How taxonomic diversity, community structure, and sample size determine the reliability of higher taxon surrogates

THOMAS M. NEESON,[1] ITAI VAN RIJN, AND YAEL MANDELIK

Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76100 Israel

Abstract. Ecologists and paleontologists often rely on higher taxon surrogates instead of complete inventories of biological diversity. Despite their intrinsic appeal, the performance of these surrogates has been markedly inconsistent across empirical studies, to the extent that there is no consensus on appropriate taxonomic resolution (i.e., whether genus- or family-level categories are more appropriate) or their overall usefulness. A framework linking the reliability of higher taxon surrogates to biogeographic setting would allow for the interpretation of previously published work and provide some needed guidance regarding the actual application of these surrogates in biodiversity assessments, conservation planning, and the interpretation of the fossil record. We developed a mathematical model to show how taxonomic diversity, community structure, and sampling effort together affect three measures of higher taxon performance: the correlation between species and higher taxon richness, the relative shapes and asymptotes of species and higher taxon accumulation curves, and the efficiency of higher taxa in a complementarity-based reserve-selection algorithm. In our model, higher taxon surrogates performed well in communities in which a few common species were most abundant, and less well in communities with many equally abundant species. Furthermore, higher taxon surrogates performed well when there was a small mean and variance in the number of species per higher taxa. We also show that empirically measured species–higher-taxon correlations can be partly spurious (i.e., a mathematical artifact), except when the species accumulation curve has reached an asymptote. This particular result is of considerable practical interest given the widespread use of rapid survey methods in biodiversity assessment and the application of higher taxon methods to taxa in which species accumulation curves rarely reach an asymptote, e.g., insects.

Key words: biodiversity assessment; complementarity; conservation planning; higher taxa; surrogate; taxonomic sufficiency.

INTRODUCTION

Ecologists and paleontologists rarely obtain complete inventories of all of the species in a community (the "Wallacean shortfall"; Whittaker et al. 2005, Bini et al. 2006). For ecologists, this is due to the high costs of exhaustive field surveys; for paleontologists, the incompleteness of the fossil record. A common alternative is the use of biodiversity indicators or surrogates, which are features of a community, its environment, or the fossil record, that are more easily measured yet highly correlated with species richness, rarity, or composition (Andelman and Fagan 2000, Moreno et al. 2007). Surrogates are often classified into three types: environmental indicators, which are abiotic factors; taxonomic indicators, which are taxa whose distribution is correlated with those of other taxa; and higher taxon indicators, in which the richness of genera or families substitutes for species richness (Moreno et al. 2007).

Higher taxa are particularly appealing as surrogates because of potential savings in taxonomic identification effort (Gaston and Williams 1993, Williams and Gaston 1994) and because, unlike other surrogates, they are directly based on the focal taxa (Mandelik et al. 2007).

Despite their intrinsic appeal, the performance of higher taxon surrogates in conservation biology has been markedly inconsistent across empirical studies; as a result, there is no clear consensus on appropriate taxonomic resolution or the overall usefulness of these surrogates. For example, Gaston and Blackburn (1995) and Brennan et al. (2006) found that family level surrogates contained adequate information about species richness, while Balmford et al. (2000), Grelle (2002), and Villasenor et al. (2005), suggested that genus-level surrogates were more appropriate. Prance (1994) found that even genera did not adequately represent centers of species endemism in the neotropics and so rejected the use of higher taxa altogether. It appears then that higher taxa perform well as surrogates in some applications, but not in others, and that the appropriate level of taxonomic resolution (i.e., family, genus, or neither) also varies among biogeographic settings. Despite the fact that there have been close to 300 case studies examining

the performance of higher taxon surrogates (Bevilacqua et al. 2012), conservation biologists still do not have a mechanistic basis for explaining why the performance of these surrogates appears to be so variable.

A framework linking the performance of higher taxon surrogates to biogeographic or paleogeographic setting would allow for the interpretation of previously published work and provide some needed guidance regarding the actual application of these surrogates in biodiversity assessment, conservation planning, and the interpretation of the fossil record. Such a framework might predict the reliability of higher taxon surrogates (including expectations of error or uncertainty) for a particular community, taxonomy, and sampling program. In the end, an ideal situation would be one in which an ecologist or paleontologist could say a priori whether higher taxon surrogates might be a useful tool for a particular application.

Toward this goal, we investigated how taxonomic diversity, community structure, and sampling effort might affect the performance of higher taxon surrogates. We chose to focus on these three specific factors for several reasons. Taxonomic diversity, which we define as the mean and variance of the number of species per genus, and species per family, has long been suspected to exert a strong influence on the performance of higher taxon methods (Gaston and Williams 1993, Williams and Gaston 1994). We hypothesized that higher taxon surrogates would perform poorly in taxa with a large mean and variance in the species–higher-taxon ratios. Community structure, by which we mean the abundance of each of the species in the community (i.e., the species abundance distribution), determines the relationships between sampling effort and the relative numbers of species and higher taxa observed. Given that higher taxon methods have to date been applied in environments as diverse as soil litter (Rosser and Eggleton 2012), freshwater streams (Heino and Soininen 2007), marine benthos (Bevilacqua et al. 2012), tropical forests (Prance 1994), and many others, we suspected that differences in community structure might explain a large part of the reported variation in higher taxon performance. In particular, we hypothesized that higher taxon surrogates would perform poorly in very diverse communities. Finally, we chose to focus on sampling effort, due to the widespread use of rapid survey methods in biodiversity assessment (Duelli 1997, Jones and Eggleton 2000) and because, for many types of organisms (e.g., insects), the species-accumulation curve rarely reaches an asymptote under typical field survey efforts (Gotelli and Colwell 2001). In focusing on sample size, we hoped to identify any pitfalls associated with rapid or incomplete field surveys.

We began by formulating a mathematical model for generating taxonomies and communities. In our model, taxonomies and communities are generated by drawing samples from probability distributions describing the species abundance distribution, and the genus–family and species–genus distributions. We performed a series of computer simulation experiments using this model to describe how taxonomic diversity, community structure, and sampling effort together influence the performance of higher taxon methods. Specifically, we examined three aspects of the efficiency of the higher taxa approach: (1) the correlations between species richness, genus richness, and family richness, including potential sources of spurious correlation; (2) the relative shapes and asymptotes of species, genus, and family accumulation curves; and (3) the performance of higher taxa in a simple site selection algorithm for the design of a reserve network.

MODEL AND METHODS

Model overview

We organized our model to represent a series of nested spatial scales. At the coarsest scale is the regional species pool, or metacommunity, from which local communities are derived. Local communities are created by taking random samples from the metacommunity. In the course of a simulated higher taxon analysis, each community is characterized by a random sample of n individuals from which inferences about the diversity and structure of the community are made.

We adopted this hierarchical structure in order to model the most common scenario in conservation planning: the estimation of species richness for each site or community in a set of communities that differ in their diversity and structure, but that are still more similar to each other than to communities in, for example, a different biome (i.e., beta diversity lower than gamma diversity). In our model, the species abundance distribution of the metacommunity can be considered a description of the average community of a certain type (e.g., communities of plants in grasslands might have some average species abundance distribution, tropical marine invertebrates another). By varying metacommunity structure (i.e., community type), we used our model to ask how higher taxon methods might perform in and be affected by a particular biogeographic setting.

In our model, the taxonomic relatedness of species does not influence the likelihood of their co-occurrence in a community. All of the species in a metacommunity are members of a single taxonomic tree whose structure is generated at the beginning of each model run. The taxonomic tree itself is an independent data structure containing the taxonomic relationships of some large number of species, genera, and families; some subset of these appear in any one metacommunity. When populating a metacommunity, we selected species from the taxonomic tree independently of their relatedness. This relationship is the simplest among a variety of observed patterns in the co-occurrence, or lack of co-occurrence, of related species (Webb et al. 2002). Finally, although we use the terms "genus" and "family" throughout this paper, our results are generalizable to any three-level hierarchical classification (e.g., subfamilies or tribes).
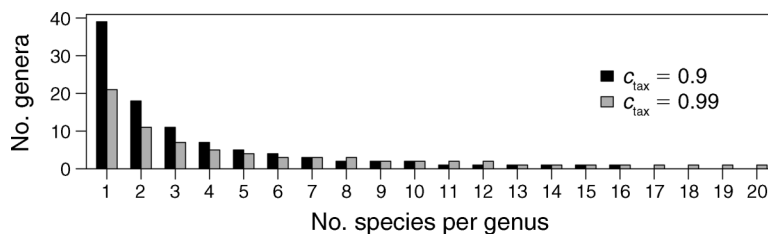
FIG. 1. The "hollow curve" of the species–genus distribution generated using the log-series distribution, for two values of the taxonomic diversity parameter c_{tax}. The larger value of c_{tax} results in fewer monospecific genera, more species-rich genera, and a larger mean and variance in the species : genus ratio.

Taxonomic diversity (c_{tax})

Taxonomic trees in our model were generated with a top-down approach in which we began with a set number of families (for all analyses, 100 families), and then, for each family, generated genera and species according to the log-series distribution (Fisher et al. 1943). We chose to use the log-series distribution on the basis of the evidence provided by Williams (1964), who found a generally excellent fit between the log-series and the taxonomic diversity of insects, birds, fishes, and flowering plants. In the log-series distribution, the proportion of genera that contain exactly y species is given by

$$f(y) = a \frac{c_{tax}{}^{y}}{y} \qquad \text{for } y = 1, 2, 3, \ldots$$

where

$$a = \frac{-1}{\log(1 - c_{tax})}.$$

The distribution gives rise to the classic "hollow curve" shape, in which mono-specific genera are most common, and genera containing n species are always more common than genera with $n + 1$ species. The distribution has a single parameter c_{tax} ($0 \leq c_{tax} \leq 1$); larger values of c_{tax} increase the mean, and also the variance, of the species–genus ratio (Fig. 1). This coupling of the mean and variance is not unique to the log-series distribution, but is instead a general characteristic of biologically realistic "hollow curves" (Williams 1964).

In order to create realistic levels of taxonomic diversity, we fixed the parameter c_{tax} of the genus–family distribution at 0.9, and set the parameter c_{tax} of the species–genus distribution to values ranging from 0.9 (resulting in a taxonomic tree with 1353 species in 100 families) to 0.9999 (resulting in 27 942 species in 100 families; Table 1). This range of taxonomic diversity is well within the bounds of the taxonomic diversity of past empirical studies of higher taxon surrogates. At the low end, for example, Grelle (2002) evaluated higher taxon methods for mammals in the neotropics, where just over 1000 species occur in 50 families (Cole et al. 1994). At the other extreme, Villasenor et al. (2005) used higher taxa as surrogates of plant diversity in Mexico, where 22 000 to 30 000 plant species occur in 248 families (Villasenor 2003, cited in Villasenor et al. 2005). Although our model is not explicitly spatial, model parameterizations that lead to very large taxonomic trees are most reflective of the application of higher taxon methods at large spatial scales or in species-rich taxa.

Community structure (c_{comm})

We also used the log-series distribution to determine the species abundance distribution of the metacommunity. In this application, the density $f(y)$ determines the proportion of species in the metacommunity that contain exactly y individuals. We chose to use the log-series distribution based again on the evidence of Williams (1964), although much support also exists for Preston's (1962) lognormal distribution (for reviews of these and other distributions, see Gotelli and Graves [1996]). Because these two distributions are in most

TABLE 1. Summary statistics for five taxonomic trees generated by fixing taxonomic diversity c_{tax} = 0.9 for the genus–family distribution and by setting c_{tax} of the species–genus distribution to each of the values in the first column.

c_{tax}	No. families	No. genera	No. species	Species/genus	Species/family
0.9	100	358	1353	3.78 (4.28)	13.53 (39.59)
0.95	100	358	2203	6.15 (8.08)	22.03 (72.41)
0.99	100	358	6190	17.29 (23.72)	61.90 (210.20)
0.999	100	358	17 289	48.29 (55.78)	172.90 (504.02)
0.9999	100	358	27 942	78.05 (76.16)	279.40 (711.80)

Note: Values in parentheses are SDs.

TABLE 2. Summary statistics for four communities generated using four values of community structure c_{comm}, the diversity parameter of the log-series distribution.

c_{comm}	No. individuals	No. species	Individuals/species	Commonest species (% of community)
0.95	10 000	3945	2.54 (2.47)	0.36
0.99	10 000	1484	6.74 (9.71)	1.12
0.999	10 000	257	38.91 (8.47)	6.15
0.9999	10 000	37	270.30 (612.85)	32.00

Note: Values in parentheses are SD.

respects nearly identical (Harte 2003), we assumed that either the lognormal or the log-series distribution would have been equally appropriate for this model.

The species abundance distribution also takes the form of a hollow curve in which many species are relatively rare, but a few species are very abundant. For some fixed number of individuals, a single parameter c_{comm} determines both the mean and variance of this distribution. When c_{comm} is small, the mean and variance of the individuals : species ratio is small, the metacommunity contains a large number of species, and the most dominant species constitutes only a small proportion of the total number of individuals. When c_{comm} is large, the variance of the individuals/species ratio is large, and the most dominant species constitutes a large proportion of the metacommunity.

To construct a metacommunity, we first calculated the species abundance distribution, and then assigned specific species to this distribution (i.e., decided which species are to be abundant and which rare) by selecting species at random from the taxonomic tree. An important consequence is that interactions between taxonomic diversity and community structure (e.g., whether the most abundant species came from species-rich or species-poor families) resulted in variability across model runs even when c_{tax} and c_{comm} were held constant. For each combination of taxonomic diversity, community structure, and sample size, we were interested in describing both this variability (i.e., variation in the performance of higher taxon methods across identically parameterized model runs) as well as the average behavior of the model.

In order to create realistic patterns of community structure, we set the parameter c_{comm} to values ranging from 0.95 to 0.9999. For communities of 10 000 individuals, these parameter values resulted in communities in which the most abundant species constituted less than 1% of the total number of individuals (c_{comm} = 0.95), up to communities in which the most abundant species constituted 32% of the community (c_{comm} = 0.9999; Table 2). This range is again biologically realistic. Williams (1964) reported a census of 170 462 birds in which the single most dominant species constituted 52.8% of the individuals. At the other extreme, He et al. (1997) reported a census of 334 077 trees in which the most dominant species accounted for only 2.5% of the individuals.

Experimental framework

We used the R programming language (R Core Development Team 2012) to conduct a series of computer simulation experiments to answer three different research questions.

Question 1: Which factors most influence the species–genus and species–family correlations?—The reliability of higher taxon surrogates is often measured as the correlation between the number of species and the number of higher taxa observed. To quantify how this correlation might be affected by taxonomic diversity, community structure, and sample size, we conducted a full-factorial experiment (Experiment 1) in which we simultaneously varied taxonomic diversity, community structure, and sample size. We used a series of three taxonomic diversity treatments (c_{tax} = 0.99, 0.999, 0.9999). Within each treatment, we ran a series of three community structure treatments (c_{comm} = 0.99, 0.999, 0.9999). From each metacommunity, we then created 30 communities of 10 000 individuals each, and measured the correlation between the number of species and the number of genera and families in random samples ranging in size from 100 to 2500 individuals. To describe variability across identically parameterized model runs, we repeated this process 30 times for each combination of taxonomic diversity, community structure, and sample size.

When analyzing these results, we considered the fact that species–higher-taxon correlations can be partly spurious at small sample sizes (Appendix).

Question 2: Which factors influence the shapes and asymptotes of species and higher taxon accumulation curves?—One appealing feature of higher taxon surrogates is that smaller sample sizes may be needed to describe higher taxon richness, due to the fact that higher taxon accumulation curves necessarily reach an asymptote earlier than species accumulation curves (Gotelli and Colwell 2001). Understanding how taxonomic diversity and community structure might affect the shapes and relatives asymptotes of species and higher taxon accumulation curves is therefore an important step toward understanding where higher taxon methods might offer the greatest advantages over species-based approaches. Even for the types of communities in which asymptotes are rarely reached in practice (e.g., many insects communities [Fisher 1999, Gotelli and Colwell 2001]), this information can provide

important clues about appropriate scaling of accumulation curves.

We used our model to show how taxonomic diversity and community structure might determine the shapes and asymptotes of species, genus, and family accumulation curves (Experiment 2). Specifically, we calculated species, genus, and family rarefaction curves (which are statistically averaged accumulation curves [Gotelli and Colwell 2001]) for all combinations of three levels of taxonomic diversity (c_{tax} = 0.9, 0.95, 0.99) and three levels of community structure (c_{comm} = 0.95, 0.99, 0.999).

Question 3: Which factors influence the performance of higher taxa in a site selection algorithm for the design of a reserve network?—We also tested how taxonomic diversity and community structure might influence the performance of higher taxa in a basic site selection algorithm for the design of a reserve network. Here we consider the common conservation task of identifying a minimum set of reserves (that is, sites or communities) that together contain all species. In an ideal case, the size of the reserve network chosen on the basis of higher taxa would be the same size as the reserve network chosen on the basis of species (Balmford et al. 1996). In practice, the higher taxon network will often be slightly larger, and the difference in the size of the two reserve networks is a measure of the efficiency of higher taxon surrogates.

To select reserve networks, we used a simple algorithm based on site complementarity, i.e., the principle that sites selected should contain species not already present in the reserve network (Justus and Sarkar 2002). Our algorithm is identical to that used by Balmford et al. (1996), except that, in the event of a tie, we chose the site with the greatest species richness; Balmford et al. selected a site at random. The algorithm is as follows:

1) Select the site with the greatest species richness.
2) For each site not yet in the reserve network, tally the number of species at that site that are not yet represented in the reserve network. Choose the site with the greatest species complementarity and add it to the network. In the event of a tie, choose the site with the greatest richness.
3) Repeat step 2 until all sites have been added to the network.

To measure the efficiency of higher taxa in selecting reserve networks, we used the species accumulation index (SAI) of surrogate efficiency (Ferrier and Watson 1997, Ferrier 2002), which is widely used (Rodrigues and Brooks 2007). The calculation of SAI is based on the relative areas under three species accumulation curves: an optimal curve (O) that results from selecting the reserve network using species complementarity, a surrogate curve (S) that results from selecting the reserve network using higher taxon surrogates, and a random curve (R), a statistically averaged accumulation curve that results from selecting sites at random. The value of SAI is calculated as follows:

$$SAI = (S - R)/(O - R).$$

SAI attains its maximum value of one when the surrogate curve exactly aligns with the species curve, indicating perfect surrogacy. When SAI is equal to or less than zero, the surrogate performs no better than random.

We used our model to calculate the effects of taxonomic diversity and community structure on SAI by performing an experiment (Experiment 3) in which we calculated SAI for genus-level surrogates, and SAI for family-level surrogates, for all combinations of three levels of taxonomic diversity (c_{tax} = 0.9, 0.95, 0.99) and three levels of community structure (c_{comm} = 0.99, 0.999, 0.9999). For each model run, we created a set of 30 sites by drawing communities of size 1000 individuals from the metacommunity. We chose here to use small communities in order to ensure high complementarity among sites, i.e., no single site would contain a high proportion of the total species richness.

RESULTS

Question 1

The species–genus and species–family correlations depended in a complex way on community structure and sample size (Experiment 1; Fig. 2). For any combination of taxonomic diversity and sample size, the species–genus and species–family correlations always increased as c_{comm} increased (i.e., as the overall number of species decreased). The species–genus and species–family correlations also tended to decrease slightly with increasing sample size, but this effect was strongest at small sample sizes (i.e., less than 1000 individuals), and was small or absent for combinations of taxonomic diversity and community structure, which led to very high or very low correlations. Taxonomic diversity had little effect on either the species–genus or species–family correlations. Variability in the species–genus correlations across identically parameterized model runs (i.e., the standard deviation of the correlations across runs) was highest in species-rich communities (i.e., small values of c_{comm}), but did not depend on taxonomic diversity nor sample size (Fig. 2). Variability in the species–family correlations depended on neither taxonomic diversity nor community structure.

Question 2

Species, genus, and family accumulation curves differed in their dependence on taxonomic diversity and community structure (Exp. 2; Fig. 3). Overall, the shapes and asymptotes of the genus and family accumulation curves were influenced by both community and taxonomic diversity, while the species accumulation curves were influenced only by community structure. Genus and family accumulation curves saturated most quickly, and reached a lower asymptote, for species-poor communities (i.e., c_{comm} = 0.999) and for highly diverse taxonomies (i.e., c_{tax} = 0.99). Species
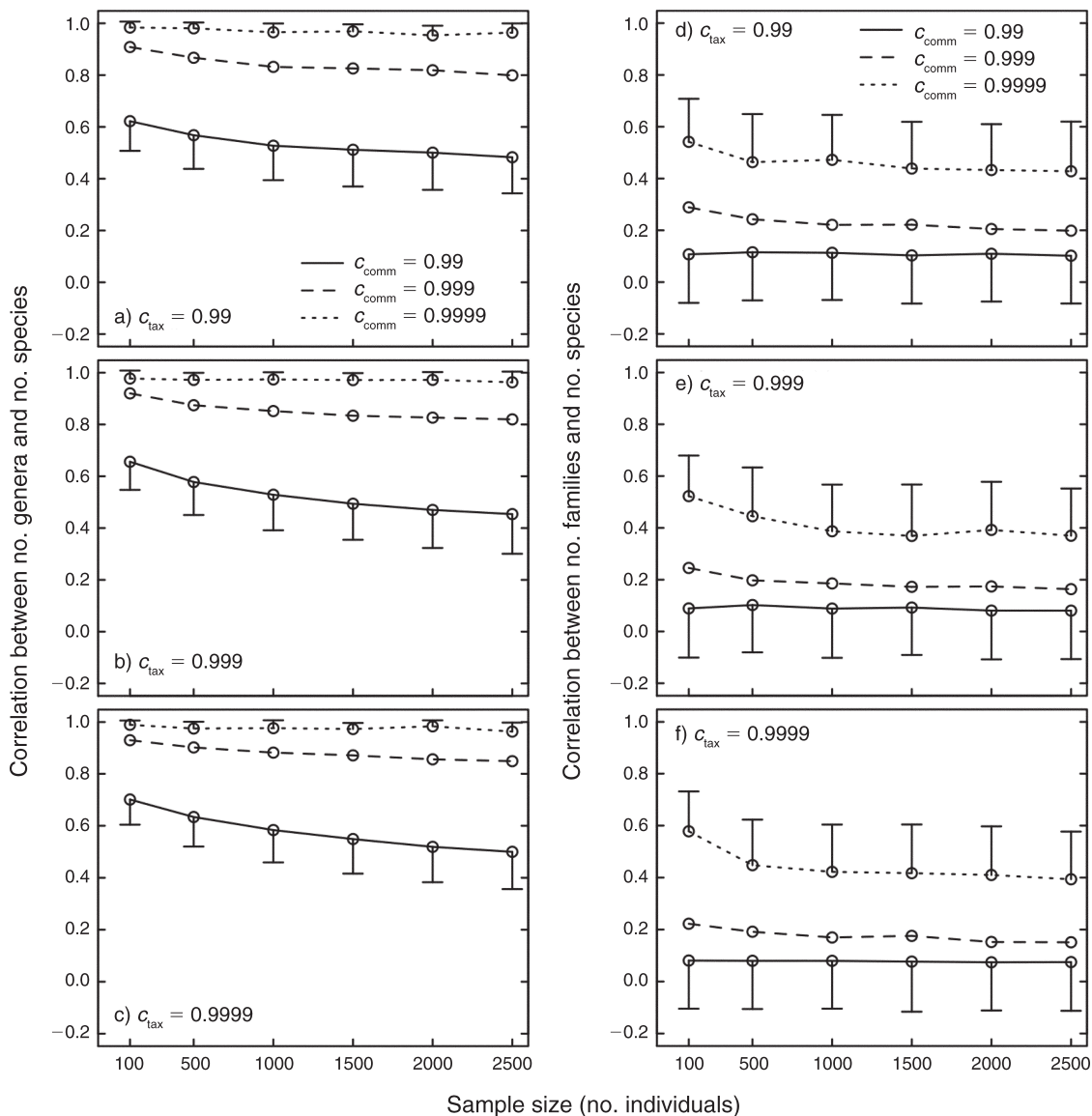
Fig. 2. Effects of taxonomic diversity (values of c_{tax}), community structure (values of c_{comm}), and sample size on the correlation between (a–c) the number of species and the number of genera and (d–f) the number of species and number of families in random samples of 30 communities (Experiment 1). Plotted points show mean values across 100 model runs; error bars give standard deviation across these model runs. Error bars are one-sided for clarity, but standard deviations are two-sided and symmetric. Error bars for $c_{comm} = 0.999$ are omitted for clarity; standard deviations for $c_{comm} = 0.999$ are intermediate between those of $c_{comm} = 0.99$ and $c_{comm} = 0.9999$.

accumulation curves saturated more quickly, and reached a lower asymptote, in species-poor communities, regardless of taxonomic diversity.

Question 3

The performance of higher taxa as the basis for the selection of a reserve network, as measured by SAI, depended on taxonomic diversity, community structure, and also their interaction (Experiment 3; Fig. 4). For both genera and families, SAI was highest (i.e., higher taxon surrogates were most efficient) for communities with the lowest species richness ($c_{comm} = 0.9999$), and for

taxonomies with the lowest species–genus and species–family ratios and variance ($c_{tax} = 0.9$). Due to the interactive effects of taxonomic diversity and community structure on SAI, the effects of community structure on SAI were strongest when taxonomic diversity was lowest. For example, when $c_{tax} = 0.9$, the difference in SAI for family-level surrogates between $c_{comm} = 0.999$ and $c_{comm} = 0.9999$ was 0.26; but when $c_{tax} = 0.99$, this difference was only 0.03. Similarly, the effects of taxonomic diversity on SAI were strongest when species richness was lowest. For example, when $c_{comm} = 0.999$, the difference in SAI for family-level surrogates between
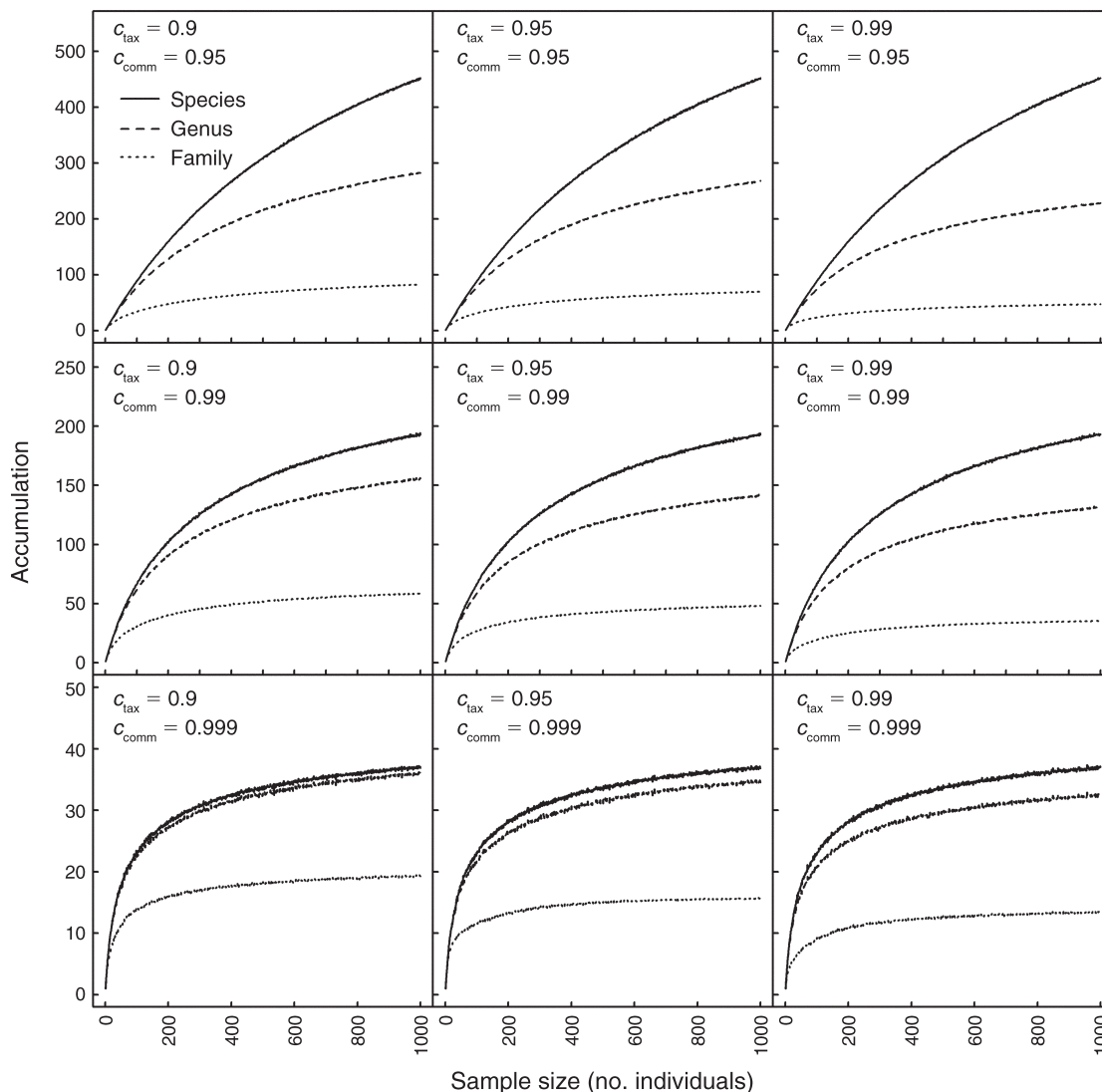
FIG. 3. Species (solid lines), genus (dashed lines), and family (dotted lines) rarefaction curves (number of individuals; Experiment 2) for all combinations of three levels of taxonomic diversity ($c_{tax} = 0.9, 0.95, 0.99$) and three levels of community structure ($c_{comm} = 0.95, 0.99, 0.999$). Confidence intervals are omitted for clarity.

$c_{tax} = 0.95$ and $c_{tax} = 0.99$ was 0.03; but when $c_{comm} = 0.9999$, this difference was 0.17.

DISCUSSION

Our simulation model provides a basis for predicting the performance of higher taxon surrogates in particular biogeographic and taxonomic settings. Model outputs show that higher taxon surrogates should perform best in communities with a shallow species abundance distribution (i.e., communities in which a few common species are most abundant; c_{comm} is large), and perform less well in communities with many equally abundant species (Figs. 2 and 4). We suspect that this is due to the fact that communities with a few abundant species will have lower variability in species–higher-taxon ratios, leading to higher surrogate reliability.

The effects of taxonomic diversity on surrogate reliability differed among experiments. Higher taxon surrogates were most efficient for reserve selection when there was a small mean and variance in the number of species per higher taxa (Experiment 3; Fig. 4). On the other hand, taxonomic diversity had little effect on species–higher-taxon correlations (Experiment 1; Fig. 2). The key difference between Experiment 1 and Experiment 3 was in the range of values of the parameter c_{tax} (0.99 to 0.9999 in Experiment 1 vs. 0.9 to 0.99 in Experiment 3). It appears then that the effect of taxonomic diversity on surrogate reliability is greatest for small values of c_{tax}.

Our results also help to explain why there is such dramatic variation in empirically measured values of the reliability of higher taxon surrogates. Despite using only
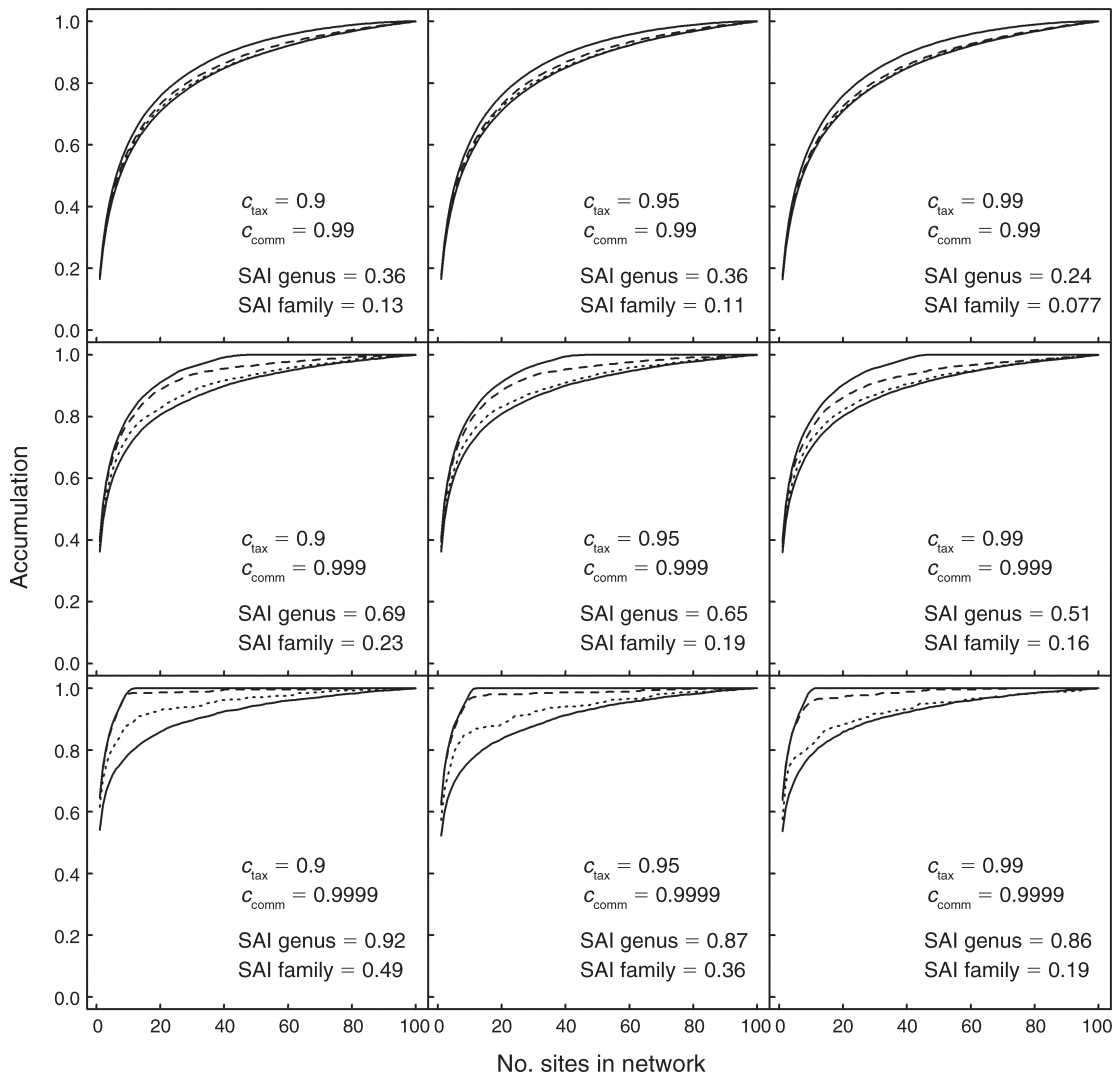
FIG. 4. The accumulation of species (as a proportion of the total; y-axis) in reserve networks of increasing size (x-axis) when sites are added to the network on the basis of species complementarity (top solid line), genus complementarity (dashed line), family complementarity (dotted line), or randomly (bottom solid line). Each panel shows average model output for a particular combination of the parameters c_{tax} and c_{comm} (Experiment 3). The species accumulation index (SAI) value gives the efficiency of each surrogate relative to reserve networks selected on the basis of species complementarity and randomly; larger values of SAI are better.

biologically realistic values of c_{tax} and c_{comm} to parameterize our model, we observed species–genus correlations that ranged from approximately 0.5 to 1.0 (Fig. 2a–c) and species–family correlations that ranged from approximately 0.05 to 0.74 (Fig. 2d–f). Given this variation, it is easy to see why some authors suggest that family richness is an adequate surrogate for species richness (Gaston and Blackburn 1995, Brennan et al. 2006), other authors advocate the use of genera (Balmford et al. 2000, Grelle 2002, Villasenor et al. 2005), and yet other authors reject the use of higher taxon methods altogether (Prance 1994). Our results suggest that, depending on the particular system, each of these three conclusions might be correct. In the actual

application of higher taxon surrogates to real-world problems in ecology and paleontology, the appropriate level of taxonomic resolution (family, genus, or neither) will depend on features of the local community, focal taxonomy, and sample size.

Although species–higher-taxon correlations are conceptually simple and easy to measure, the value of this correlation alone should not be the sole basis for deciding whether higher taxon methods might be useful for a particular conservation application. We showed that these correlations can be partly spurious when sample sizes are small (Appendix). The magnitude of this spurious correlation can be reduced, but not eliminated, if relative sample size (i.e., proportion of

total richness observed) is standardized across sites. Within our model, we suspect that this pattern (of diminishing spurious correlation with increasing sample size) accounts for the declining species–higher-taxon correlations with increasing sample size in Fig. 2.

The existence of these spurious correlations is of considerable practical interest due to the widespread use of rapid survey methods in biodiversity assessment (Duelli 1997, Jones and Eggleton 2000), as well as the application of higher taxon methods to organisms for which accumulation curves rarely saturate under typical field survey efforts (e.g., insects [Fisher 1999, Anderson and Ashe 2000, Gotelli and Colwell 2001]). For these types of organisms, and for data collected via rapid survey methodologies, empirically measured species–higher-taxon correlations will always be partly spurious and so overstate the extent to which sampled higher taxon richness can be used to infer true species richness. Whenever sample sizes are small, biologists should not use the value of an empirically measured correlation as the sole evidence that surrogates have performed well.

We found that higher taxon surrogates were an efficient basis for selecting reserve networks, relative to cross-taxon surrogates (i.e., unrelated taxa) and environmental surrogates (i.e., abiotic factors). This is a more direct measure of the usefulness of higher taxon surrogates than the species–higher-taxon correlation (Balmford et al. 1996). In a review of 575 surrogacy tests from 27 studies, Rodrigues and Brooks (2007) report median SAI values (a measure of surrogate efficiency) of 0.41 for cross-taxon surrogates and 0.08 for environmental surrogates. Higher taxon surrogates in our model always outperformed the median SAI for environmental surrogates, suggesting that higher taxon surrogates may be a more useful type of surrogate. Genus level surrogates in our model usually outperformed the median SAI for cross-taxon surrogates, but family-level surrogates were usually less efficient than cross-taxon surrogates. In other words, genus-level categories may be more useful than cross-taxon surrogates, but family-level categories are usually not.

Applications

Based on our results, ecologists and paleontologists should be able to say a priori whether higher taxon surrogates would be reliable in a particular study system. To do this, researchers should combine available data and expert opinion to estimate where their system lies along the continuum of communities and taxonomies described in Tables 1 and 2. For example, researchers studying birds in Great Britain might assume that those communities, although each slightly different, are generally similar to those described in Williams (1964); in that study, the most abundant species accounted for 52.8% of the individuals (i.e., c_{comm} was very large), suggesting that higher taxon surrogates should perform well. At the other end of the spectrum, researchers studying trees in tropical rainforests might

consider the results of He et al. (1997); in that study, the single most dominant species accounted for only 2.5% of individuals (i.e., c_{comm} was very small), suggesting that higher taxon surrogates might be less reliable in similar communities.

In some cases, higher taxon surrogates are likely to remain in use even when they perform only moderately well. Insects are a case in point. Insect communities are highly diverse (Stork 1988), and species accumulation curves rarely saturate in typical field surveys (Fisher 1999, Gotelli and Colwell 2001). For insects, then, higher taxon surrogates might be less reliable than they are for other, less diverse taxa. Nevertheless, identifying collections of insects to the species level is time consuming and expensive, and taxonomic expertise is limited (Beattle and Oliver 1994, Wilson 2000, Wheeler 2004). Higher taxon surrogates are therefore likely to remain an indispensable tool for insect ecologists, but researchers should have realistic expectations of their reliability.

Literature Cited

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes. Proceedings of the National Academy of Sciences USA 97:5954–5959.

Anderson, R. S., and J. S. Ashe. 2000. Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphilidae, Curculionidae). Biodiversity Conservation 9:617–653.

Balmford, A., A. H. M. Jayasuriya, and M. J. B. Green. 1996. Using higher taxon richness as a surrogate for species richness: II. Local applications. Proceedings of the Royal Society B 263:1571–1575.

Balmford, A., A. J. E. Lyon, and R. M. Lang. 2000. Testing the higher taxon approach to conservation planning in a megadiverse group: the macrofungi. Biological Conservation 93:209–217.

Beattle, A. J., and I. Oliver. 1994. Taxonomic minimalism. Trends in Ecology and Evolution 9:488–490.

Bevilacqua, S., A. Terlizzi, J. Claudet, S. Fraschetti, and F. Boero. 2012. Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. Journal of Applied Ecology 49:357–366.

Bini, L. M., J. A. F. Diniz-Filho, T. F. L. V. B. Rangel, R. P. Bastos, and M. P. Pinto. 2006. Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. Diversity and Distributions 12:475–482.

Brennan, K. E. C., L. Ashby, J. D. Majer, M. L. Moir, and J. M. Koch. 2006. Simplifying assessment of forest management practices to invertebrates: How effective are higher taxon and habitat surrogates for spiders following prescribed burning? Forest Ecology and Management 231:138–154.

Cole, F. R., D. M. Reeder, and D. E. Wilson. 1994. A synopsis of distribution patterns and the conservation of mammal species. Journal of Mammalogy 75:266–276.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agriculture, Ecosystems, and Environment 62:81–91.

Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Systematic Biology 51:331–363.

Ferrier, S., and G. Watson. 1997. An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity. Environment Australia, Canberra, Australian Capital Territory, Australia.

Fisher, B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. Ecological Applications 9:714–731.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12:42–58.

Gaston, K. J., and T. M. Blackburn. 1995. Mapping biodiversity using surrogates of species richness: macro-scales and new world birds. Proceedings of the Royal Society B 262:335–341.

Gaston, K. J., and P. H. Williams. 1993. Mapping the world's species—the higher taxon approach. Biodiversity Letters 1:2–8.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Grelle, C. E. V. 2002. Is higher taxon analysis an useful surrogate of species richness in studies of Neotropical mammal diversity? Biological Conservation 108:101–106.

Harte, J. 2003. Tail of death and resurrection. Nature 424:1006–1007.

He, F., P. Legendre, and J. V. LaFrankie. 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. Journal of Vegetation Science 8:105–114.

Heino, J., and J. Soininen. 2007. Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? Biological Conservation 137:78–89.

Jones, D. T., and P. Eggleton. 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. Journal of Applied Ecology 37:191–203.

Justus, J., and S. Sarkar. 2002. The principle of complementarity in the design of reserve networks to conserve biodiversity: a preliminary history. Journal of Biosciences 42:421–435.

Mandelik, Y., T. Dayan, V. Chikatunov, and V. Kravchenko. 2007. Reliability of a higher taxon approach to richness, rarity, and composition assessments at the local scale. Conservation Biology 21:1506–1515.

Moreno, C. E., E. Pineda, F. Escobar, and G. Sanchez-Rojas. 2007. Shortcuts for biodiversity evaluation: a review of terminology and recommendations for the use of target groups, bioindicators and surrogates. International Journal of Environment and Health 1:71–86.

Prance, G. T. 1994. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. Philosophical Transactions of the Royal Society of London B 345:89–99.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: part I. Ecology 43:182–215.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics 38:713–737.

Rosser, N., and P. Eggleton. 2012. Can higher taxa be used as a surrogate for species-level data in biodiversity surveys of litter/soil insects? Journal of Insect Conservation 16:87–92.

Stork, N. E. 1988. Insect diversity: facts, fiction and speculation. Biological Journal of the Linnean Society 35:321–337.

Villasenor, J. L., G. Ibarra-Manriquez, J. A. Meave, and E. Ortiz. 2005. Higher taxa as surrogates of plant biodiversity in a megadiverse country. Conservation Biology 19:232–238.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Wheeler, Q. D. 2004. Taxonomic triage and the poverty of phylogeny. Philosophical Transactions of the Royal Society B 359:571–583.

Whittaker, R. J., M. B. Araujo, P. Jepson, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation biogeography: assessment and prospect. Diversity and Distributions 11:3–23.

Williams, C. B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, New York, New York, USA.

Williams, P. H., and K. J. Gaston. 1994. Measuring more of biodiversity: Can higher taxon richness predict wholesale species richness? Biological Conservation 67:211–217.

Wilson, E. O. 2000. A global biodiversity map. Science 29:2279.

SUPPLEMENTAL MATERIAL

Appendix

Demonstration and discussion of spurious relationships in empirically measured correlations between species and higher taxon richness (*Ecological Archives* A023-063-A1).