 10.6% more than for the full species pool. For 6 of the 13 groups, canonical analysis explained less within-group variance

in species' abundance than the full species pool on average (Table 2). The ability of the single best species to explain variance in abundance of other in-group species varied markedly among a priori species groups (Table 3). Across groups, the single best species explained on average 18.8% (range 8.2–31.5%) of variance in abundance of other in-group species. No one species was consistently the best indicator species across groups.

Empirical Grouping and Plot-Level Analysis

The dendrogram and scree plot (Fig. 1) suggest a strong three-cluster solution. This cluster solution produced an agglomeration coefficient of 0.80, indicating substantial coherence in group assignment. This agglomeration coefficient was substantially higher than the range produced in the 1000 column-randomized cluster analyses (0.25–0.31; Fig. 1b). The scree plot of cluster dissimilarity across number of clusters was strongly inflected and departed from the distribution of scree plots of the column-randomized cluster analyses over most of the range of cluster numbers (Fig. 1b). Thus, the cluster solution indicated significant patterns of co-occurrence after controlling for random process.

All three empirically identified clusters at the plot level had statistically significant positive within-group correlations (Table 1). The grouping variable accounted for 5.5%, 0.38%, and 21.0% of the variance in correlations among clusters 1, 2, and 3, respectively (Table 1). The paired *t* test of differences in variance explained by

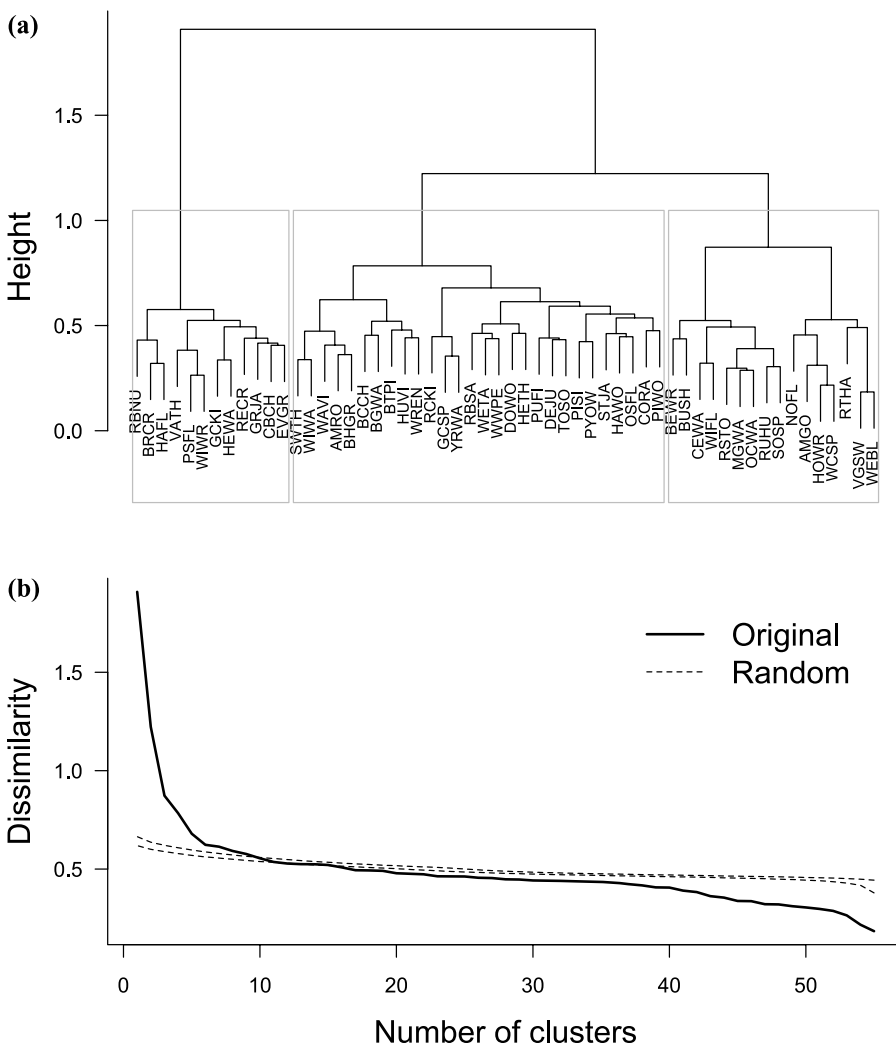


Figure 1. (a) Dendrogram and (b) scree plot for plot-scale empirical grouping of bird species. Clustering was done with polythetic agglomerative hierarchical clustering on the Spearman correlation distance matrix of species' abundances and Ward's minimum-variance fusion strategy. The range of values of the agglomerative coefficient and scree plots for 1000 column randomizations of the species matrix are shown as null comparisons. (Abbreviations of species' names are provided in Appendix 1.)

species within groups to variance explained in the full species pool was statistically significant for clusters 1 and 3 (Table 2). Species in cluster 1 on average explained 10.6% of the variance in the abundances of other in-group species, 9.1% more than the variance explained on average by these species in the full species pool. Species in cluster 3 on average explained 1.3% of the variance in abundances of other in-group species, 0.3% more than for the full species pool. The ability of the single best species to explain variance in abundance of other in-group species varied markedly among clusters (Table 3). Across clusters, the single best species explained on average 12.6% (range 0.5–34.9%) of the variance in abundance of other in-group species.

Empirical Grouping and Sub Basin Analyses

Cluster analyses at the sub basin level also suggested a strong three-cluster solution on the basis of interpretation of the dendrogram and scree plot (Fig. 2). This cluster solution produced an agglomeration coefficient of 0.94, which indicated substantial coherence in group assign-

ment. This agglomeration coefficient was higher than the range produced in the 1000 column-randomized cluster analyses (0.77–0.84; Fig. 2), which indicated the cluster solution identified significant patterns of co-occurrence after controlling for random process.

There were significant positive within-group correlations for all three empirically identified clusters at the sub basin level (Table 1). The grouping variable accounted for 5.8%, 6.1%, and 19.2% of the variance in correlations among species in clusters 1, 2, and 3, respectively (Table 1).

The paired *t* test of differences in variance explained by species within groups to variance explained in the full species pool was statistically significant for clusters 1 and 2 (Table 2). Species in cluster 1 on average explained 16.7% of variance in abundances of other in-group species, 9.0% more than the variance explained on average by these species in the full species pool. Species in cluster 2 explained on average 7.7% of variance in abundances of other open-canopy species, 1.6% more than for the full species pool. The ability of the single best species to explain variance in abundance of other

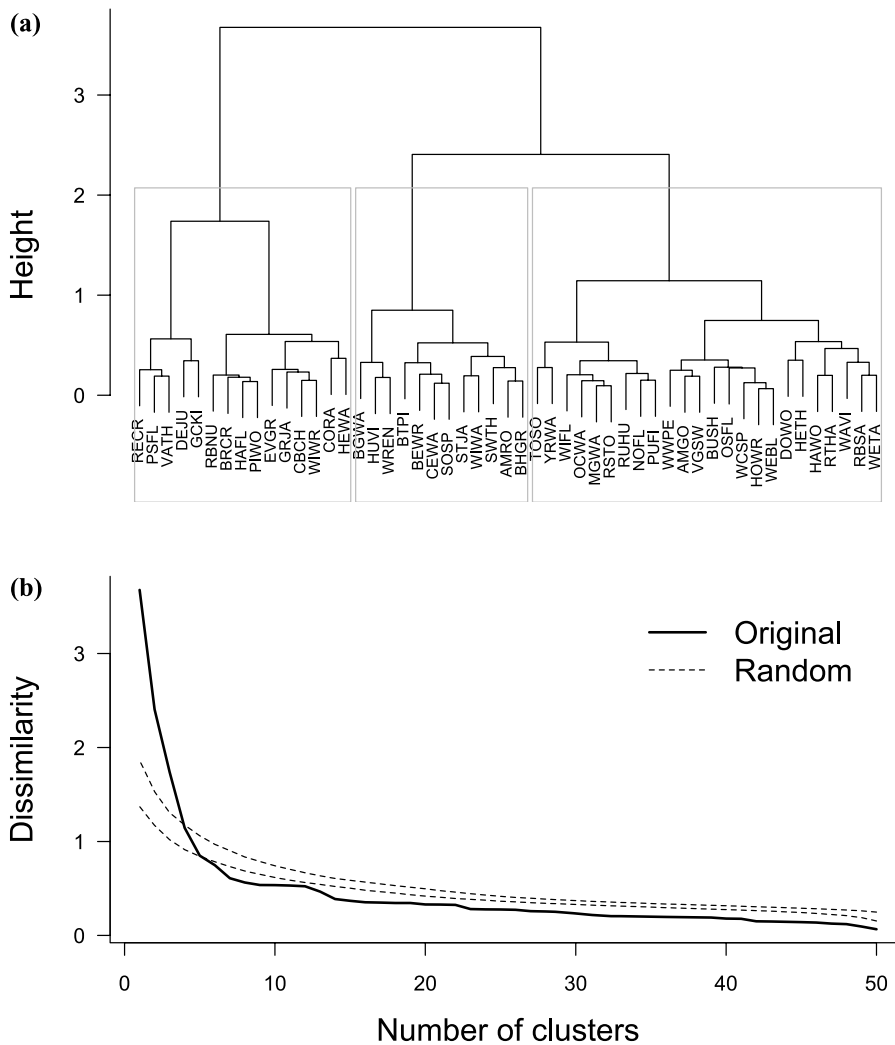


Figure 2. (a) Dendrogram and (b) scree plot for sub basin-scale empirical grouping of bird species. Clustering was done with polythetic agglomerative hierarchical clustering on the Spearman correlation distance matrix of species' abundances and Ward's minimum-variance fusion strategy. The range of values of the agglomerative coefficient and scree plots for 1000 column randomizations of the species matrix are shown as null comparisons. (Abbreviations of species' names are provided in Appendix 1.)

in-group species varied markedly among clusters (Table 3). Across clusters, the single best species explained on average 19.5% (range 12.7–31.5%) of variance in abundance of other in-group species.

Discussion

Scale Dependence in Species Surrogacy

Patterns of species co-occurrence are likely to be scale dependent. For example, the American Redstart (*Setophaga ruticilla*) and Least Flycatcher (*Empidonax minimus*) are positively associated regionally, indicating overlap in range, but exhibit negative patterns of co-occurrence locally, reflecting different fine-scale habitat selection (Sherry 1979). We found that surrogacy strength at the sub basin level was not substantially different than at the plot level for most species groups on the basis of both a priori or empirical grouping (Tables 1 & 2). On the basis of number and strength of significant statistical tests, there was little difference in the strength of species surro-

gacy between plot and sub basin scales. This suggests that in this system there do not appear to be substantial differences in patterns of species co-occurrence between plot scales and the scale of small hydrological basins. This, however, does not preclude scale-dependent changes in co-occurrence patterns at broader spatial scales than those we evaluated.

Grouping Rule and Species Surrogacy

The most objective tests of species surrogacy would use a priori groups that were defined independently of the data set used for evaluation. Wiens et al. (2008) suggest forming groups through cluster analysis on species' ecological characteristics and choosing a member of each group as a surrogate for the others. This is very similar to the a priori grouping in our analysis.

Our analysis indicates that the empirical grouping provided stronger patterns of surrogacy than the a priori grouping. It is not surprising that groups formed empirically to maximize within-group similarity in abundance patterns are significantly better predictors of in-group

abundance for the same data set than are a set of independently derived groups. The empirically derived groups can be considered a best-case scenario which provides the maximum possible strength of surrogacy. These results are likely close to the maximum possible variance explained by grouping these data. Nevertheless, they may be idiosyncratic to the particular data set and study area used to produce them.

Species groupings assigned objectively based on a priori consideration of species autecological characteristics are likely to be more generalizable across populations and ecosystems than empirical groupings and their observed surrogacy patterns. In addition, a priori groupings are more easily interpreted ecologically than empirical groupings in that they are based on definable ecological characteristics, such as seral-stage association, migratory status, or functional group, rather than on the happenstance of the patterns of co-occurrence in a given ecosystem at a given time.

Splitting species into 13 a priori groups on the basis of migratory status, seral-stage association, microhabitat association, and functional group produced few statistically significant surrogate relationships. Seral-stage association showed the strongest surrogacy, with significant within-group correlations for closed- and open-canopy-associated species at both the plot and sub basin level. All the other grouping categories were largely devoid of statistically significant surrogacy relationships. Statistically significant patterns of co-occurrence in relation to seral-stage association are not surprising in this system, given that the major differences among plots and sub basins that formed the samples for this study were related to seral-stage conditions of forest succession (McGarigal & McComb 1995). One would expect to find significant patterns of co-occurrence among species with similar seral-stage associations in a data set in which sample locations primarily differ along gradients of seral development. Even here, however, little variance was explained. No seral-condition groupings at either the plot or sub basin level explained more than 18.2% of within-group variance in abundance. The absence of significant patterns of co-occurrence for any of the other groups suggests that coarse habitat-association attributes may be the only characteristics useful for defining species surrogacy.

Utility of Species Surrogacy

Monitoring efficacy is often judged on the basis of power to detect change. Manley et al. (2004) suggest that being able to detect a 20% change in abundance, 80% of the time is a reasonable expectation for change-detection monitoring. In our analysis, the average variance in species' abundance explained by the group assignment was 9.4% at the sub basin scale and 2.7% at the plot scale (Table 2). It is nearly impossible for surrogate monitoring to have

sufficient power to detect change when over 90% of the variability of a species assemblage is independent of the abundance of indicator species.

Our results indicate that with a priori omniscience one could pick indicators that perform better than the group averages we identified (Table 3). For example, at the plot level, 3 of 13 groups had a member species that could explain more than 20% of in-group variance, whereas 6 of 13 could at the sub basin level. This, however, does not provide much encouragement because identifying these "best" indicators for each group would require a priori data collection and evaluation for all member species. Thus, the average in-group surrogate ability is the more meaningful measure of the success of group surrogacy. Nevertheless, even selection of the "best" group indicators (Table 3) for each group did not give substantial power to monitor in-group abundance. The average variance explained by the best indicator across groups was 12.6% at the plot level and 19.5% at the sub basin level. A two-stage inference is required to use a surrogate for monitoring the group; the power to measure group change would be reduced by the product of the uncertainty of the estimate of the surrogate species' abundance and the imprecision with which that surrogate species reflects abundances of its group. A useful and reliable surrogate species must be tightly associated with the group it represents. On the basis of these considerations, we believe that the rarity of statistically significant indicator relationships and the weakness of those that were found suggest that guild-level indicator species for birds are not effective in this system.

Surrogacy is a key concept in ecosystem management and the movement into multispecies conservation paradigms. Effective species surrogates, however, appear to be rare. Ecological theory provides a possible explanation. No two species can long occupy the same niche (Gause 1934; Hutchinson 1957; Pulliam 2000). Thus, all coexisting, sympatric species must differ along at least one critical niche dimension. There must be some limit to the similarity of coexisting species (MacArthur 1967), and it is expected that species that are similar in some aspects of their niche will displace others so as to minimize competition. This would tend to lead to weak or negative patterns of co-occurrence for species sharing functional ecological characteristics, as we found in our study (see also Sherry 1979). Niche displacement processes would appear destructive to the stable existence of strong species surrogacy on the basis of functional ecological characteristics.

Conclusions

We present a limited evaluation of the surrogate species concept. We limited the evaluation to bird species in a temperate forest environment. We evaluated patterns in

space and not in time. Nevertheless, the lack of strong surrogacy is compelling. The data set was large (over 75,000 bird locations at over 1000 point-count stations). These data have been used in numerous studies (McGarigal & McComb 1995; Cushman & McGarigal 2002; Cushman & McGarigal 2004; Cushman et al. 2008) and have sufficient power to detect patterns in community structure (McGarigal & McComb 1995; Cushman & McGarigal 2003). In addition, we considered two spatial scales and both a priori and empirical species grouping, which provided a comprehensive evaluation of the surrogate-species concept.

Our results suggest that certain types of surrogacy are unlikely to reliably exist. For example, groups formed on the basis of migratory status, microhabitat association, and functional group did not receive any support. Thus, the guild-indicator concept (Block et al. 1987) and management-indicator species (Landres 1992; Landres et al. 1988) do not appear to have merit, at least for these species. The idea that the dynamics of one species will represent those of others that share its functional or migratory characteristics (Wiens et al. 2008) should be verified rather than assumed. We did find significant relationships among the co-occurrence patterns of species with shared seral-stage associations. Nevertheless, these relationships were weak in terms of the ability of one of the group to predict abundance patterns of other group members.

To monitor ecosystems one must study them, determine the critical elements within the ecosystems, formulate specific hypotheses concerning ecosystem function, and collect data to evaluate those hypotheses (Nichols & Williams 2006; Cushman et al. 2008; Cushman & McKelvey 2009). For such approaches to produce stable and reliable inferences to the ecosystem, the monitored elements should be chosen on the basis of strong causal chains and be linked explicitly to either top-down or bottom-up controls. One should not, however, make the error of assuming that by monitoring any species or group of species one is monitoring an ecosystem. There is no statistical basis to believe a priori that the dynamics or distribution of an individual species is representative of a species group. These relationships need to be demonstrated rather than assumed. Lacking these understandings, the emphasis for species monitoring should be on the perceived importance of the species itself and not on its presumed ecological surrogacy.

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Supporting Information

Results for analysis of all four forms of the data set are available as part of the on-line article (Appendix S1) and include results for Mantel analysis of within-group correlation that are interpreted the same as in Table 1. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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