Beyond Species Richness: Community Similarity as a Measure of Cross-Taxon Congruence for Coarse-Filter Conservation

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Abstract: *The use of a surrogate taxon in conservation planning has become questionable because recent evidence suggests that the correlation of species richness between pairs of taxa is highly variable both taxonomically and geographically. Species richness is only one measure of species diversity, however, and recent studies suggest that investigations of cross-taxon congruence should consider a broader range of assessment techniques. The cross-taxon congruence of community similarity between sites among taxa has rarely been examined and may be the most relevant measure of species diversity in the context of coarse-filter conservation strategies. We examined cross-taxon congruence patterns of species richness and community similarity (Bray-Curtis similarity) among birds, butterflies, and vascular plants in montane meadow habitats in the Greater Yellowstone Ecosystem. Although patterns of species richness (Spearman rank correlation) varied between taxa, we consistently found a positive correlation in community similarity (Mantel test) between all pair-wise comparisons of the three taxa (e.g., sites with similar bird communities also had similar butterfly communities). We suggest that the success of a surrogate taxon depends on the technique used to assess surrogacy and the specific approach to conservation planning. In the context of coarse-filter conservation, measures of community similarity may be more appropriate than measures of species richness. Furthermore, the cross-taxon congruency of community similarity in our study suggests that coarse-filter conservation may be tenable in montane meadow communities.*

Más Allá de la Riqueza de Especies: Similitud de Comunidades como una Medida de Congruencia Trans-Taxones para la Conservación de Grano Grueso

Resumen: *El uso de un taxón sustituto en la planeación de la conservación se ha vuelto cuestionable porque información reciente sugiere que la correlación de riqueza de especies entre pares de taxones es altamente variable taxonómica y geográficamente. Sin embargo, la riqueza de especies es solo una medida de la diversidad de especies, y estudios recientes sugieren que las investigaciones de congruencia trans-taxón debieran considerar una mayor variedad de técnicas de evaluación. La congruencia trans-taxón de la similitud de comunidades entre sitios entre taxones rara vez se ha examinado y puede ser la medida de diversidad de especies más relevante en el contexto de las estrategias de conservación de grano grueso. Examinamos patrones de congruencia trans-taxón de riqueza de especies y similitud de comunidades (similitud Bray-Curtis) en aves, mariposas y plantas vasculares en hábitats de praderas montanas en el Ecosistema Greater*

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Yellowstone. Aunque los patrones de riqueza de especies (correlación Spearman de rangos) variaron entre especies, encontramos consistentemente una correlación positiva en la similitud de la comunidad (prueba de Mantel) entre todas las comparaciones de pares de los tres taxones (es decir, los sitios con comunidades similares de aves también tenían comunidades similares de mariposas). Sugerimos que el éxito de un taxón sustituto depende de la técnica utilizada para evaluar la sustitución y el abordaje específico de la planeación de conservación. En el contexto de la conservación de grano grueso, pueden ser más apropiadas las medidas de similitud de comunidades que las medidas de riqueza de especies. Más aun, la congruencia trans-taxón de similitud de comunidades en nuestro estudio sugiere que la conservación de grano grueso puede ser justificable en comunidades de praderas montanas.

Introduction

As the field of conservation planning has evolved, strategies have broadened from targeting single species to focusing on biotic communities (e.g., coarse-filter conservation strategies) (Hunter 1988, 1991; Noss 1990; Franklin 1993; Simberloff 1998; Hunter 2001). Although this premise is straightforward in theory, the practice of identifying representative biotic communities is a major challenge. Generally, biotic communities are defined by a surrogate taxon (Groves et al. 2000), and it is assumed that this set of communities will be representative for other taxa as well. The use of surrogate taxa in conservation planning has become suspect, however, because recent evidence suggests that the correlation of species richness and coincidence of diversity "hotspots" between pairs of taxa is highly variable (Prendergast et al. 1993; Prendergast & Eversham 1997; Lawton et al. 1998; Prendergast et al. 1999; Ricketts et al. 1999) and may be dependent on the spatial scale examined (Weaver 1994; Blair 1999).

We should make a distinction between coarse-filter strategies and efforts to map species richness at coarse spatial scales, such as GAP analysis (Scott et al. 1993; Jennings 1995), and note criticisms thereof (Conroy & Noon 1996; Flather et al. 1997). *Coarse-filter conservation* refers specifically to the premise that a representative array of biotic communities will contain the majority of the species pool within a given area (Hunter 1991, 2001). Therefore, using species richness as the currency with which to assess patterns of cross-taxon congruency may be more relevant to single-species approaches to conservation planning than coarse-filter approaches. Measures of species richness do not provide information on species identity and therefore do not provide information about the representativeness of a set of conservation areas. Simply knowing the number of species at a given site does not give insight into whether that particular site contains species that add to the overall representation of an array or ones that are redundant.

We suggest that patterns of cross-taxon congruence in community composition are more relevant to coarse-filter strategies than patterns of species richness. Using Whittaker's (1960) terminology, tests of the cross-taxon congruency in the context of coarse-filter conservation should focus on patterns of congruence in measures of beta diversity (community similarity between two sites) rather than alpha diversity (species richness at a single site) among taxa. If an array of communities is representative for multiple taxa, then patterns of community similarity between sites among taxa should be correlated.

Few researchers have directly compared patterns of cross-taxon congruency in species richness and community composition. Researchers testing optimum reserve-selection algorithms have compared the congruency of richness hotspots to that of reserve networks based on measures of complementarity between areas (Ryti 1992; Faith & Walker 1996*a*; Williams et al. 1996; Howard et al. 1998; Reyers & van Jaarsveld 2000; Reyers et al. 2000). These algorithms build a minimum set of areas needed to maximize the diversity of a given taxon by adding areas of highest complementarity in a stepwise fashion. A given area's complementarity value is based on the number of so-far-unrepresented species. Patterns of cross-taxon congruency are then assessed by examining the proportional overlap of minimum sets built with different surrogate taxa and correlations in the order of entry into the network and by assessing the overall representation of taxa that are not surrogates by the network of sites identified with the surrogate taxa (Saetersdal et al. 1993; Pressey et al. 1996, 1997; Reyers & van Jaarsveld 2000; Pressey & Cowling 2001).

Although these approaches do incorporate species identity and assess the redundancy or complementarity of a particular area, they do not address the congruency of community composition or beta diversity per se. Although measures of complementarity are used to build the network of sites, the final currency of success is still species richness. A network of sites based on a surrogate taxa is considered successful if it also captures high species richness of nontarget taxa. Measures of proportional overlap indicate the overall spatial congruence of different taxa, and correlations in the order of entry into the network are highly affected by which algorithm is used (Reyers & van Jaarsveld 2000). Although a multitude of sophisticated algorithms has been suggested, no universal algorithm has been identified to handle all conservation planning scenarios (Pressey et al. 1997; Prendergast et al. 1999).

Howard et al. (1998) addressed community composition directly by examining the congruency of the raw complementarity scores from reserve-selection algorithms. They found variable congruency in patterns of species richness, whereas patterns of complementarity between taxa were consistently correlated. However, their analysis did not incorporate all possible pair-wise combinations of sites. To avoid pseudoreplication, they only compared each site to the site that was next smaller in physical size. Although they partitioned out the effects of size in their analysis, a more robust test would consider the community composition of all pair-wise combinations of sites. Furthermore, the complementarity scores for sites were based on the order in which they were added to the network and the criteria of the algorithm used.

Oliver et al. (1998) adopted a more straightforward approach and assessed patterns of cross-taxon congruency by directly comparing measures of community composition. They calculated measures of beta diversity (Bray-Curtis similarity; Bray & Curtis 1957) in plant, vertebrate, and invertebrate assemblages between all pair-wise combinations of sites and assessed congruency using Mantel tests (McCune & Mefford 1997; Legendre & Legendre 1998). Although they found little congruency in species richness, the community composition among all three assemblages were highly correlated.

We adopted the methods of Oliver et al. (1998) and tested for correlations of species richness and community similarity among birds, butterflies, and vascular plants in montane meadows within the Greater Yellowstone Ecosystem (GYE) in Wyoming and Montana (U.S.A.). The meadows included hydric willow and sedge communities, mesic forb-rich meadows, and xeric sagebrush flats (Debinski et al. 1999). For each taxon in each study area, we calculated the species richness in each meadow and the community similarity between all pairs of meadows and examined patterns of cross-taxon congruency.

Methods

Study Areas

We used two study areas within the GYE. The "Gallatins" included the Gallatins National Forest and a northwestern portion of Yellowstone National Park. The "Tetons" study area included portions of Grand Teton National Park. These two regions are 192 km apart and have very similar plant and animal communities. We focused specifically on low-elevation montane meadows (2000–2500 m elevation). Meadows ranged from 1 to 7861 ha and averaged 500 ha in size.

Meadow Classification and Sampling Stratification

We used remote-sensing data to identify the full range of meadow variation within the GYE and then stratified our sampling along this gradient of variation to ensure that our study areas were representative of the regional variation in species richness and community composition across the three taxa studied. We used an unsupervised computer classification of Satellite Pour l'Observation de la Terre (SPOT) multispectral satellite imagery to produce maps of six spectrally distinct meadow classes or meadow (M) types within the Gallatins and Tetons study areas, with a minimum mapping unit (MMU) of 25 pixels, or 1 ha. (Debinski et al. 1999, 2000, 2002). The spectral classes (labelled M1–M6) are arranged along a gradient of increasing hydrology, which is a major factor controlling species-distribution patterns within the GYE (Marston & Anderson 1991). The M1 and M2 contain a significantly greater richness and abundance of obligate wetland plants, whereas the dryer meadow types are composed of a greater abundance of obligate upland plants (Kindscher et al. 1998; Debinski et al. 1999, 2002).

Selection of Sampling Sites

We used global positioning devices, aerial photography, topographic maps, and compass readings from identifiable landmarks to locate sample sites in the field. We chose meadows that were a minimum of 500 m apart, and, when possible, we attempted to locate a diversity of meadow types in the same general area. There were some problems associated with the M4 classification in the Tetons study area. Field investigations in late May 1997 indicated that some areas mapped as M4 types were in fact groves of aspen (*Populus tremuloides*) with dense herbaceous understory. Therefore, we eliminated the M4 type from the Tetons study area, and sampling proceeded in the remaining five meadow types. Thus, we sampled 25 meadows in the Tetons and 30 meadows in the Gallatins. We conducted all sampling in the geographic center of each meadow.

Plant, Bird and Butterfly Sampling

We sampled plants in July of 1997 and 1998. During each sampling period, we surveyed plants in 20, 1-m^2 quadrats placed systematically within a 20 × 20 m plot in the center of each meadow. We estimated the aerial percent cover of each plant species in each 1-m^2 quadrat by using a modified Daubenmire (1959) method in which estimations were made to the nearest percentage.

We surveyed the bird community in each meadow every 2 weeks, for a total of three replications per year between early June and mid-July of 1997, 1998, and 2000. Between 0530 and 1030 hours, two observers conducted 15-minute point counts within circular plots of 50-m radius. During each survey we mapped the location of each bird observed to avoid double counting of individuals. Additionally, we recorded the behavior of each bird observed, and we did not include individuals flying through the plot in our analysis. We conducted extensive training

and validation tests at the beginning of each field season to ensure consistency across years and between observers.

We surveyed the butterfly community in each meadow every 2 weeks between mid-June and mid-August, for a total of four replications per year in 1997 and 1998 and three replications in 2000. Two people netted butterflies for 20 minutes within a 50 × 50 m plot between 0930 and 1630 hours. We placed each butterfly captured in a glassine envelope, and at the end of the survey all individuals were identified to species and most were released. Some individuals were retained as voucher specimens or for later identification.

Species Richness

We calculated bird, butterfly, and plant species richness in each meadow as the total number of species encountered across all sampling dates. Visual estimations of species-accumulation curves suggested that the majority of the species pool was sampled for each taxon in each meadow. We used Spearman rank correlations (Conover 1980) to test for cross-taxon species-richness correlations. Analyses performed with different species-richness estimators and alpha-diversity indices (e.g., Shannon index) did not alter general conclusions.

Community Similarity

We used the total abundance of each species encountered over all sample dates in each meadow to calculate Bray-Curtis similarity between each pair of meadows within each study area for each of the three taxonomic groups. We used Bray-Curtis similarity because it has many properties amenable to ecological data, including independence from scale of measurement and from joint absences (Clarke 1993; Clarke & Warwick 1994). We fourth-root-transformed raw abundance values to standardize abundance between taxa.

We summarized Bray-Curtis similarities between all pair-wise combinations of meadows in each study area as a matrix for each taxon separately, and we used Mantel tests to test for cross-taxon correlations between the similarity matrices (Legendre & Legendre 1998). The Mantel test is a multivariate measure that evaluates the null hypothesis of no relationship between two similarity matrices. It is a preferable alternative to simple Pearson correlations because it circumvents the problem of pseudoreplication by addressing partial dependence between the cells of similarity matrices (McCune & Mefford 1997; Legendre & Legendre 1998). We performed partial Mantel correlations to test for possible confounding effects of geographic distance between sites on cross-taxon congruence patterns. Partitioning out the effect of geographic distance did not alter general conclusions. All Mantel tests were performed with the R-Package statistical software (Legendre & Vaudor 1991), and significance was assessed with a Monte-Carlo procedure with 999 permutations.

Results

Cross-Taxon Congruence of Species Richness

Patterns of cross-taxon species richness were highly variable among taxa and study sites (Table 1). Butterfly and plant richness were significantly positively correlated in the Tetons (Rho = 0.478, $p = 0.015$) but not in the Gallatins ($p > 0.05$). Furthermore, other comparisons between taxa in both study areas were not statistically significant (Table 2; Fig. 1).

Cross-Taxon Congruence of Community Similarity

In contrast, community similarity between all pair-wise comparisons of taxa in both study areas was significantly ($p < 0.05$) positively correlated (Table 2; Fig. 2). Plant

Table 1. Summary statistics for bird, butterfly, and plant species richness[a] in each meadow, and bird, butterfly, and plant community similarity[b] between all pairs of meadows in two study areas within the Greater Yellowstone Ecosystem.

Study area and variable	n	*Mean*	*SD*	*Minimum*	*Maximum*
Gallatins					
bird richness	30 meadows	5.07	2.23	1.00	10.00
butterfly richness	30 meadows	19.83	4.53	8.00	27.00
plant richness	30 meadows	48.56	12.41	20.00	69.00
bird similarity	435 pairs	0.19	0.19	0.00	0.83
butterfly similarity	435 pairs	0.55	0.09	0.22	0.78
plant similarity	435 pairs	0.34	0.16	0.02	0.74
Tetons					
bird richness	25 meadows	7.76	4.32	1.00	16.00
butterfly richness	25 meadows	22.76	4.31	17.00	34.00
plant richness	25 meadows	45.20	9.78	20.00	61.00
bird similarity	300 pairs	0.25	0.20	0.00	0.97
butterfly similarity	300 pairs	0.46	0.13	0.15	0.78
plant similarity	300 pairs	0.27	0.17	0.01	0.81

[a] *Richness is the total number of species recorded in each meadow across all sampling dates.*
[b] *Bray-Curtis similarity.*

Table 2. Cross-taxon correlations among bird, butterfly, and plant species richness[a] in each meadow, and bird, butterfly, and plant community similarity[b] between all pairs of meadows in two study areas within the Greater Yellowstone Ecosystem.

Study area and comparison	*Species-richness correlation[c] (p)*	*Community-similarity correlation[d] (p)*
Gallatins		
bird vs. butterfly	0.000 (0.998)	0.291 (0.001)
bird vs. plant	−0.113 (0.548)	0.371 (0.001)
butterfly vs. plant	0.027 (0.883)	0.474 (0.001)
Tetons		
bird vs. butterfly	−0.007 (0.972)	0.661 (0.001)
bird vs. plant	−0.011 (0.958)	0.673 (0.001)
butterfly vs. plant	0.478 (0.015)	0.768 (0.001)

[a] *Richness is the total number of species recorded in each meadow across all sampling dates.*
[b] *Bray-Curtis similarity.*
[c] *Spearman's rho.*
[d] *Mantel's r calculated using Monte-Carlo permutation tests with 999 permutations.*

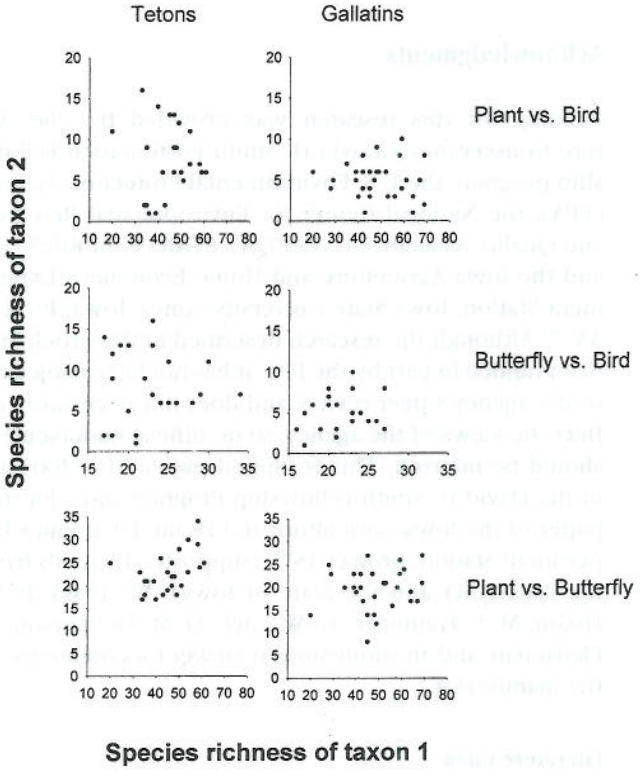

Figure 1. Cross-taxon correlations among bird, butterfly, and plant species richness in 25 meadows (Tetons study area) and 30 meadows (Gallatins study area) within the Greater Yellowstone Ecosystem. The only significant correlation (Spearman rank correlation, p < 0.05) was between plants and butterflies in the Tetons (Table 2). Axes are identical within taxa comparisons, but not across all six graphs.

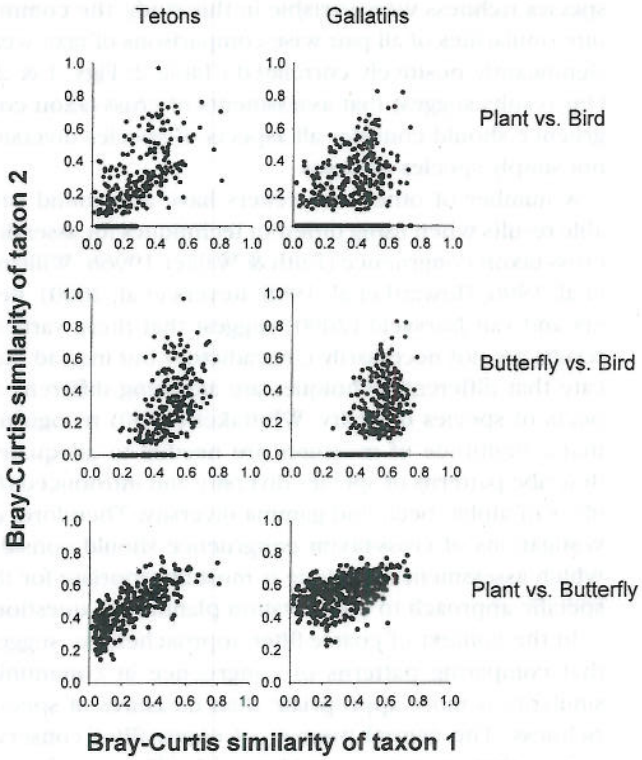

Figure 2. Cross-taxon correlations among bird, butterfly, and plant community similarity (Bray-Curtis similarity) between all pair-wise combinations of meadows (300 in the Tetons and 435 in the Gallatins) in two study areas within the Greater Yellowstone Ecosystem. All correlations were significant (Mantel test, p < 0.05, 999 permutations) (Table 2).

and butterfly similarity showed the strongest correlations in both study areas, whereas correlations involving bird similarity were more variable (Fig. 2). This may be due to the fact that the meadow classes represented a greater range in community similarity for birds than for plants and butterflies (Table 1). In general, Mantel correlation coefficients in the Tetons were higher than in the Gallatins. Nonetheless, for both study areas, sites that had similar community composition for one taxon also had more similar community composition for the other two taxa than expected by chance.

Discussion

Our results concur with the growing body of evidence suggesting that the correlation of species richness between pairs of taxa is highly variable both geographically and taxonomically. Our results also suggest, however, that incongruence of species richness among taxa does not necessarily discount the identification of surrogates for overall biodiversity. Although cross-taxon patterns of

species richness were variable in this study, the community similarities of all pair-wise comparisons of taxa were significantly positively correlated (Table 2; Figs. 1 & 2). Our results suggest that assessments of cross-taxon congruence should consider all aspects of species diversity, not simply species richness.

A number of other researchers have also found variable results when using different techniques for assessing cross-taxon congruence (Faith & Walker 1996*b*; Williams et al. 1996; Howard et al. 1998; Reyers et al. 2000). Reyers and van Jaarsveld (2000) suggest that these variable results are not necessarily contradictory but instead indicate that different techniques are assessing different aspects of species diversity. Whittaker (1960) recognized that a multitude of measures are needed to adequately describe patterns of species diversity and introduced the ideas of alpha, beta, and gamma diversity. Therefore, investigations of cross-taxon congruence should consider which assessment technique is most appropriate for the specific approach to conservation planning in question.

In the context of coarse-filter approaches, we suggest that comparing patterns of congruence in community similarity is more appropriate than measures of species richness. The central premise of coarse-filter conservation is that species assemblages of different taxa will be distributed in a nonrandom fashion across the landscape (Hunter 2001). Although patterns of species richness in our study were variable, we found that an array of meadow sites chosen to represent community composition for one taxon were representative for the other taxa as well.

The congruency of community similarity in our study likely reflects the hydrologic gradient of the meadows sampled. The community composition of all three taxa in both study areas shifted from hydric willow meadows to xeric sagebrush meadows. Previous research suggests the use of abiotic variables such as hydrology, climate, elevation, and geomorphology as direct surrogates for biodiversity (Develice et al. 1988; Hunter 1988; Belbin 1993; Faith & Walker 1996*a*, 1996*b*; Burnett et al. 1998; Nichols et al. 1998; Chase et al. 2000). Although it is unclear whether the results of our study can be generalized to systems with a greater complexity of factors affecting community composition, our results suggest that abiotic approaches to conservation planning may be tenable.

Cross-taxon congruence in community similarity was higher in the Tetons than in the Gallatins, and the overall representation of community variation of the three taxa was not identical. The hydrologic gradient represented a greater range in community similarity for birds than for plants or butterflies (Table 1). Despite this geographic and taxonomic variation, however, all patterns of cross-taxon congruency were significantly correlated (Table 2).

Although we partitioned out the effects of geographic distance on cross-taxon congruence patterns, our approach did not address spatial issues directly. Future studies should examine the relationship between species richness and community similarity in a spatially explicit manner. Furthermore, our approach considers patterns of cross-taxon congruency only for coarse-filter conservation. In many cases, coarse-filter conservation needs to be paired with fine-filter conservation that specifically targets rare, endemic, or threatened species. Our analysis did not consider the congruency of overall community similarity with these fine-filter targets.

In practice, no single approach to conservation planning will be sufficient for all projects (Prendergast et al. 1999); therefore, there is no single measure of success for cross-taxon congruency. Additional studies in a variety of ecological systems are necessary to fully evaluate the use of biotic communities and abiotic variables as surrogates for overall biodiversity. Our results demonstrate, however, that these approaches are effective for montane meadow communities within the Greater Yellowstone Ecosystem. Furthermore, we demonstrated that measures of community similarity and not simple species richness should be used as the measure of surrogacy success in future studies of coarse-filter conservation strategies.

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