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E-Article

Phylogenetic Measures of Biodiversity

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abstract: We developed a theoretical framework based on phylogenetic comparative methods to integrate phylogeny into three measures of biodiversity: species variability, richness, and evenness. These metrics can be used in conjunction with permutation procedures to test for phylogenetic community structure. As an illustration, we analyzed data on the composition of 58 lake fish communities in Wisconsin. The fish communities showed phylogenetic underdispersion, with communities more likely to contain closely related species. Using information about differences in environmental characteristics among lakes, we demonstrated that phylogenetic underdispersion in fish communities was associated with environmental factors. For example, lakes with low pH were more likely to contain species in the same clade of acid-tolerant species. Our metrics differ from existing metrics used to calculate phylogenetic community structure, such as net relatedness index and Faith's phylogenetic diversity. Our metrics have the advantage of providing an integrated and easy-to-understand package of phylogenetic measures of species variability, richness, and evenness with well-defined statistical properties. Furthermore, they allow the easy evaluation of contributions of individual species to different aspects of the phylogenetic organization of communities. Therefore, these metrics should aid with the incorporation of phylogenetic information into strategies for understanding biodiversity and its conservation.

Keywords: phylogenetic species diversity, phylogenetic community structure, freshwater fish.

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One of the oldest questions in ecology is what processes govern the species composition of communities (Gleason 1926; Clements 1936). Abiotic factors, such as climate, soil type, and water chemistry, may limit which species occur in a community and what densities they achieve, while biotic factors, such as the presence of predators, competitors, or suitable prey, can have similarly important effects. Undoubtedly, both abiotic and biotic factors are acting in all communities, yet their relative importance and the outcomes of their interactions are often difficult to identify. This is in large part due to the difficulty of knowing enough about species and how they interact with the environment and one another to predict community composition.

In the face of this challenge, an approach that has generated growing interest is the incorporation of species phylogenies into community ecology (e.g., Losos 1996; Grandcolas 1998; Webb et al. 2002). Phylogenies can be used to summarize anticipated similarities among species in traits that affect their potential abiotic and biotic interactions within communities. Closely related species might have similar tolerances to similar environmental stressors and thus be more likely to occur within the same community than with less related species (e.g., Webb 2000). Conversely, closely related species might share the same resource requirements, and therefore competition could prevent similar species in the same community (Elton 1946). Thus, identifying phylogenetic patterns in community composition can generate hypotheses about the abiotic and biotic factors structuring communities.

Here, we develop three metrics that incorporate phylogenies into measures of different aspects of community composition: species variability, species richness, and species evenness. Our work builds on the ideas put forth in previous efforts to incorporate species phylogeny into biodiversity metrics (e.g., Williams et al. 1991; Faith 1992; Clarke and Warwick 1998; Webb 2000). The three metrics we present here are derived statistically by considering the value of some unspecified neutral trait shared by all species in a community. As this neutral trait evolves up a phylogenetic tree, speciation occurs, and from this point forward, evolution proceeds independently along each phylogenetic lineage. Our metric of phylogenetic species

variability (PSV) quantifies how phylogenetic relatedness decreases the variance of this hypothetical unselected trait shared by all species in the community. To calculate PSV, only information about the phylogenetic relatedness of species in a community is needed, not information about any particular trait. Nonetheless, framing this measure in the context of a hypothetical neutral trait gives a metric that has not only an intuitive interpretation but also appealing statistical properties. The second metric quantifies phylogenetic species richness (PSR) as the number of species in a community multiplied by the community's PSV. This metric is directly comparable to the traditional metric of species richness but includes phylogenetic relatedness. The third metric measures phylogenetic species evenness (PSE). It is the metric of PSV modified to incorporate relative species abundances. The maximum attainable value of PSE (i.e., 1) occurs only if species abundances are equal and species phylogeny is a star (i.e., a phylogeny that depicts a burst of radiation with each species evolving independently from a common starting point; fig. 1; Felsenstein 1985). Thus, PSE is a measure of both phylogenetic and species evenness.

We derive these three metrics and develop permutation tests that compare the compositions of multiple communities under hypotheses about community assembly. We illustrate the metrics using a data set of lake fish communities. In appendix A, we compare similar metrics to ours: the net relatedness index (NRI) and the nearest taxon index (NTI), developed by Webb and colleagues (Webb 2000; Webb et al. 2002); Faith's phylogenetic diversity (PD; Faith 1992); and McIntosh evenness (*E*; Magurran 1988). A major advantage of our metrics is that they provide a comprehensive set of measures for different aspects of community composition.

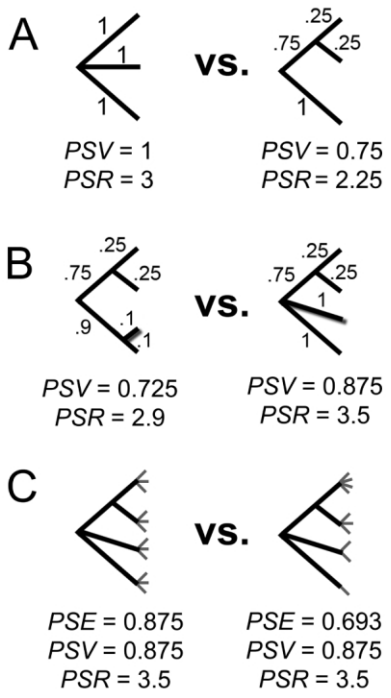

Figure 1: Phylogenies with values for the metrics of phylogenetic species variability (PSV), phylogenetic species richness (PSR), and phylogenetic species evenness (PSE). *A*, PSV and PSR are at their maxima (1 and species richness, respectively) when a community phylogeny is a star. Because two species of the right-hand phylogeny are related, PSV and PSR values are less than the values of the left-hand phylogeny. *B*, When a species is added to a community, the resulting values of PSV and PSR are dependent on the species branch length and where on the phylogeny the species is added. Relative to the right-hand phylogeny of *A*, PSV decreased in the left-hand phylogeny of *B*, while PSV increased in the right-hand phylogeny of *B*. *C*, Our metric PSE essentially grafts each individual of a community onto the tip of the phylogeny of its species with branch lengths of 0. For the left-hand phylogeny, PSE is equal to PSV because all species abundances are equal. When abundances are uneven, PSE is generally less than PSV, as in the right-hand phylogeny. When species are phylogenetically even, as in the left-hand phylogeny of *A*, and have even abundances, PSE = 1.

Methods

Phylogenetic Species Variability

Our measure of phylogenetic species variability summarizes the degree to which species in a community are phylogenetically related. When a community phylogeny is a star, the index equals 1, indicating maximum variability. As relatedness increases, the index approaches 0, indicating reduced variability. To derive the measure, suppose a community contains n species whose evolutionary relationships are given by a known phylogenetic tree (hereafter called the community phylogeny). We assume that branch lengths of the community phylogeny are proportional to the evolutionary divergence between species. Thus, community phylogenies derived from studies of neutral molecular markers are ideal. In the absence of a neutral-based phylogeny, phylogenies based on phenotypic traits or fossil records can be used solely, or in combination with a simple sorting of species by taxonomy, to create trees with arbitrary branch lengths separating taxonomic levels (e.g., Grafen 1989; Webb 2000).

To translate a community phylogeny into the measure of phylogenetic species variability, consider a hypothetical unselected (neutral) continuous-valued trait that evolves randomly and independently among separate phylogenetic lineages. In this Brownian motion model of evolution, branch lengths of the community phylogeny are proportional to the expected variance in the unselected trait value for each species (Felsenstein 1985; Garland et al. 1993). Specifically, let X_i denote the value of neutral trait X for

species i, and suppose that as time progresses, X_i randomly increases or decreases incrementally. The value of X_i at any point in time will be normally distributed, and if time is proportional to branch lengths, then the variance of X_i, v_{ii}, is proportional to the distance from base to tip i of the tree. Similarly, the covariance between the neutral trait values X_i and X_j of species i and j, v_{ij}, is proportional to the length of the shared branch between the lineages. Thus, the community phylogeny defines a multivariate normal distribution with an $n \times n$ covariance matrix $\mathbf{V}$ whose elements, v_{ij}, give the expected evolutionary covariance between species (Martins and Hansen 1997).

Matrix $\mathbf{V}$ can be written $\mathbf{V} = \sigma^2\mathbf{C}$, where σ^2 is a scalar that gives the rate of evolutionary divergence of all n species and $\mathbf{C}$ is a covariance matrix that summarizes the correlation structure of the community phylogeny. The units of matrix $\mathbf{C}$ are arbitrary, and if $\mathbf{V}$ is a tree with contemporaneous tips, then $\mathbf{C}$ may be scaled such that the average value of the diagonal elements is 1, making $\mathbf{C}$ a correlation matrix. This scaling implies that σ^2 gives the average evolutionary divergence of all n species from the base of the tree to the tips (Garland and Ives 2000).

The total phylogenetic species variability of the community can be measured by the variance in neutral trait values X_i among species given by the expectation (app. B)

$$\mathrm{E}\{(X_i - \bar{x})^2\} = \frac{\sigma^2}{n^2}(n\mathrm{tr}\mathbf{C} - \Sigma\mathbf{C}), \tag{1}$$

where $\bar{x} = 1/n\sum_{i=1}^{n} X_i$ is the average of X, tr$\mathbf{C}$ is the trace (sum of diagonal elements) of $\mathbf{C}$, and $\Sigma\mathbf{C}$ denotes the sum of all elements of $\mathbf{C}$. Increasing phylogenetic correlation increases the off-diagonal elements of $\mathbf{C}$ but does not change the diagonal elements of $\mathbf{C}$, so from equation (1), phylogenetic correlation acts to decrease the variance in neutral trait values among species. In the special and unrealistic case in which all species are unrelated, the phylogenetic tree would be a star, with n unarticulated branches radiating from the base of the tree. For this case, $\mathrm{tr}\mathbf{C} = \Sigma\mathbf{C} = n$. To obtain a measure of PSV that scales between 0 and 1, divide equation (1) by its maximum attainable value that would occur under a star phylogeny, $\sigma^2(n - 1)/n$, to give

$$\mathrm{PSV} = \frac{n\mathrm{tr}\mathbf{C} - \Sigma\mathbf{C}}{n(n-1)} = 1 - \bar{c}, \tag{2}$$

where $\bar{c}$ is the average of the off-diagonal elements of $\mathbf{C}$.

Figure 1 illustrates the calculation of PSV for simple community phylogenies. Although scaling $\mathbf{C}$ to have diagonal elements equal to 1 constrains PSV between 0 and 1, $\mathbf{C}$ need not be scaled, in which case PSV will be in units of the community phylogeny and equation (2) will not reduce to $1 - \bar{c}$. Note also that the only information needed to calculate PSV for a given community is the phylogeny of the species it contains. Even though we derived PSV in the context of a hypothetical neutral trait, this was only a tool to conceptually generate the measure. While the metric was derived and can be interpreted in terms of the variance in values of a neutral trait among species in a community, no trait needs to be specified.

The mean and variance of the sampling distribution of PSV can be calculated under the assumption that communities are random draws of species from a species pool. Let PSV_n be the phylogenetic species variability of a community with n species randomly selected from a pool of N species, and let $\mathbf{C}_{\mathrm{pool}}$ be the phylogenetic correlation matrix for the species pool. Because the probability of selecting each species is independent of n, the expected value of the off-diagonal elements of $\mathbf{C}$ for the n species community is the average of the off-diagonal elements of $\mathbf{C}_{\mathrm{pool}}$, $\tilde{c}$. Therefore, one would anticipate from equation (2) that the expectation of PSV_n is $\mathrm{E}\{\mathrm{PSV}_n\} = 1 - \tilde{c}$, which is independent of n; this intuition is confirmed formally in appendix B. Note that this conclusion remains true even if species are selected with unequal probabilities (i.e., have different prevalence among communities), provided these probabilities do not depend on species richness. In this case, $\tilde{c}$ is the average of the off-diagonal elements of $\mathbf{C}_{\mathrm{pool}}$ weighted by the probabilities of including each species pair.

In contrast to the mean of PSV_n, the variance of PSV_n does depend on n. For the case in which species are randomly selected from a species pool, the variance of PSV_n is given by

$$V\{\mathrm{PSV}_n\} = \frac{2}{n(n-1)}[S_{ii} + (n-2)S_{i\tilde{i}} + (n-2)(n-3)S_{\tilde{i}\tilde{i}}], \tag{3}$$

where $S_{ii} = \overline{(c_{ij} - \tilde{c})^2}$ is the sample variance of the off-diagonal elements of $\mathbf{C}_{\mathrm{pool}}$, $S_{i\tilde{i}} = \overline{(c_{ij} - \tilde{c})(c_{ik} - \tilde{c})}$ is the sample covariance for elements in the same row of $\mathbf{C}_{\mathrm{pool}}$, and $S_{\tilde{i}\tilde{i}} = \overline{(c_{ij} - \tilde{c})(c_{lk} - \tilde{c})}$ is the sample covariance for elements in different rows of $\mathbf{C}_{\mathrm{pool}}$ (app. B). If species are not selected with equal probability, a similar expression for the variance of PSV_n still holds, but calculations of S_{ii}, $S_{i\tilde{i}}$, and $S_{\tilde{i}\tilde{i}}$ must be weighted according to the probability of selecting species. This arises for the case in which species are selected according to their prevalence among communities. When species are selected with unequal probabilities, it is easiest to compute $V\{\mathrm{PSV}_n\}$ by numerically simulating community assembly while selecting species with their prescribed probabilities.

For the case when species are selected with equal probabilities, communities containing only two species have

$V\{\text{PSV}_2\} = \overline{(c_{ij} - \tilde{c})^2}$, and $V\{\text{PSV}_n\}$ decreases monotonically to 0 as n approaches N. Finding the greatest variability in PSV_n for small communities is understandable because small communities represent a small and potentially unrepresentative subset of the species pool. In general, equation (3) can be used in statistical tests to obtain confidence intervals in the estimate of PSV for a single community, to calculate confidence intervals for PSV for multiple communities analyzed together, and to correct for heteroscedasticity in the variance of PSV under the assumption that species composition does not depend on species richness.

Phylogenetic Species Richness

The phylogenetic species richness of a community can be measured by multiplying the number of species in the community, n, by their evolutionary relatedness, PSV, to give

$$\text{PSR} = n\text{PSV}. \tag{4}$$

The sampling variance of PSR for a given n is

$$V\{\text{PSR}_n\} = n^2 V\{\text{PSV}_n\}. \tag{5}$$

PSR will be less than or equal to n, with the difference greater for communities with less PSV. PSR is a measure of the richness of a community in which phylogenetically distinct species add relatively more biodiversity than phylogenetically related species. Computation of PSR is illustrated in figure 1.

Phylogenetic Species Evenness

PSV can be modified to incorporate species abundances, thereby giving a metric for phylogenetic species evenness. As before, suppose there is a community of n species with a community phylogeny given by $\mathbf{C}$ but with each species represented by $m_i (i = 1, \ldots, n)$ individuals. Species abundances are included in PSE by envisioning an "individuals phylogeny" in which each individual organism is grafted onto the tip of the community phylogeny corresponding to its species. Thus, the individuals phylogeny has polytomies of m_i individuals with branch length of 0 at each of the n species tips. The individuals phylogeny gives an $m \times m$ covariance matrix $\sigma^2\Phi$, where $\sum_{i=1}^{n} m_i = m$ is the total number of individual organisms in the community. Note that $\text{tr}\Phi = \Sigma m_i c_{ii}$, where c_{ii} is the diagonal elements of $\mathbf{C}$; thus, modifying equation (2) for the individuals phylogeny gives a phylogenetic "individuals" variability of

$$\text{PSV}_{\text{ind}} = \frac{m\text{tr}\Phi - \Sigma\Phi}{m(m-1)} = \frac{m\text{diag}(\mathbf{C})'\mathbf{M} - \mathbf{M}'\mathbf{C}\mathbf{M}}{m(m-1)}, \tag{6}$$

where the prime denotes transpose, $\mathbf{M}$ is an $n \times 1$ column vector containing values of m_i, and diag gives an $n \times 1$ column vector of the main diagonal of $\mathbf{C}$. If $\mathbf{C}$ is scaled so that the average of the diagonal elements is 1, then $\text{tr}\Phi = m$.

To derive PSE, compare a community with a phylogeny given by $\mathbf{C}$ to a community having evolutionarily independent species (i.e., a star phylogeny) with equal species abundances ($m_i = \bar{m}_i$). For this case, $\text{tr}\Phi = n\bar{m}_i = m$ and $\Sigma\Phi = n\bar{m}_i^2$. The ratio of PSV_{ind} calculated using the true phylogeny with true abundances to PSV_{ind} calculated using the star phylogeny with even abundances is

$$\text{PSE} = \frac{m\text{diag}(\mathbf{C})'\mathbf{M} - \mathbf{M}'\mathbf{C}\mathbf{M}}{m^2 - \bar{m}_i m}. \tag{7}$$

This expression is always less than or equal to 1, with 1 occurring when $\mathbf{C}$ is the identity matrix and all species have equal density. The metric PSE has the property that PSE = PSV if all species have the same abundance (fig. 1*C*), and in this case, the extent to which PSE is less than 1 reflects the unevenness arising from the phylogenetic relationships among species rather than their abundances. Thus, we term PSE "evenness" because when a community phylogeny is set to be a star, PSE is simply a measure of the evenness of species abundances and is mathematically related to the E metric (app. A).

The sampling distribution of PSE_m for communities containing m individuals can be calculated from simulations, although this requires numerous assumptions about how species are selected from the species pool. For example, species could be selected at random and the abundance of selected species chosen at random from the observed abundances of this species among communities. Because of the numerous ways in which the sampling distribution of PSE_m can be calculated, we do not pursue this in detail here.

Statistical Inference for Multiple Communities

These three metrics can be used to infer phylogenetic structure for single communities. More often, data will be available for multiple communities, and a researcher will be interested in identifying phylogenetic structure across the collection of communities. For this, the metrics PSV and PSR require species presence/absence data from all communities and the phylogenetic tree for all species (i.e., the species pool phylogeny). The metric PSE additionally requires the abundance of each species in each community. The question we address here is whether, on average, communities represent a nonrandom sampling of species from the species pool phylogeny, thereby indicating that there is phylogenetic signal in community composition.

We describe three null hypotheses that can be used in permutation tests for nonrandom patterns in PSV. The same approach can be used for PSR and PSE. Suppose a researcher has a presence/absence matrix in which rows correspond to communities and columns to species. The first null hypothesis, null 1, randomly shuffles cells within each row, while null 2 randomly shuffles cells within each column. Null 1 preserves the number of species within each community but makes each species have the same expected prevalence. Null 2 preserves the observed prevalence of each species but makes each community have the same expected species richness. Nulls 1 and 2 are identical to SIM3 and SIM2, respectively, in an article by Gotelli (2000) and have been used in other studies of phylogenetic structure (e.g., null 1: Clarke and Warwick 1998; Tofts and Silvertown 2000; Kembel and Hubbell 2006; null 2: Cavender-Bares et al. 2004).

Our permutation test null 3 maintains both column and row totals by using the trial-swap algorithm of Miklos and Podani (2004). The trial-swap algorithm differs from other swap algorithms in that the number of attempts to swap submatrices (i.e., checkerboard units; Stone and Roberts 1990), not the number of successful swaps of submatrices, is set before the algorithm is run (e.g., Stone and Roberts 1990; Gotelli 2000). This difference results in a distribution of randomized presence/absence matrices that can be considered neutral (Miklos and Podani 2004).

The first two permutations address specific hypotheses about the causes of phylogenetic structure. Null 1 assumes that all species have the same expected prevalence in the data. Under this hypothesis, the expected value of PSV in each community, $\overline{\text{PSV}}_{\text{null1}}$, is the PSV value of the entire species pool, PSV_{pool}. Permutation under null 1 tests the hypothesis that $\overline{\text{PSV}}_{\text{obs}} = \text{PSV}_{\text{pool}}$, where $\overline{\text{PSV}}_{\text{obs}}$ is the observed mean PSV among communities. Null 1 will be rejected if communities, on average, have species compositions that do not represent random samples from the species pool. This could be caused by differences in the overall prevalence of species (e.g., species A and B are closely related, and they occur in every community, thereby decreasing PSV in all communities) and/or by communities differing from random draws of the species pool phylogeny in different ways (e.g., each community contains pairs of closely related species, but these pairs are different in each community).

In contrast to null 1, the expected value of PSV under null 2, $\overline{\text{PSV}}_{\text{null2}}$, does not necessarily equal the value of PSV_{pool}. Instead, $\overline{\text{PSV}}_{\text{null2}}$ equals the value of PSV that would be calculated from the supercommunity constructed by combining all communities, with multiple occurrences of a given species among communities incorporated into the phylogenetic tree by grafting each occurrence onto the tip for that species, to form a polytomy with branch lengths of 0. Null 2 will be rejected by nonrandom associations between species among communities (e.g., species A and B are closely related, and they are more likely to occur in the same communities than expected by chance). Null 2 will not be rejected because closely related species are more or less prevalent than expected by chance across all communities, as is the case under null 1. Note that even though permutation under null 2 changes the species richness of communities, because the expected value of PSV is independent of species richness, null 2 will not be rejected by differences in species richness among communities. Note also that null 2 may be rejected while null 1 is not. This pattern indicates that there are nonrandom phylogenetic associations among species within communities, even though $\overline{\text{PSV}}_{\text{obs}}$ is not statistically different from $\overline{\text{PSV}}_{\text{pool}}$.

Finally, null 3 maintains any observed correlation between species richness and prevalence in the null data sets. Unlike nulls 1 and 2, the interpretation of null 3 is complicated because null 3 preserves much of the community structure; therefore, the conclusion drawn when null 3 is rejected is less straightforward. Because swap algorithms like null 3 have received considerable favorable attention for other applications in the literature (e.g., Gotelli 2000) and are used to test for phylogenetic community structure (e.g., Webb 2000; Cavender-Bares et al. 2004; Kembel and Hubbell 2006), our description and use of null 3 with PSV should be taken as a cautionary report. Like null 2, null 3 factors out differences in prevalence among species across all communities, so null 3 will not be rejected solely because closely related species are more or less prevalent. Also like null 2, null 3 will be rejected if closely related species are more or less likely to occur in the same community. The difference between nulls 2 and 3, however, is that null 3 places constraints on the distribution of species among communities according to their prevalence across all communities. Specifically, null 3 requires that communities with more species have a greater probability of containing species with low prevalence (i.e., rare species) than would be predicted by species prevalence alone. To see this, consider a simple case of five communities, two of which contain species A, B, C, D, and E; two of which contain species A and B; and one of which contains species B and C. In permutations under null 3, no two-species permutation community is produced containing species D and/or E because the occurrences of these species are restricted to the two communities containing all five species. Therefore, under null 3, species D and E never occur without all other species, even though together they make up 1/4 (four out of 16) of the species occurrences in the data set.

When using PSV, this constraint of null 3 will reduce its power to detect phylogenetic patterns in the co-occur-

rence of species relative to null 2. For example, imagine that species D and E are closely related species with phylogenetically conserved narrow niches that allow them to exist only in complex habitats. Although these species are rare, they nonetheless coexist more frequently than expected according to prevalence. Unlike null 2, null 3 will not be rejected because of this type of phylogenetic signal. For this reason, we cannot recommend using null 3 with PSV until further work is performed to show the hypothesis null 3 tests. Thus, we prefer null 2 to null 3. We point out, however, that null 2 is particularly well suited for application to PSV because, mathematically, PSV does not depend on the number of species in a community under null 2. Therefore, null 2 will not be rejected because of differences in species richness that are unrelated to phylogeny. This removes the main argument against null 2 in other applications where the metric of interest does depend on species richness (Gotelli 2000).

To test each of the null hypotheses, we permuted the data under each hypothesis to create 1,000 permutation data sets, with 50,000 trial swaps assigned to null 3. For each null data set, we calculated the mean value of PSV across all communities. Statistical significance is obtained by comparing the distribution of the 1,000 null means to the observed mean value; the null hypotheses are rejected at the confidence level α if $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ is less than the $\alpha/2$ or greater than the $1 - \alpha/2$ quantiles of the permutation distributions of null means (i.e., 0.005 and 0.995 for $\alpha = 0.01$). On average, communities contain relatively less related species (i.e., phylogenetic overdispersion) if $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ is greater than found under a null hypothesis, and the converse is true for phylogenetic underdispersion (also termed phylogenetic clustering).

To address how individual species contribute to $\overline{\mathrm{PSV}}_{\mathrm{obs}}$, each species i can be removed in turn and the average PSV among the resulting communities, $\overline{\mathrm{PSV}}_i$, calculated. The effect of species i on $\overline{\mathrm{PSV}}_{\mathrm{obs}}$, $\Delta\overline{\mathrm{PSV}}_i$, was calculated as

$$\Delta\overline{\mathrm{PSV}}_i = \frac{\overline{\mathrm{PSV}}_i - \overline{\mathrm{PSV}}_{\mathrm{obs}}}{\sum_{i=1}^{N} (|\overline{\mathrm{PSV}}_i - \overline{\mathrm{PSV}}_{\mathrm{obs}}|)}. \tag{8}$$

Thus, $\Delta\overline{\mathrm{PSV}}_i$ is expressed as a signed proportion of the total deviation from $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ that occurs when all species are removed from the data set one at a time. In addition, statistical significance of $\overline{\mathrm{PSV}}_i$ under null 2 was determined to see whether phylogenetic structure changed from $\overline{\mathrm{PSV}}_{\mathrm{obs}}$. The permutation test under null 2 was made from a phylogenetic covariance matrix and presence/absence matrix with species i removed.

All Matlab code used to perform these and the following analyses are included as zip files. A list of the downloadable codes is in appendix C.

Example Data Set and Analyses

During the summers of 2001–2004, 58 lakes in the Northern Highland Lakes District of Vilas County, Wisconsin, were sampled for fish species at eight 50-m sections along the lake shoreline. Lake and site selection procedures are described by Marburg et al. (2006). Six minnow traps per site were baited and set for 24 h, and one pass by an electroshocking boat was made after dusk. All captured fish were identified to species and released. Thirty-eight species were found. For our analysis, we aggregated the data from each method of capture and for each site within each lake to form a lake-by-species presence/absence matrix and a lake-by-species abundance matrix.

We determined the phylogenetic relationships among species from published molecular phylogenies in peer-reviewed literature. If no phylogenetic data for species were found, then species were aggregated with congeners or confamilials. We used TreeView, version 1.6.6 (Page 1996), to aggregate the phylogenetic data into a Newick format phylogeny. The Newick format tree was used with the function "newick2phylog" of the library "ade4" in statistics program R (R Project 2005) to give a phylogenetic covariance matrix based on the nodal covariance between species. Because we did not have information on branch lengths, we rescaled the covariance matrix in three different ways and ran all statistical analyses separately for each matrix. First, we standardized the nodal matrix to have diagonal elements equal to 1. Second, we used R with the function "corGrafen" of library "ape" to rescale the phylogeny using Grafen's (1989) method with $\rho = 1$. Third, we constructed a supertree by hand of all species found in the state of Wisconsin (Watermolen and Murrell 2001) and used the submatrix of the 38 sampled species as our species pool phylogeny (see app. C). The first and third methods of phylogeny construction assume that the number of nodes shared between two species is proportional to the evolutionary time before the pair's last common ancestor (see Webb 2000). All statistical conclusions using the three methods were the same, so we present only the results from the third method.

Metrics of phylogenetic composition can be regressed against environmental factors to determine possible underlying causes for variation in phylogenetic structure among communities. The PSV and PSR values for each lake were regressed against variables: lake area, dissolved organic carbon, shoreline development (buildings per kilometer of shoreline), pH, conductivity, and grade (average slope of the shoreline). Marburg et al. (2006) describe calculation of these variables, and all variables except grade have been shown to affect fish populations, species richness, and community structure in lakes of the sampled region (e.g., Rahel 1984; Schindler et al. 2000; Jackson et

al. 2001; Hrabik et al. 2005; Sass et al. 2006). Grade may have impacted the efficiency of our sampling because across lakes, it negatively correlates with species richness (Pearson correlation coefficient, $r = -0.48$) and the natural log of total fish abundance ($r = -0.33$). We first used least squares regressions and weighted PSV and PSR values by the inverse of the expected variances given by equations (3) and (5). Diagnostics from the linear models of both metrics revealed heteroscedasticity of the residuals and nonlinearities in the predicted matrix values. Therefore, we also used weighted linear quantile regression to infer the relationship between the phylogenetic metrics and the environmental variables found in the best-fitting least squares models (Cade and Noon 2003; Cade et al. 2005). Quantile regression is better than least squares regression at finding patterns when data are heterogeneous. An estimated quantile coefficient is the rate of change associated with a specific independent variable over the dependent values less than or equal to τ, the quantile value (Cade and Noon 2003). Quantile regressions were made for values between $\tau = 0.05$ and $\tau = 0.95$ in steps of 0.05. All quantile regressions were calculated with the function "rq" of the library "quantreg" (Koenker and Hallock 2001) in the statistics program R. The metrics PSV and PSR were weighted as above. Significance for each coefficient in each quantile regression was based on confidence intervals (0.10) calculated by inverting the quantile rank score test (Cade and Noon 2003; Cade et al. 2005) with the "summary.rq" function of library "quantreg."

We used nulls 1, 2, and 3 with PSV and nulls 1 and 2 with PSE to test for phylogenetic signal in the fish communities. The metrics PSV, PSR, and PSE were correlated with each other and with species richness. In addition, we tested the hypothesis that lakes with low pH have less PSV than lakes with high pH. We split our data set of 58 lakes into two groups. The low-pH group contained seven lakes with pH values ranging from 5.43 to 6.91, while the high-pH group contained 51 lakes with pH values ranging from 7.09 to 8.98. For each fish community, we computed $V[\mathrm{PSV}_n]$ with numerical simulations using the species prevalence of the group in which the community was assigned. We then calculated standard errors around the mean PSVs of both groups using the individual variances of the estimates for each community.

Results

Phylogenetic Species Variability

Our metric PSV summarizes the degree of relatedness among a group of species. The observed variability in PSV for the fish data set is greater in communities with lower species richness *n*, as expected from equation (3) (fig. 2*D*). However, the mean value of PSV is positively correlated with *n* across communities, even though PSV should be independent of *n* if communities represent random samples from the species pool. This illustrates an unexpected, and possibly biologically significant, relationship between *n* and PSV.

The permutation tests under nulls 1 and 2 indicate strong phylogenetic underdispersion for the fish communities ($\overline{\mathrm{PSV}}_{\mathrm{obs}} = 0.4530$; $\overline{\mathrm{PSV}}_{\mathrm{null1}} = 0.5056$, $P_{\mathrm{null1}} \ll 0.01$; $\overline{\mathrm{PSV}}_{\mathrm{null2}} = 0.4666$, $P_{\mathrm{null2}} \ll 0.01$; fig. 3). The value of $\overline{\mathrm{PSV}}_{\mathrm{null3}}$ is closer to $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ than is either $\overline{\mathrm{PSV}}_{\mathrm{null1}}$ or $\overline{\mathrm{PSV}}_{\mathrm{null2}}$ for the fish communities ($\overline{\mathrm{PSV}}_{\mathrm{null3}} = 0.4583$), which is anticipated because null 3 preserves the most observed structure of the data. Null 3 is not statistically rejected. The fact that $\overline{\mathrm{PSV}}_{\mathrm{null2}}$ is much closer to $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ than is $\overline{\mathrm{PSV}}_{\mathrm{null1}}$ (i.e., $\overline{\mathrm{PSV}}_{\mathrm{null1}} = \mathrm{PSV}_{\mathrm{pool}}$) indicates that most of the variability of fish communities occurs because of differences in prevalence among species; those species that are most prevalent are, on average, related (for an example of the opposite pattern, see Anderson et al. 2004). Even though null 2 factors out these differences among species prevalence, there is still underdispersion in the fish communities, according to this model.

In general, the magnitude of the effect of each species on $\overline{\mathrm{PSV}}_{\mathrm{obs}}$, $|\Delta\overline{\mathrm{PSV}}_i|$, is strongly and positively related to species prevalence (Kendall rank correlation, $k = 0.7552$, $z = 6.6746$, $P < .001$). This result is anticipated by the smaller departure of $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ from $\overline{\mathrm{PSV}}_{\mathrm{null2}}$ versus $\overline{\mathrm{PSV}}_{\mathrm{null1}}$ in the data set. The third most prevalent fish species, bluntnose minnow (*Pimephales notatus*), has the largest effect ($\Delta\overline{\mathrm{PSV}}_{P.\ notatus} = -0.1401$; see app. C). This large effect can be explained by the location of the bluntnose minnow in the species pool phylogeny, which is split at the root into two major clades (see app. C). These clades generally correspond to the order Perciformes and the order Cypriniformes. The species of the major clade containing the bluntnose minnow (i.e., Cypriniformes) are generally much less prevalent than the perciform clade species (see app. C). The $\Delta\overline{\mathrm{PSV}}_i$ values for almost all species of the major clade containing the bluntnose minnow are negative. Thus, adding species from the cypriniform clade increases the PSV of fish communities that generally have perciform species. The bluntnose minnow has a large effect on $\overline{\mathrm{PSV}}_{\mathrm{obs}}$ because it is the most prevalent member of the cypriniform clade.

Finally, we asked whether a particular subset of data was significantly different in PSV than another subset. We divided the fish data set into two groups for lakes above or below pH = 7.0. On average, low-pH lakes were significantly lower in PSV than high-pH lakes ($\overline{\mathrm{PSV}}_{\mathrm{low}} = 0.3634 \pm 0.03$, $\overline{\mathrm{PSV}}_{\mathrm{high}} = 0.4653 \pm 0.005$; fig. 3).

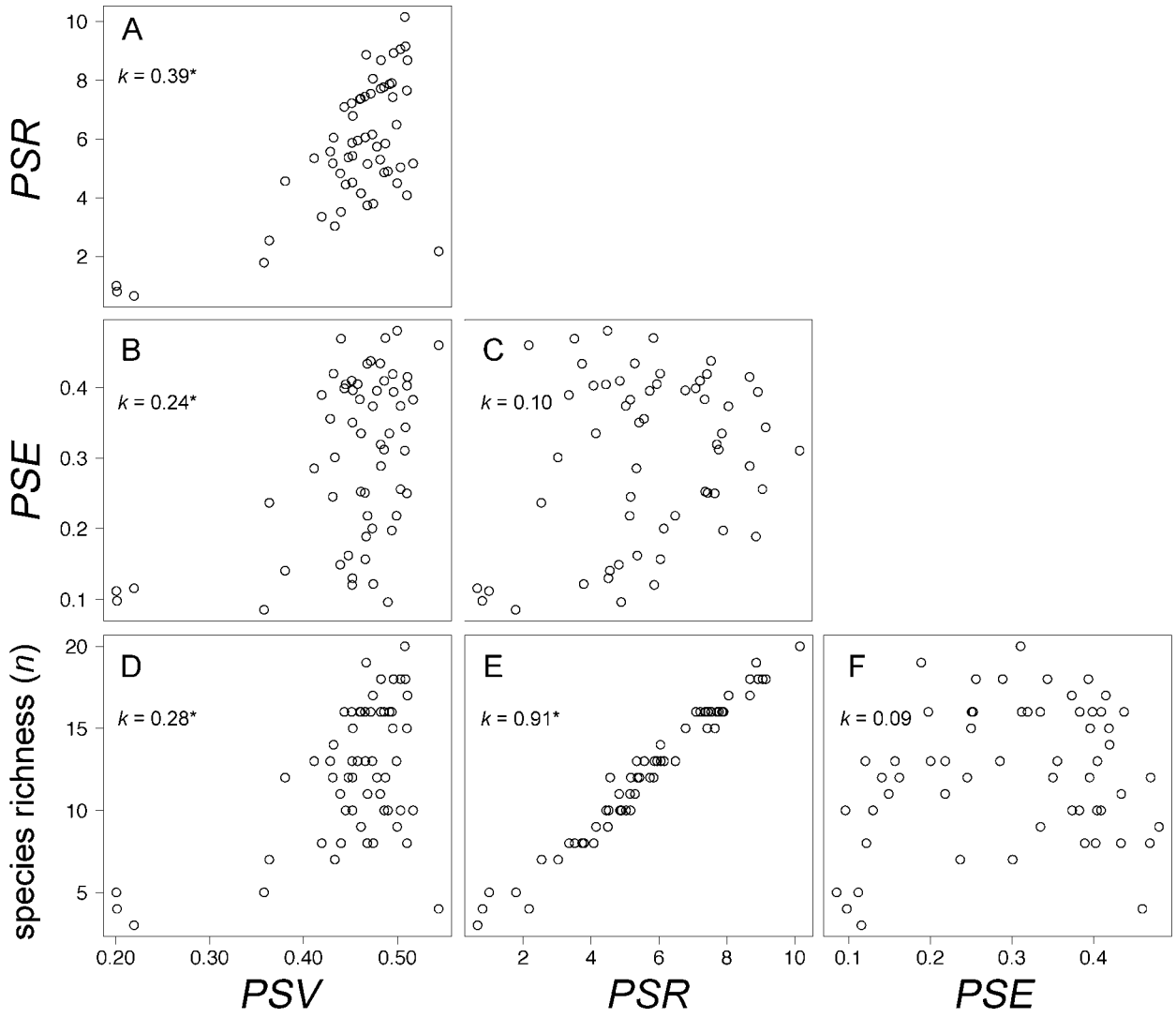

Figure 2: Fish community scatterplots of species richness (n), phylogenetic species variability (PSV), phylogenetic species richness (PSR), and phylogenetic species evenness (PSE). Asterisks indicate nonparametric Kendall rank correlations (k) that are significant at $\alpha = 0.01$.

Phylogenetic Species Richness

Our metric PSR is the product of PSV and species richness, n. Not surprisingly, PSR is strongly correlated with n (fig. 2*E*). Nonetheless, there is residual variability in PSR around n that affects the rankings of communities according to the two measures. These differences are significant if communities are ranked by n versus PSR for conservation priority. To illustrate this, we ranked the 58 fish communities using either PSR or n. Between the two ranking systems, fish communities differ, on average, 2.9 (± 0.40) positions. While these two metrics are simply two different ways of measuring richness, they can give different rankings of communities, and the differences in ranking maybe biologically important.

Phylogenetic Species Evenness

Our metric PSE is related to our metric PSV but incorporates differences in species abundances within communities. For the fish data set, $\overline{\text{PSE}}_{\text{obs}}$ (0.3016) is less than $\overline{\text{PSV}}_{\text{obs}}$ (0.4530) because of unevenness in species abundances within communities. Furthermore, PSE and PSV are correlated, indicating the role of phylogeny in PSE (fig. 2*B*). While PSV is correlated to both PSR and species richness n, PSE is not (fig. 2). Also, note in figure 2 that

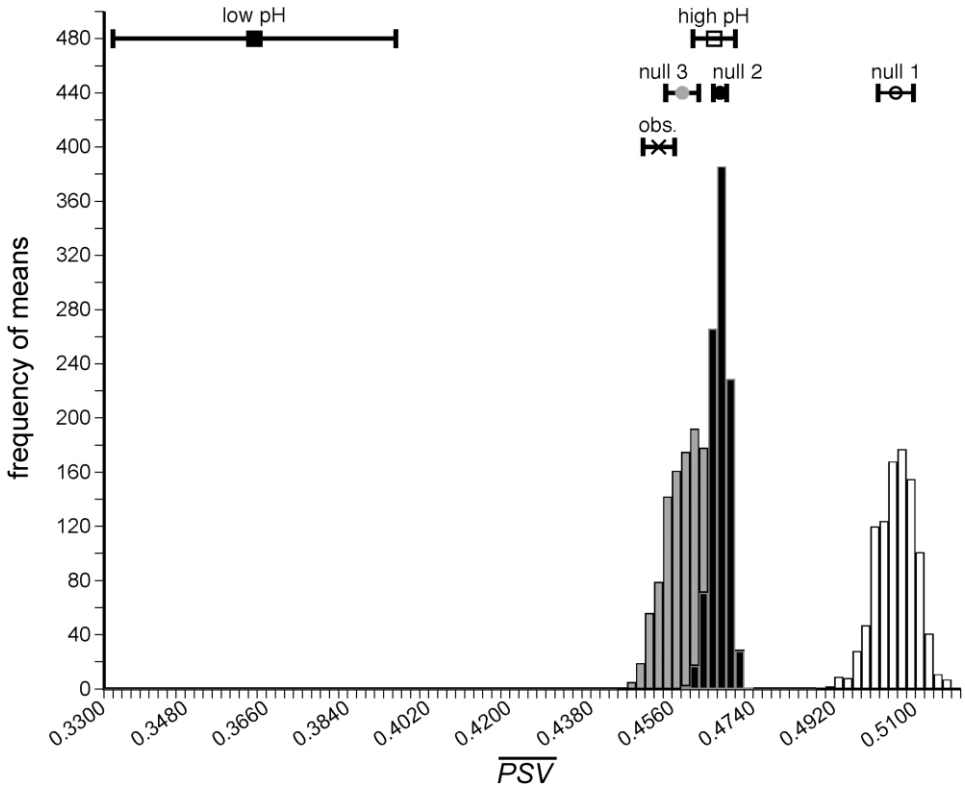

Figure 3: Observed and permuted mean phylogenetic species variability ($\overline{\text{PSV}}$) values for northern Wisconsin lake fish communities. Null distributions are produced from 1,000 permutations of the data set under null models 1 (*white bars*), 2 (*black bars*), and 3 (*gray bars*). Circles directly above histograms are the means of those distributions ± 1 SE. The observed mean PSV value (*cross*) is indicated, with ± 1 SE calculated by combining the variances of each community (eq. [3]). The fish communities are phylogenetically underdispersed according to nulls 1 and 2, but not null 3, because the observed mean is below the null 1 and 2 distributions but within the 0.005 and 0.995 quantiles of the null 3 distribution ($\alpha = 0.01$). Squares are the mean PSV values of the subset analysis, ± 1 SE (see "Methods" for standard error calculation). Low-pH lakes contain species with significantly less phylogenetic species variability than do high-pH lakes.

the variability of PSE correlates little with n, while variability in PSV does. This occurs because PSE values are dominated by common species and are therefore less sensitive than PSV values to the presence/absence of rare species (eq. [3]).

Tests of PSE under null 1 show the same underdispersed structure as found for PSV ($\overline{\text{PSE}}_{\text{null1}} = 0.3473$, $P_{\text{null1}} \ll 0.01$); however, the permutation test does not statistically reject null 2 ($\overline{\text{PSE}}_{\text{null2}} = 0.3153$, $P_{\text{null2}} > 0.01$). This indicates that the observed PSE of the fish communities can primarily be explained by differences in species prevalence. To show this further, we calculated the number of standard deviations the null mean values are away from the observed mean values of PSV and PSE. The observed mean PSE, $\overline{\text{PSE}}_{\text{obs}}$, is about 6 and 2 SD lower than $\overline{\text{PSE}}_{\text{null1}}$ and $\overline{\text{PSE}}_{\text{null2}}$, respectively, while $\overline{\text{PSV}}_{\text{obs}}$ is about 12 and 7 SD lower than $\overline{\text{PSV}}_{\text{null1}}$ and $\overline{\text{PSV}}_{\text{null2}}$. This shows that the strong phylogenetic underdispersion indicated by the null 1 and null 2 analyses of PSV begins to break down once species abundances are incorporated into PSV.

Environmental Regressions

To explain patterns of PSV and PSR in the fish data, we regressed these measures against environmental variables for each lake community. The best-fitting weighted least squares models have lake pH and shoreline grade explaining variation in both PSV and PSR, while conductivity and dissolved organic carbon (DOC) also explain variation in PSR (PSV: pH sum of squares [SS] = 27.09, grade SS = 23.87, residual SS = 136.66, adjusted $R^2 = 0.21$; PSR: pH SS = 331.65, grade SS = 526.27, conductivity SS = 417.74, DOC SS = 279.87, residual SS = 1,582.76, adjusted $R^2 = 0.59$). The coefficients for pH in the PSV and PSR models are positive (PSV: pH coefficient = 0.02; PSR: pH coefficient = 1.08), as are the coefficients for

conductivity and DOC in the PSR model (conductivity coefficient = 0.02, DOC coefficient = 0.22). The coefficients for grade in both models are negative (PSV: grade coefficient = −0.17; PSR: grade coefficient = −9.77). These analyses show that the species present in lakes with high grade and/or low pH are phylogenetically related. On the other hand, as lake conductivity and DOC increase, more phylogenetically diverse groups of species are added to communities.

We also performed weighted linear quantile regression. For PSV, coefficients assigned to shoreline grade are negative and significant across all quantiles, while pH coefficients are positive but significant only up to $\tau = 0.65$. Similarly, pH coefficients of PSR are significant only below $\tau = 0.30$, while coefficients for grade, conductivity, and DOC are significant across all quantiles. The relationship between pH and PSV is wedge shaped; while high-pH lakes all have high PSV, low-pH lakes may have either high or low variability (fig. 4). Thus, the low explanatory power of pH in the least squares regression models is because pH only explains variation in the lower end of the metrics' distributions.

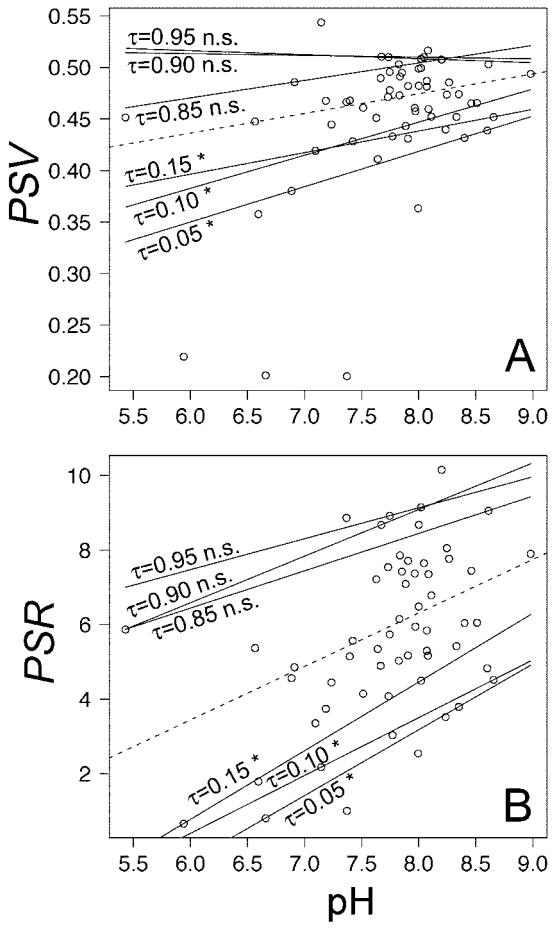

Figure 4: Quantile regressions (*solid lines*) of phylogenetic species variability (PSV; *A*) and phylogenetic species richness (PSR; *B*) of lake fish communities show pH to be significant only at the lower ends of the metrics' distributions. Regressions are weighted by the inverse of the expected variance of PSV and PSR. Asterisks denote a quantile regression pH coefficient to be significant (see "Methods"), while *n.s.* indicates no statistical difference from 0. Dashed lines are weighted least squares regressions.

Discussion

We developed three related metrics of phylogenetic community composition—PSV, PSR, and PSE—designed to integrate phylogenies into ecological studies of biodiversity (Webb et al. 2002). This manuscript builds on the ideas presented in other works that develop metrics to quantify the phylogenetic component of biodiversity (e.g., Faith 1992; Clarke and Warwick 1998; Webb 2000). Our metrics are easy to compute from the phylogenetic tree giving the evolutionary relatedness among species and have an intuitive explanation in terms of covariation in neutral trait values among species. We illustrated simple permutation tests under different null hypotheses that reveal different patterns underlying nonrandom community structure and demonstrated how our metrics can be used in conjunction with environmental covariates to infer environmental processes that may underlie community structure. The strong mathematical relationship among the three metrics gives an integrated package for assessing the effects of phylogeny on different aspects of community composition.

Fish Community Structure

For the fish communities we analyzed, PSV is phylogenetically underdispersed according to null models 1 and 2. This is due both to phylogenetic signal in species prevalence (nulls 1 and 2) and to phylogenetically related species occurring in the same community more commonly than expected from their prevalence (null 2). Weighted least squares regression shows that pH is the strongest environmental driver of PSV. However, the explanatory power of pH is low. The quantile regressions show that pH is most strongly associated with values at the lower end of the PSV and PSR distributions (fig. 4). Our data set has few low-pH lakes, making detection of strong pH effects on fish composition unlikely. Nonetheless, low-pH lakes have significantly lower PSV values than do high-pH lakes (fig. 3).

This result is supported by previous research on the effects of pH on fish community structure (e.g., Rahel and Magnuson 1983; Rahel 1984). The prevalent species of the order Perciformes found in Wisconsin (e.g., yellow perch *Perca flavescens*) have broad pH tolerance, while many

species from the order Cypriniformes (e.g., bluntnose minnow) cannot tolerate low pH (Rahel and Magnuson 1983). Furthermore, pH generally correlates with fish species richness (Rahel and Magnuson 1983), and we found this correlation in our data ($r = 0.43$). Also, in our data set, lakes that have low species richness are generally dominated by perciforms. These two patterns may have contributed to the correlation we found between species richness and PSV, which is not predicted if communities represent random draws from the species pool. In summary, this data set is an example of how environmental filtering may drive phylogenetic underdispersion (Webb et al. 2002; Ackerly 2003; Cavender-Bares et al. 2004), and future studies on how pH affects fish phylogenetic community structure should use data sets containing more lakes with low pH (e.g., Rahel and Magnuson 1983; Rahel 1984).

Null Model Selection and Interpretation

Different null models test different hypotheses, and null models should be selected strategically to elucidate a data set. Null 1 exposes any difference between the observed data and a random sampling of species from the species pool. Therefore, it includes both phylogenetic signal in the prevalence of species (e.g., two closely related species are highly prevalent among communities) and phylogenetic signal in the composition of individual communities (e.g., two closely related species, though both prevalent, never occur in the same community). Null 2 factors out differences in prevalence among species to expose the sole effect of phylogenetic signal in the composition of individual communities. In combination, these null models can indicate whether there is phylogenetic signal at the regional/metacommunity scale (nulls 1 and 2) and at the local community scale (null 2; Leibold et al. 2004). In contrast, null 3 is designed to retain as much structure in the data set as possible, but it does so at the expense of a simple interpretation of the results. For example, null 3 is not rejected in our fish data set, yet this provides little help in explaining the data (see "Methods"). Because the phylogenetic hypothesis that null 3 tests cannot currently be interpreted, we advise caution when using null 3 with our metrics to test for phylogenetic signal in community composition. We also recommend more work on all null hypotheses, including swap-algorithm null models such as null 3, used to test for phylogenetic community structure.

Which Index to Use?

All three metrics we developed measure phylogenetic signal in community data; however, deciding which index to use depends on the research question. To measure phylogenetic structure, we recommend using PSV because PSV measures pure phylogenetic signal that is not confounded with species richness and abundance. There is a close mathematical link between PSV and NRI (Webb 2000; Webb et al. 2005), but the two metrics did not draw the same conclusions from the fish data set (i.e., null 2 was not rejected using NRI; app. A). A major difference between PSV and NRI is that computing NRI requires an extra step to standardize its variance across communities and center its mean at 0 using random selections from the species pool based on a hypothesis identical to null 1. In contrast, PSV is standardized against a hypothetical community of species that are unrelated (i.e., a star phylogeny). An important distinction between these metrics is that the standardization of NRI makes it difficult to interpret the results of permutations nulls 1 and 2, which, when used with PSV, test specific hypotheses about the causes of phylogenetic structure. Webb (2000) also proposed the metric NTI to measure the branch tip clustering of a community's species. PSV can be modified to give a metric to measure phylogenetic species clustering of species across the tips of a phylogeny (app. A).

Any research questions that use species richness as a response variable or as a surrogate for biodiversity can also use PSR. For example, PSR can be compared to well-known spatial and temporal relationships of species richness (Rosenzweig 1995; Adler et al. 2005) and can be manipulated in biodiversity/ecosystem functioning experiments (Hooper et al. 2005). Similarly, because PSR is PSV multiplied by species richness, PSV can be used to explain residual variation in existing data sets of the effects of biodiversity on ecosystem functioning. The commonly used metric of conservation biology, Faith's PD (Faith 1992), is related to PSR (app. A). The difference between the metrics is that PSR uses more of the information contained within a phylogeny than does PD, which is only the sum of branch lengths. Furthermore, the relationship between PSR and PSV demonstrates a simple way to integrate what are termed distance- (PSR) and topology- (PSV) based phylogenetic metrics (see Mooers et al. 2005 and references therein). Finally, species evenness is a major aspect of biodiversity (Magurran 1988), and our new measure PSE makes it possible to integrate evenness in species abundances and evenness in species phylogeny.

Conclusion

Biodiversity is not an easy concept to measure. While classic approaches have equated diversity with a combination of richness and evenness (Magurran 1988), this ignores factors that might influence the role or function of species in a community (e.g., Mason et al. 2005). We take the approach that phylogenetic species variability may encap-

sulate broad similarities and differences among species. While phylogenies will not perfectly reflect the relationships among species in physiology, behavior, and ecology that affect species' roles within and impacts on communities, phylogenetic relatedness gives an easily applied surrogate that can be used in initial analyses to understand how communities are structured.

In the literature, there are multiple metrics designed to summarize phylogenetic community composition (e.g., Williams et al. 1991; Faith 1992; Clarke and Warwick 1998; Webb 2000; Shimatani 2001; Barker 2002; Ricotta 2004). Rather than employ unrelated metrics of community composition, we have provided a common framework for integrating phylogenetic information into metrics of species variability, richness, and evenness. Our metrics are easy to apply, and we have shown how they can be used in statistical tests to help identify the underlying causes of phylogenetic patterns in species composition.

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APPENDIX A

Comparison with Existing Metrics

Phylogenetic Species Variability

We compared our metric of phylogenetic species variability (PSV) to the net relatedness index (NRI), an index developed to reveal nonrandom patterns in community phylogenetic structure (Webb 2000),

$$\mathrm{NRI} = -\frac{\bar{d} - \bar{r}}{\mathrm{SD}(r)}, \tag{A1}$$

where $\bar{d}$ is the mean phylogenetic distance between all pairs of species in a community of n species and $\bar{r}$ and $\mathrm{SD}(r)$ are the mean and standard deviation, respectively, of pairwise phylogenetic distances calculated numerically by randomly drawing n species multiple times from the species pool phylogeny (Webb et al. 2002, 2005). The $\bar{r}$ and $\mathrm{SD}(r)$ are calculated under the same assumption as null 1 in our permutation tests (see "Statistical Inference for Multiple Communities"). Because $\bar{d} = 2(1 - \bar{c}) = 2\mathrm{PSV}$ (assuming the average of diagonal elements of **C** is 1), NRI and PSV are closely related (see eq. [2]). However, we derived PSV by standardizing against a star phylogeny (rather than $\bar{r}$ and $\mathrm{SD}(r)$ as for NRI), and therefore reference to a species pool is not required. Thus, rather than numerically standardizing PSV to have a mean of 0 and 1 SD, like NRI, we instead derived its sampling properties explicitly so that they may be incorporated into any statistical tests.

To compare PSV and NRI, we correlated their values for the fish data set and compared the mean observed NRI, $\overline{\mathrm{NRI}}_{\mathrm{obs}}$, to distributions of null means derived under nulls 1 and 2. (Because phylogenetic overdispersion corresponds to larger values of PSV and smaller values of NRI, strong negative correlations imply they give the same results.) NRI is correlated with PSV for the fish data set (Kendall rank correlation, $k = -0.78$, $z = -8.7$, $P < .001$); these correlations are approximate because NRI values differ slightly with each recalculation because of the numerical standardization procedure. For NRI, null 1 shows phylogenetic underdispersion ($\overline{\mathrm{NRI}}_{\mathrm{obs}} = 1.17$, $\overline{\mathrm{NRI}}_{\mathrm{null1}} = -0.003$, $P \ll .01$), but null 2 is not rejected for the fish communities ($\overline{\mathrm{NRI}}_{\mathrm{null2}} = 1.57$, $P > .01$). Therefore, while both NRI and PSV are correlated as expected from their mathematical relationship, they do not give the same descriptions of phylogenetic structure.

Webb (2000) also developed the nearest taxon index (NTI) to measure the branch tip clustering of species of a community,

$$\mathrm{NTI} = -\frac{\bar{t} - \bar{a}}{\mathrm{SD}(a)}, \tag{A2}$$

where $\bar{t}$ is the mean nearest neighbor distance of species on the tips of the community phylogeny and $\bar{a}$ and $\mathrm{SD}(a)$ are the mean and standard deviation, respectively, of pairwise nearest neighbor phylogenetic distances calculated numerically by randomly drawing n species multiple times from the species pool phylogeny. Equation (2) can be modified to give a metric of phylogenetic species clustering, PSC,

$$\mathrm{PSC} = 1 - \frac{\sum_{i=1}^{n} \max(c_{i-})}{n}, \tag{A3}$$

where c_{i-} represents the off-diagonal elements in row i of matrix **C** with the average of the diagonal elements as 1. As PSC increases to 1, species are less related to one another at the tips of the phylogeny. Here, only PSV and NRI are compared.

Phylogenetic Species Richness

As an alternative to our metric of phylogenetic species richness (PSR), the metric phylogenetic diversity (PD) is the sum of all the branch lengths of the community phylogeny (Faith 1992). This metric is calculated from a phylogenetic distance matrix using an algorithm, and consequently there is no simple equation to relate PD to PSR (Barker 2002). The two metrics are similar because both generally increase as species richness n increases across communities. Nonetheless, they differ in detail, with PD being based on the summation of branch lengths and PSR being based on the averaging of pairwise phylogenetic correlation among species (i.e., PSV).

For the fish data, we correlated PSR with PD values calculated from the "pd" function of the program "phylocom" (Webb et al. 2005). PSR and PD were highly correlated ($k = 0.93$, $z = 10.3$, $P < .001$). Despite the correlation, the metrics differed by an average of 4.2 (± 0.44 SE) in the ranking of each community. Thus, they summarize phylogenetic species richness differently.

Phylogenetic Species Evenness

We know of no measure that incorporates both phylogenies and relative species abundances as done by our measure of phylogenetic species evenness (PSE). Nonetheless, PSE is related to McIntosh evenness (E), a nonphylogenetic evenness metric (Magurran 1988):

$$E = \frac{m - \sqrt{\sum_{i=1}^{n} m_i^2}}{m - m/\sqrt{n}}, \tag{A4}$$

where n is species richness, m is the total number of individuals, and m_i is the number of individuals of species i. When the community phylogeny is a star but species differ in abundance,

$$\mathrm{PSE} = \frac{m^2 - \sum_{i=1}^{n} m_i^2}{m^2 - m^2/n}. \tag{A5}$$

This differs from E only in that each term of the equation is squared.

For the fish data set, we correlated the values of E, PSE, and m. McIntosh's E and PSE were strongly correlated ($r = 0.68$, $t = 7.01$, $P < .001$). Thus, PSE depends not only on phylogeny but also on the relative abundance of species. However, E was significantly negatively correlated to the natural logarithm of m ($r = -0.48$, $t = -4.13$, $P < .001$), while PSE was not ($r = -0.17$, $t = -1.30$, $P > .19$). This indicates that large fish communities are less even in species abundances than are small communities, but the individuals in large communities are generally not more or less related to each other than individuals in small communities.

APPENDIX B

Derivation of Phylogenetic Species Variability

The derivation of our metric of phylogenetic species variability (PSV) envisions a hypothetical neutral (unselected) trait shared by all species. While the calculation of PSV does not involve trait values, deriving PSV in this context gives it a concrete, phylogenetic interpretation. Under the assumption of Brownian motion evolution, the distribution of X_i is given by $\mathbf{x} = x_b + \boldsymbol{\varepsilon}$, where $\mathbf{x}$ is a vector containing values of X_i, x_b is the neutral trait value of the common ancestor at the base of the phylogeny, and $\boldsymbol{\varepsilon}$ contains values of ε_i that have a multivariate normal distribution with mean 0 and covariance matrix $\mathrm{E}\{\boldsymbol{\varepsilon}\boldsymbol{\varepsilon}'\} = \sigma^2\mathbf{C}$. The expectation of the sample variance calculated from the values of X_i is

$$\frac{1}{n}\mathrm{E}\{(\mathbf{x} - \bar{x})'(\mathbf{x} - \bar{x})\} =$$

$$\frac{1}{n}\mathrm{E}\{\boldsymbol{\varepsilon}'\boldsymbol{\varepsilon}\} + \frac{2}{n}\mathrm{E}\{(x_\mathrm{b} - \bar{x})\boldsymbol{\varepsilon}\} + \mathrm{E}\{(x_\mathrm{b} - \bar{x})^2\}, \tag{B1}$$

where $\bar{x} = (1/n)\sum_{i=1}^{n} X_i$. The terms in this expression can be expanded as $\mathrm{E}\{\boldsymbol{\varepsilon}'\boldsymbol{\varepsilon}\} = \sigma^2\mathrm{tr}\mathbf{C}$, $\mathrm{E}\{(x_\mathrm{b} - \bar{x})\boldsymbol{\varepsilon}\} = (-1/n)\sigma^2\boldsymbol{\Sigma}\mathbf{C}$, and $\mathrm{E}\{(x_\mathrm{b} - \bar{x})^2\} = (1/n^2)\sigma^2\boldsymbol{\Sigma}\mathbf{C}$. This leads directly to equation (1).

When communities are constructed under the null hypothesis of randomly selecting n species from a pool containing N species, it is possible to obtain expressions for the expectation and variance of PSV_n. For the species pool, let $\tilde{c} = (2/Q)\sum_{i=1}^{N}\sum_{j=i+1}^{N} c_{ij}$ denote the average of the $Q = N(N-1)/2$ off-diagonal elements of $\mathbf{C}_\mathrm{pool}$. The expectation of PSV_n is $\mathrm{E}\{\mathrm{PSV}_n\} = 1 - \mathrm{E}\{(1/q)\sum_{i=1}^{n}\sum_{j=i+1}^{n} c_{ij}\}$, where c_{ij} are the $q = n(n-1)/2$ randomly selected values of c_{ij} that correspond to species in a n species community. There is a total of

$$\binom{N}{n}$$

different communities, and therefore the probability of a given community is

$$p = 1\Big/\binom{N}{n}.$$

Of these,

$$\binom{N-2}{n-2}$$

contain a given pair of species. Therefore,

$$\begin{aligned}\mathrm{E}\left\{\frac{1}{q}\sum_{i=1}^{n}\sum_{j=i+1}^{n}c_{ij}\right\} &= \frac{1}{q}\left(p\sum_{i=1}^{N}\sum_{j=i+1}^{N}c_{ij}\right)\binom{N-2}{n-2}\\ &= \frac{2}{n(n-1)}\left(\sum_{i=1}^{N}\sum_{j=i+1}^{N}c_{ij}\right)\left[\frac{n(n-1)}{N(N-1)}\right] \qquad \text{(B2)}\\ &= \frac{2}{N(N-1)}\left(\sum_{i=1}^{N}\sum_{j=i+1}^{N}c_{ij}\right) = \tilde{c},\end{aligned}$$

and the expression for the expectation of PSV_n follows immediately.

The variance of PSV_n can be calculated in a similar way. Briefly,

$$\begin{aligned}V\{\mathrm{PSV}_n\} &= \mathrm{E}\left\{\left(\frac{1}{q}\sum_{i=1}^{n}\sum_{j=i+1}^{n}c_{ij}-\tilde{c}\right)^2\right\}\\ &= \frac{1}{q^2}\mathrm{E}\left\{\left(\sum_{i=1}^{n}\sum_{j=i+1}^{n}(c_{ij}-\tilde{c})\right)^2\right\}. \qquad \text{(B3)}\end{aligned}$$

Letting $d_{ij} = c_{ij} - \tilde{c}$,

$$\begin{aligned}V\{\mathrm{PSV}_n\} = \frac{p}{q^2}\Bigg[&\binom{N-2}{n-2}\frac{1}{2}\sum_{i=1}^{N}\sum_{j=i+1}^{N}d_{ij}^2\\ &+\binom{N-3}{n-3}\sum_{i=1}^{N}\sum_{j=i+1}^{N}\sum_{k\neq j,\,i}^{N}d_{ij}d_{ik} \qquad \text{(B4)}\\ &+\binom{N-4}{n-4}\sum_{i=1}^{N}\sum_{j=i+1}^{N}\sum_{k\neq j,\,i}^{N}\sum_{l\neq k,\,i}^{N}d_{ij}d_{lk}\Bigg].\end{aligned}$$

Here, the first, second, and third terms count the numbers of communities with the same pair, triplet, and quartet of species, respectively. Thus, for example,

$$\binom{N-3}{n-3}$$

communities contain species 1, 2, and 3, and in the expansion of the term $\{[\sum_{i=1}^{n}\sum_{j=i+1}^{n}(c_{ij}-\tilde{c})]^2\}$ for these communities, the term $d_{12}d_{13}$ occurs twice. These two occurrences of $d_{12}d_{13}$ are counted in the sum $\sum_{i=1}^{N}\sum_{j=i+1}^{N}\sum_{k\neq j,i}^{N}d_{ij}d_{ik}$. Equation (B4) reduces to equation (3).

APPENDIX C

List of Downloadable Files, Including Computer Programs in Matlab

All Matlab code used to perform the analyses, Newick format phylogenies, and species prevalence/effect data is provided in a zip file. A list of the included elements follows.

PSV2nulls.m—Gives phylogenetic species variability (PSV; eq. [2]) and tests for phylogenetic structure with nulls 1 and 2.

PSE2nulls.m—Gives phylogenetic species evenness (PSE; eq. [7]) and tests for phylogenetic structure with nulls 1 and 2.

quantile.m—Used with PSV2nulls.m and PSE2nulls.m to calculate quantiles. Code written by Peter J. Acklam (pjacklam@online.no).

varPSV.m—Calculates the variance of PSV (eq. [3]).

varPSV2.m—Bootstraps the variance of PSV using species prevalence.

non2compcov.m—Standardizes a covariance matrix to have diagonal elements of ones.

sppPSVeffect.m—Gives $\Delta\overline{\mathrm{PSV}_i}$ (eq. [8]) and tests for phylogenetic structure with null 2.

NRI.m—Gives net relatedness index (NRI; eq. [A1]) and tests for phylogenetic structure with nulls 1 and 2.

means.m—Gives mean phylogenetic distances through permutation, used with NRI.m (eq. [A1]).

trialswap.m—Trial swaps a presence/absence matrix using code written by Brice X. Semmens (semmens@u.washington.edu) but modified to produce null 3.

PSVtrialswap.m—Calculates PSV (eq. [2]) and tests for phylogenetic structure using null 3.

fish_spp_pool_newick_phylo.txt—Newick phylogeny of the fish sampled in this study.

WI_fish_newick_phylo.txt—Fish of Wisconsin, Newick phylogeny.

table_of_spp_effects.txt—Table of fish species prevalence and $\Delta\overline{\mathrm{PSV}_i}$ (eq. [8]) value.

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