Phylogenetic Metrics of Community Similarity

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abstract: We derive a new metric of community similarity that takes into account the phylogenetic relatedness among species. This metric, phylogenetic community dissimilarity (PCD), can be partitioned into two components, a nonphylogenetic component that reflects shared species between communities (analogous to Sørensen's similarity metric) and a phylogenetic component that reflects the evolutionary relationships among nonshared species. Therefore, even if a species is not shared between two communities, it will increase the similarity of the two communities if it is phylogenetically related to species in the other community. We illustrate PCD with data on fish and aquatic macrophyte communities from 59 temperate lakes. Dissimilarity between fish communities associated with environmental differences between lakes often has a phylogenetic component, whereas this is not the case for macrophyte communities. With simulations, we then compare PCD with two other metrics of phylogenetic community similarity, Π_{ST} and UniFrac. Of the three metrics, PCD was best at identifying environmental drivers of community dissimilarity, showing lower variability and greater statistical power. Thus, PCD is a statistically powerful metric that separates the effects of environmental drivers on compositional versus phylogenetic components of community structure.

Keywords: environmental gradient, phylogenetic community structure, phylogenetic beta diversity, Sørensen's similarity index, species turnover, UniFrac.

Introduction

Metrics of community similarity (or dissimilarity) measure differences in species composition among communities (Whittaker 1972; Wilson and Shmida 1984; Vellend 2001). By condensing the comparison between communities into a single number, these metrics give a simple tool for identifying possible drivers that lead to species differences among communities. For example, Whittaker (1960) computed the similarity among plant communities across three different soil types, finding that the most dissimilar com-

munities occurred on the most dissimilar soils (quartz diorite and serpentine soils). Therefore, he concluded that soil type is a driver of community composition. A large number of metrics of community similarity have been devised, and these metrics have been used in a large number of diverse studies (Whittaker 1972; Pielou 1977; Wilson and Shmida 1984; Legendre and Legendre 1998).

Metrics of community similarity are of two types, those that measure beta diversity and those that measure species turnover between communities. The distinction is that beta diversity is the overall variability in composition among a collection of communities, whereas species turnover is the pairwise differences between communities (Vellend 2001). Although they are distinct, there is often a close mathematical relationship between the two (Legendre et al. 2005); for example, when comparing only two communities, Whittaker's measure of beta diversity, β_W, is identical to $2 - D_S$, where D_S is Sørensen's similarity index, which measures species turnover (Vellend 2001). In general, metrics of beta diversity become metrics of turnover when applied to pairs of communities, and here we will simply refer to metrics used to compare pairs of communities as similarity metrics (including dissimilarity metrics).

A limitation of traditional metrics of community similarity is that they do not account for the possible similarity among species that are not shared between communities yet might nonetheless share traits through a common ancestry (Warwick and Clarke 1998; Izsak and Price 2001; Graham and Fine 2008). Suppose we were comparing three communities that have no species in common. If communities A and B have numerous congeners in common while sharing no congeners with community C, it is sensible to conclude that communities A and B are more similar. Communities A and B might not share the same species, but they have congeners that likely share similar environmental requirements or experience biotic and abiotic forces in the same way. There are a growing number of metrics to compare communities that use information about phylogenetic relationships among species (Rao 1982;

Warwick and Clarke 1995; Watve and Gangal 1996; Izsak and Price 2001; Pavoine et al. 2004; Lozupone and Knight 2005; Bacaro et al. 2007; Ferrier et al. 2007; Hardy and Senterre 2007; Bryant et al. 2008; Graham and Fine 2008). Most phylogenetic metrics can be fitted into the general "quadratic-entropy" framework established by Rao (1982), in which communities are compared on the basis of any measure of similarity of the species contained (e.g., Pavoine et al. 2004; Hardy and Jost 2008; Villéger and Mouillot 2008).

Metrics of beta diversity that incorporate phylogenetic information were derived independently by Chave et al. (2007) and Hardy and Senterre (2007) from the population genetics metrics F_{ST} and N_{ST}; these methods are examples of the quadratic-entropy framework (Rao 1982) using phylogenetic distance. The metric Π_{ST} (using the notation of Hardy and Senterre 2007) is defined for species presence/absence data. It is based on the average pairwise distance on a phylogenetic tree between species randomly selected from the same community, Δ_S, and that between species randomly selected from any community, Δ_T. The metric Π_{ST} then measures the degree to which Δ_S exceeds Δ_T (see also Hardy and Jost 2008; Villéger and Mouillot 2008). Both Chave et al. (2007) and Hardy and Senterre (2007) apply their metrics to give summary estimates of beta diversity and pairwise estimates of community similarity. In the latter case, the authors compared community similarities with similarities in environmental variables to identify environmental factors correlated with community composition, as did Whittaker (1960) in his analysis of plant communities on different soil types.

A second group of metrics that incorporate phylogenetic information is designed only to measure species turnover (Izsak and Price 2001; Lozupone and Knight 2005; Bacaro and Ricotta 2007; Ferrier et al. 2007; Lozupone et al. 2007; Bryant et al. 2008). These metrics are based on the phylogenetic distance between species in different communities measured by the shared branch lengths of species on their phylogenetic tree. For example, Lozupone and Knight (2005) compute the metric UniFrac as the sum of the branch lengths two communities share on a phylogenetic tree; if, for example, two communities contained no species in common and each community contained separate clades that join only at the base of the joint phylogeny of the species in the two communities, then the community dissimilarity would be maximal because the species from different communities share no phylogenetic branches.

Here, we develop a new metric of phylogenetic community dissimilarity, PCD, for pairwise differences between communities. The PCD metric is derived by asking how much of the variance among species in the values of a hypothetical nonselected trait in one community can be predicted by the known trait values of species in another community. The variance in the trait values among all species in a single community, say, community 1, can be computed from their phylogenetic relationships (Helmus et al. 2007). If the values of the hypothetical trait for species in community 2 were known, then this information may be used to reduce the unexplained trait variance among species in community 1. For example, if community 1 has all species in common with community 2, then knowing the trait values in community 2 will explain all of the trait variance in community 1. On the other hand, if communities 1 and 2 share no species in common, knowing the trait values in community 2 might still reduce the unexplained trait variance in community 1 if community 2 contains species phylogenetically related to species in community 1. The PCD metric is defined so that the greater the variance in community 1 explained by community 2, the more similar are the communities. While both Π_{ST} and UniFrac are based on measuring the branch lengths on the phylogenetic trees of species among communities, PCD is based on computing the variance in a hypothetical trait; these are conceptually distinct approaches, and there is no simple mathematical relationship between PCD and the other two metrics.

The PCD metric has two advantages over previous metrics of community similarity that incorporate phylogenetic information. First, we have designed PCD so that it does not depend on the numbers of species in the two communities. Commonly used metrics of (nonphylogenetic) community similarity, such as Sørensen's index and Jaccard's index (Legendre and Legendre 1998), depend on species richness. For example, in a comparison of communities made up of different combinations from a pool of 100 species, two large communities with close to 100 species are more likely to share species just by chance than two small communities; this causes most metrics of community similarity to indicate that larger communities are more similar. Existing phylogenetic metrics of community similarity, such as UniFrac, also show this dependence on species richness. Second, when phylogenetic information is removed (i.e., when all species among communities are assumed to be phylogenetically independent), PCD is identical to a modification of Sørensen's index that removes the bias caused by community size. Therefore, we partition PCD into a nonphylogenetic component determined solely by the compositional similarity between communities (i.e., which species they have in common) and a phylogenetic component that depends on the phylogenetic relationships of nonshared species. We show here that this refinement helps to interpret the effects of phylogenetic signal in species turnover across communities.

Below, we first derive PCD and apply it to data on the fish and aquatic macrophyte communities of 59 temperate

lakes. We use PCD to identify which of 16 environmental drivers are associated with greater similarity for each set of communities. We then perform a similar set of analyses using two other phylogenetic metrics of community similarity, Π_{ST} and UniFrac; as we show, other common phylogenetic metrics of community similarity are closely related to one or the other of these two metrics. Finally, we compare PCD, Π_{ST}, and UniFrac, using simulations.

Methods

The metric of phylogenetic community dissimilarity, PCD, can be derived by using the conceptual framework of phylogenetic comparative methods (Gotelli and Pyron 1991; Abouheif 1999; Garland and Ives 2000). Our approach builds on that used by Helmus et al. (2007) to derive the metric PSV (phylogenetic species variability), which measures the phylogenetic diversity of species within a community. The PSV metric is derived by considering a hypothetical, nonselected trait that evolves in a Brownian motion fashion up a phylogenetic tree. The PSV metric measures the variance in this hypothetical trait among species. In reality, we are not interested in any particular trait shared by all species within a community. This manner of constructing PSV is abstract, in the sense that once the metric is derived, we do not use any trait information or make any inferences about species traits. Nonetheless, this derivation of PSV around a hypothetical trait leads to a metric of phylogenetic diversity that has useful statistical properties, and we take advantage of these properties to derive PCD.

Under a Brownian motion model of evolution, any phylogenetic tree with n species defines an $n \times n$ covariance matrix whose diagonal elements contain the theoretical variances in trait values for each of the n species and whose off-diagonal elements contain the covariances in trait values between species caused by phylogenetic relatedness. These matrices are constructed by use of the mathematical result that variances in nonselected trait values are proportional to the base-to-tip distance on the phylogenetic tree and that covariances are proportional to the shared branch length between species (Martins and Hansen 1997; Garland and Ives 2000). Suppose communities 1 and 2, with n_1 and n_2 species, have phylogenetic covariance matrices $\mathbf{C}_{11}$ and $\mathbf{C}_{22}$, respectively. An $n_1 \times n_2$ intercommunity covariance matrix, $\mathbf{C}_{12}$, can be defined whose elements c_{ij} give the hypothetical covariance between species i in community 1 and species j in community 2. The covariance matrix for the trait in community 2 that is conditional on the trait values in community 1 is

$$\mathbf{S}_{22} = \mathbf{C}_{22} - \mathbf{C}'_{12}\mathbf{C}_{11}^{-1}\mathbf{C}_{12}, \qquad (1)$$

with the prime denoting a transpose; this relationship comes from the result that the covariance matrix for a conditional multivariate normal distribution is derived from the Schur complement of the unconditional multivariate normal distribution (e.g., Harvey 1989; Martins and Hansen 1997). From this, the PSV for community 2 conditional on information from community 1 is

$$\text{PSV}_{2|1} = \frac{n_2\text{tr}\mathbf{S}_{22} - \Sigma\mathbf{S}_{22}}{n_2(n_2 - 1)}, \qquad (2)$$

where $\text{tr}\mathbf{S}_{22}$ is the trace of $\mathbf{S}_{22}$ (the sum of diagonal elements), and $\Sigma\mathbf{S}_{22}$ is the sum of all elements of $\mathbf{S}_{22}$. The $\text{PSV}_{2|1}$ will always be less than the unconditional PSV of community 2 when community 1 has species that are related to species in community 2.

To derive an overall measure of dissimilarity, we combine the conditional PSVs for both communities (eq. [2]) and standardize these by the unconditional PSVs to give

$$D = \frac{n_1\text{PSV}_{1|2} + n_2\text{PSV}_{2|1}}{n_1\text{PSV}_1 + n_2\text{PSV}_2}. \qquad (3)$$

Here, the PSVs for each community are weighted by the number of species in the community, n_i, because PSV gives the expected variance in a neutral trait for a single randomly selected species. Thus, multiplying PSV by the number of species in a community gives the total neutral trait variance for the community; Helmus et al. (2007) call nPSV "phylogenetic species richness." If two communities contain no species in common and if species from the two communities are phylogenetically unrelated according to the phylogeny used, then $D = 1$. If both communities contain exactly the same species, then all trait variation within community i is explained by variation in community j (i.e., $\mathbf{S}_{ii}$ becomes a zero matrix), and hence $D = 0$.

An appealing property of D is that in the absence of phylogenetic covariance among species, D is identical to 1 minus Sørensen's similarity index, D_S, which equals 1 when communities have no species in common and 0 when their composition is identical. If n_{shared} is the number of species shared by the two communities, then

$$D_S = 1 - \frac{2n_{\text{shared}}}{n_1 + n_2} \qquad (4)$$

(Bacaro et al. 2007). In the absence of phylogenetic covariance among species (i.e., in eq. [1], $\mathbf{C}_{11} = \mathbf{C}_{22} = \mathbf{C}_{12} = \mathbf{I}$, the identity matrix), the measure of dissimilarity D given by equation (3) equals D_S.

A difficulty arises if one were to use D as a measure of

community dissimilarity, because the expectation of D decreases with increasing numbers of species, n_1 and n_2. To remove this bias, we can calculate the expectation of D under the assumption that the n_1 and n_2 species in communities 1 and 2 are selected at random from the species pool,

$$\overline{D}(n_1, n_2, \mathbf{C}_{\text{pool}}) = \frac{n_1\overline{\text{psv}_{i|j}}(n_2) + n_2\overline{\text{psv}_{i|j}}(n_1)}{n_1\text{PSV}_{\text{pool}} + n_2\text{PSV}_{\text{pool}}}, \quad (5)$$

where PSV_{pool} is the unconditional PSV calculated for all N species in the species pool, $\mathbf{C}_{\text{pool}}$ is their phylogenetic covariance matrix, and $\overline{\text{psv}_{i|j}}(n_j)$ is the mean conditional $\text{PSV}_{i|j}$ (eq. [2]) for community i, given the composition of n_j species randomly drawn from the species pool. Note that $\overline{\text{psv}_{i|j}}(n_j)$ is independent of n_i, which greatly aids computations. In our analyses here, we define the species pool as the list of all species in the set of communities that we are analyzing, but the species pool can be defined under any hypothesis of community assembly.

The metric PCD is

$$\text{PCD} = \frac{n_1\text{PSV}_{1|2} + n_2\text{PSV}_{2|1}}{n_1\text{PSV}_1 + n_2\text{PSV}_2} \frac{1}{\overline{D}(n_1, n_2, \mathbf{C}_{\text{pool}})}, \quad (6)$$

which is independent of n_1 and n_2. If species within communities 1 and 2 represent random samples of n_1 and n_2 species from the species pool, then PCD has an expected value of 1; values greater than 1 correspond to communities that are more dissimilar than randomly selected communities, whereas values less than 1 correspond to more similar communities. Because PCD is standardized on the basis of the number of species in the species pool and their phylogenetic relationships, PCD cannot be used to compare among different data sets.

The PCD of two communities is a function of two components: the shared species among communities and the phylogenetic relationships among species that are not shared among communities. We refer to these as the compositional and phylogenetic components, respectively. To measure the compositional component, we use 1 minus Sørensen's index modified to remove its dependence on community size. For n_1 and n_2 species randomly selected from the community pool of size N, the expectation of D_S is

$$\overline{D}_S(n_1, n_2) = 1 - \frac{2n_1n_2}{(n_1 + n_2)N}. \quad (7)$$

Therefore, we define the compositional component of PCD, PCDc, as

$$\text{PCDc} = \frac{D_S}{\overline{D}_S(n_1, n_2)}. \quad (8)$$

If all species in the species pool were phylogenetically unrelated, then PCD = PCDc. The component of PCD that depends on nonshared species, and hence on the phylogeny, can be defined as PCD/PCDc so that

$$\text{PCD} = \text{PCDc} \times \text{PCDp}. \quad (9)$$

We have formulated the decomposition of PCD as the multiplicative combination of PCDc and PCDp so that their values can be interpreted in a way consistent with each other. When PCD = 1, communities are no more or less similar than communities selected at random from the species pool. If PCDp = 1, then PCD = PCDc, so that any departure of community similarities (PCD) from random is due solely to compositional differences between communities (PCDc). Similarly, if PCDc = 1, then any departure of community similarities from random is due solely to the phylogenetic relationships of nonshared species (PCDp). Because the expectations of PCD and PCDc are both 1 when communities are constructed by randomly selecting species, the geometric expectation of PCDp is 1; although the arithmetic expectation of PCDp is not 1, in practice we have found it to be very close to 1.

The behaviors of PCD, PCDc, and PCDp can be illustrated with examples comparing two communities, each containing eight species from a pool of 16 species (fig. 1). In example A, PCD = PCDc = PCDp = 1, which is the expectation if species were randomly selected from the species pool. In this particular example, the compositions are highly structured to give the exact case of PCD = PCDc = PCDp = 1. The "neutral" dissimilarity of this example can be seen in the fact that if the presence/absence of species in both communities were swapped (changing presences to absences and vice versa), the species patterns between communities would remain the same; this symmetry leads to PCD = PCDc = PCDp = 1.

In example B, the communities share four of eight species out of the pool of 16 species, so PCDc = 1. Note that PCDc = 1 whenever four species are shared, regardless of where on the phylogeny the species occur, demonstrating that PCDc does not incorporate any phylogenetic information. However, the nonshared species in the second community (species i, j, m, and n) occur in a clade different from that containing all the species in the first community (species a–h), so there is high phylogenetic dissimilarity caused by the distribution of the nonshared species, leading to PCDp = 1.66. This illustrates the interpretation of PCDp as that part of PCD that depends on the nonshared species' phylogenetic relationships with each other and with the shared species. In example C, the
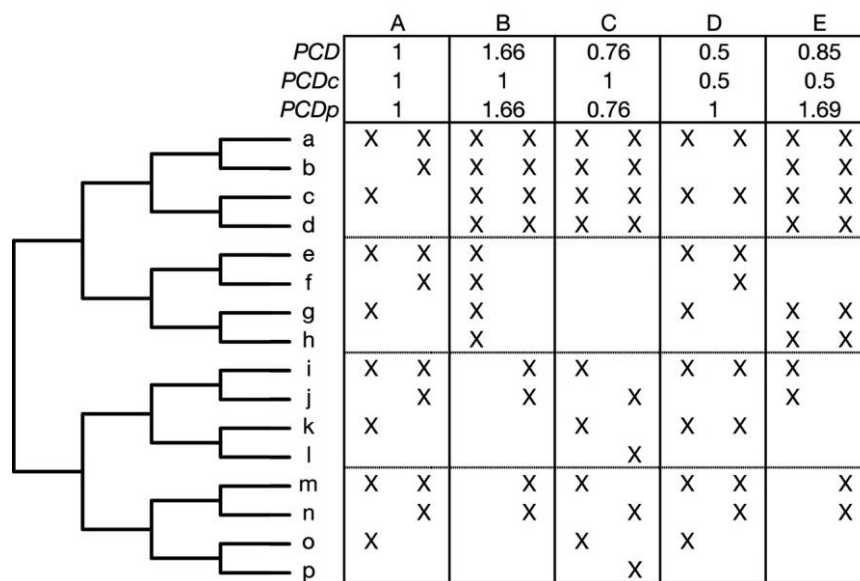
	A		B		C		D		E	
PCD	1		1.66		0.76		0.5		0.85	
PCDc	1		1		1		0.5		0.5	
PCDp	1		1.66		0.76		1		1.69	
a	X	X	X	X	X	X	X	X	X	X
b		X	X	X	X	X			X	X
c	X		X	X	X	X	X	X	X	X
d			X	X	X	X			X	X
e	X	X	X				X	X		
f		X	X					X		
g	X		X				X		X	X
h			X						X	X
i	X	X			X		X	X	X	
j		X				X			X	
k	X				X		X	X		
l						X				
m	X	X			X		X	X		X
n		X				X		X		X
o	X				X		X			
p						X				

Figure 1: Examples of five pairs of communities, each containing eight species from a species pool of 16. Values of PCD, PCDc, and PCDp are given for each pair.

communities share four of eight species, so again PCDc = 1. In contrast to example B, however, the nonshared species are all closely related, so there is low phylogenetic dissimilarity, with PCDp = 0.76.

In example D, the communities share six of eight species from the pool of 16, so on the basis of the shared species, the communities are more similar than expected if species from different communities were distributed randomly with respect to each other. The PCDc value of 0.5 reflects this. The nonshared species (f, g, n, and o) are distributed evenly across the phylogeny; the two nonshared species in the first community (g and o) occur in subclades different from those of the nearest species in the second community (e or f and m or n), while the two nonshared species in the second community (f and n) occur in the same subclades as the nearest species in the first community (e and m). Thus, PCDp = 1.

Finally, in example E, PCDc = 0.5 because there are six shared species. Furthermore, PCDp = 1.69 because the nonshared species in both communities occur in a clade different from that of the shared species and are themselves in different subclades. Because of the opposing effects of PCDc and PCDp, the resulting value of PCD = 0.85 is close to 1. We should point out that the range of possible values of PCDp (and conversely PCDc) depends on the particular value of PCDc (PCDp); to give an extreme example, if all eight species are shared between the two communities, then PCD = PCDc = 0, and PCDp is undefined because there are no nonshared species. This

functional interaction between PCDc and PCDp is expected, however, because the overall metric PCD is bounded.

To determine the effect of environmental drivers on communities, PCD can be compared to the environmental dissimilarity between communities (e.g., the absolute value of the pairwise difference in an environmental variable). For statistical inference, randomization tests can be performed in which the values of environmental variables are permuted among communities many times, with correlations calculated for each permutation data set. The resulting permutation distribution is then compared to the observed correlations to obtain *P* values. In most applications, many environmental variables will be considered, and therefore the *P* values should account for multiple comparisons. To do this, we first created 10,000 data sets by randomly permuting m environmental variables among communities and correlating these to the observed PCD values. Thus, each of the 10,000 permutation data sets produced m permutation correlations, one for each of the m environmental variables. We then tested the significance of the environmental variable with the highest observed correlation in the real data by comparing it with the distribution of the highest correlations from each of the 10,000 permutation sets (regardless of the actual environmental variable); this distribution of the highest correlations from the 10,000 permutation data sets is the distribution expected under the null hypothesis that there is no correlation between PCD values and all m environmental

variables. To test the significance of the second-highest observed correlation, we removed a randomly selected environmental variable from each of the 10,000 permutation data sets, created a null distribution of the highest correlations for the remaining $m - 1$ environmental variables, and then compared this distribution with the second-highest observed correlation. We repeated this procedure for the third-highest observed correlation, and so on. Technically, this procedure assumes that there are no Type I errors (rejecting the null hypothesis when it is true); this assumption is the justification that underlies the random removal of environmental variables to test the next-lower correlation. In practice, the Type I errors are very small, and the *P* values resulting from this procedure are very accurate. Statistical inference for correlations between environmental variables and either PCDc or PCDp can be performed in the same way.

In our permutation test, we permute the environmental variables among communities rather than the species among communities. We do this in order to preserve the phylogenetic structure of the communities while testing the null hypothesis that the composition of communities is independent of the environmental drivers. The alternative approach of permuting species among communities (e.g., Bryant et al. 2008) breaks up phylogenetic structure and leads to a more complicated null hypothesis: that species are distributed among communities independently of both environmental drivers and phylogenetic relationships. Because we are explicitly interested in the effects of environmental drivers, we use the more conservative null hypothesis by leaving the phylogenetic structure of community composition intact. One situation in which permuting species among communities could test a simple null hypothesis is when communities are a priori binned into categories and average similarities between communities in different categories are of interest. For example, Parmentier and Hardy (2009) binned 311 plots into five plant formation categories and then permuted species among communities to test the similarity between groups; the analysis did not use any environmental information. This situation differs from ours, however, because we are testing whether continuously valued environmental drivers are associated with community similarity rather than with differences between two groups. We are interested not in whether phylogenetic patterns exist in community composition (Faith 1992; Webb 2000; Helmus et al. 2007) but instead in what environmental drivers underlie differences among communities, when the differences are measured by composition (PCDc), phylogenetic relationships of nonshared species (PCDp), or both (PCD).

In addition to separating PCD into PCDc and PCDp, we explored two alternative ways that PCD can be used to assess

the compositional and phylogenetic components of community structure. These are described in appendix A.

Example Data Sets

We illustrate the application of PCD by using data on fish and aquatic macrophyte communities in 59 lakes sampled in 2001–2004 in the Northern Highland Lakes District of Vilas County, Wisconsin. These data were collected as part of a larger project that surveyed many variables, such as coarse-woody habitat abundance (Marburg et al. 2006; Sass et al. 2006) and shoreline tree characteristics (Marburg 2006), with the goal of understanding how shoreline residential development affects lake ecology. Lakes were selected to maximize variation in two variables, the degree of shoreline development and lake water conductivity. Conductivity is an indicator for other chemical variables, including pH and phosphorus concentration, and correlates with biological variables such as species richness (Kratz et al. 1997, 2006; Hrabik et al. 2005).

Within each of the 59 lakes, eight 50-m segments of shoreline (sites) were randomly selected, with two sites selected per compass quadrant of each lake (northeast, northwest, southeast, and southwest). Fish sampling consisted of six minnow traps per site set for 24 h, and one pass by an electroshocking boat made after dusk at each site. All captured fish were identified to species and released. It was impossible to launch an electroshocking boat in Little Rock Lake, and therefore we obtained fish community data for this lake from Sass (2004), who sampled Little Rock Lake in 2001–2004 using minnow traps, seining, and angling. The macrophytes in the lakes consisted of emergent, submerged, and floating plants. For macrophyte sampling, at the center of each site a transect was made perpendicular to shore that extended to a depth of 2 m. At every meter along the transect, the macrophyte species present, the substrate composition, and the total percent vegetation cover were recorded in a 0.25-m^2 quadrat. All data are available online at the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) Web site (http://www.lternet.edu/sites/ntl/). All sampling data were aggregated up to the lake scale to produce two presence/absence matrices of 59 lakes × 43 fish and 59 lakes × 64 macrophyte taxa. We use the term "taxa" here because not all fish and macrophytes could be identified to the species level.

We used published phylogenies to construct informal supertrees of our fish and macrophyte taxa. When no phylogenetic data were found, taxa were grouped according to Linnaean taxonomy. The resulting phylogenies were highly resolved, with four polytomies in the fish phylogeny and two in the macrophyte phylogeny. We dated as many nodes in each phylogeny as possible. All dates on the mac-

rophyte phylogeny and most dates on the fish phylogeny were from the TimeTree of Life project (Hedges et al. 2006). Branches and nodes were then adjusted with the *bladj* function of the program Phylocom to be evenly spaced between the dated nodes (Webb et al. 2008*b*). The two phylogenies and references for the dated nodes are given in appendix B.

We constructed a lake × environment data matrix of 16 variables that we hypothesized would correlate with fish and macrophyte community differences across lakes. These variables divide into three groups: lake water chemistry (dissolved organic carbon, dissolved inorganic carbon, alkalinity, conductivity, pH, water color, total phosphorus, and total nitrogen), lake physical characteristics (lake area, lake maximum depth, coarse woody habitat abundance, and benthos substrate diversity), and human disturbance (lake shoreline building density, invasive rusty crayfish abundance, a metric of human shoreline disturbance). Sampling methods are provided on the NTL-LTER Web site (http://www.lternet.edu/sites/ntl/).

Comparison with Other Phylogenetic Metrics

With our fish community data set, we compared PCD with two other metrics, Π_{ST} (Chave et al. 2007; Hardy and Senterre 2007) and unweighted UniFrac (Lozupone and Knight 2005). We considered only these two metrics because other metrics in the literature are similar to UniFrac. In fact, the metric Δ_T of Bacaro et al. (2007) is identical to UniFrac. The metric PhyloSør of Bryant et al. (2008) is identical to the phylogenetic version of the Bray-Curtis similarity metric proposed by Ferrier et al. (2007), and both of these are mathematically so closely related to UniFrac that they will give similar results. We define these five metrics mathematically in appendix C and provide code for computing PCD, Π_{ST}, and UniFrac in the R statistical computing language (R Development Core Team 2008) in the package Picante (Kembel et al. 2010).

It is possible to derive composition-only versions of both Π_{ST} and UniFrac that could be compared to PCDc; this can be done by calculating Π_{ST} and UniFrac with a hypothetical "star" phylogeny (a tree with a single polytomy at the base), so that all species are phylogenetically unrelated (app. C). Nonetheless, because the resulting composition-only versions of Π_{ST} and UniFrac have not previously been investigated, here we confine our comparisons to the overall metrics of community similarity PCD, Π_{ST}, and UniFrac.

We first analyzed the data on fish communities, using Π_{ST} and UniFrac to compare with the analyses using PCD. We then performed a simulation study based on our fish community data, in which we specified the underlying relationship between community composition and a single

environmental driver. Thus, we used the simulations to compare the statistical ability of the metrics of dissimilarity to detect a known environmental driver. We recognize that the relative performance of metrics may depend on the particular structure of the simulation model; to avoid bias in the comparison, we constructed the simulation model to mimic key features of the fish and macrophyte data that we analyzed. We assumed that communities occur along a continuous gradient of environmental driver x and that each species has a unimodal optimal value of x, x_{opt}. The probability that a species occurs in a community decreases according to a Gaussian curve centered on x_{opt} with a standard deviation σ; the smaller the value of σ, the more sensitive each species is to the environmental gradient (fig. 2). We incorporate phylogenetic information by assuming that x_{opt} evolves according to a Brownian motion process up the fish phylogenetic tree. This is illustrated in figure 2*A*, 2*C*, and 2*E* by the red lines for four closely related species that all respond similarly to the simulated environment; these correspond to members of the *Lepomis* group in the fish community data set (app. B).

We compared how the three metrics performed under four different simulation scenarios. The first simulation model has a low σ value that causes strong phylogenetic signal in species turnover (fig. 2*A*, 2*B*). The second is the same as the first but has a stochastic element that causes realistic variation in species richness across simulated communities independent of the environmental driver x (fig. 2*C*, 2*D*). Because this scenario most closely matches the data, we treated it as the baseline scenario. The third scenario randomly assigns x_{opt} values to species to simulate communities with no phylogenetic signal in species turnover. The final scenario has a larger σ value that weakens the sensitivity of species to the gradient in x (fig. 2*E*, 2*F*). This scenario allowed us to address the power of the different metrics to determine whether x has a statistically significant effect on community composition. For each scenario, we simulated 61 communities across an environmental gradient 1,000 times; calculated the corresponding PCD (PCDc and PCDp), Π_{ST}, and UniFrac values for each of the 1,000 data sets; and then correlated these values to the dissimilarities in the simulated communities' values of x.

Finally, we performed a power analysis to address which metric provides the most statistical power to identify the effect of a single environmental driver on community composition. Using simulations, we manipulated the environmental sensitivity of species by decreasing σ (to increase species sensitivities to the environmental gradient) in increments. At each increment, we simulated 1,000 data sets and determined the proportion for which the environmental driver x was statistically significant. The higher
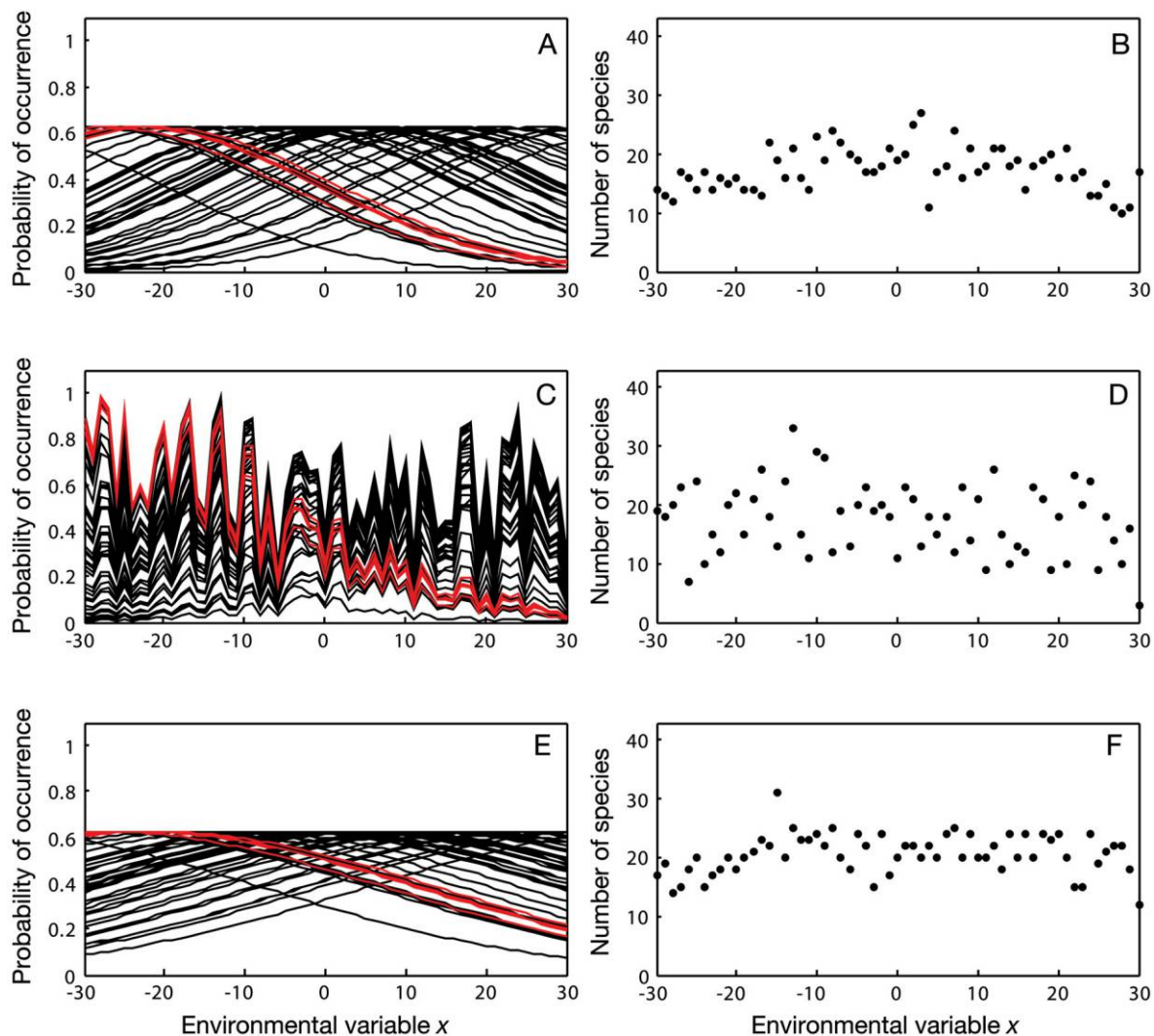
Figure 2: Simulations of community composition along an environmental gradient. We assume that there is a pool of 43 species among 61 communities that are distributed evenly along a gradient of a hypothetical environmental driver x. This mimics the structure of our fish community data set. A, The distribution of probabilities of each species occurring in each community is plotted along the environmental gradient. The optimal value of x for each species, x_{opt}, is assumed to evolve by a Brownian motion process; the four species shown in red are a cluster of four *Lepomis* species (see app. B). B, The number of species in each community in A. C, When stochasticity is introduced into the community occurrence probabilities, there is greater variation in the number of species per community (D). E and F give similar relationships for the case in which the effect of x on the probability that species will occur within a community is reduced compared to that in A and B; the tolerance of each species to x is broader (σ is larger). Note that in B, the number of species in communities at either end of the environmental gradient tends to decrease; this occurs because we constrained the values of x_{opt} to be within the environmental gradient, and this produces an asymmetry, so that species at the edge of the environmental gradient can contain only species having x_{opt} greater (lower boundary) or less (upper boundary) than the boundary values of x. The R code that produced these simulations is available in the Picante package (Kembel et al. 2010).

this proportion for a given σ, the greater the power of the metric to identify the environmental driver.

Results

Fish and Macrophyte PCD-Environmental Analyses

For fish communities, the only statistically significant environmental variable correlated with PCD when multiple

comparisons are taken into account was pH (table 1). Furthermore, the compositional and phylogenetic components of PCD—PCDc and PCDp, respectively—were each correlated with pH. These results indicate that not only are lakes with similar pH likely to contain the same species (PCDc) but their nonshared taxa are also likely to come from the same phylogenetic clade (PCDp). The im-

Table 1: Spearman rank correlations between metrics of phylogenetic community dissimilarity (PCD) and the absolute values of differences in 16 environmental variables between lakes

Community, variable	PCD	PCDc	PCDp
Fishes:			
Chemical:			
pH	**.31****	**.22***	**.19***
Water color	**.20**	.11	**.16**
Conductance	**.18**	.17	.10
Dissolved inorganic carbon	**.17**	**.19**	.07
Alkalinity	**.16**	**.19**	.07
Dissolved organic carbon	.10	.00	**.13**
Total nitrogen	−.03	−.01	−.04
Total phosphorus	−.04	.02	−.08
Physical:			
Substrate richness	.10	.02	**.13**
Depth	.03	**.13**	−.09
Area	−.09	−.05	−.08
Human:			
Total cover	.11	**.13**	.02
Buildings	.08	.00	.11
Coarse woody habitat	.03	.02	.03
Human impact	.03	.04	.00
Rusty crayfish	.00	.07	−.06
Macrophytes:			
Chemical:			
Dissolved inorganic carbon	**.46*****	**.63*****	−.01
Alkalinity	**.46*****	**.58*****	.04
Conductance	**.38*****	**.50*****	−.01
pH	**.26****	**.25*****	.13
Water color	**.15**	**.14***	.04
Total phosphorus	.05	**.11**	−.05
Dissolved organic carbon	.05	.02	.05
Total nitrogen	−.02	−.01	−.02
Physical:			
Substrate richness	.07	**.10**	.00
Depth	.04	.07	−.02
Area	−.06	−.02	−.06
Human:			
Rusty crayfish	**.14**	.09	**.13**
Coarse woody habitat	**.11**	**.18****	−.02
Buildings	.10	−.05	**.16**
Total cover	.09	**.13**	.00
Human impact	.08	−.02	**.12**

Note: Statistical significance was determined by a permutation test accounting for comparisons using multiple environmental variables (see text). Boldface indicates significance ($P < .05$) without accounting for multiple comparisons. PCDc = compositional component of PCD; PCDp = phylogenetic component of PCD.

* $P < .05$.
** $P < .01$.
*** $P < .001$.

portance of phylogeny is seen not only in the statistically significant correlation with PCDp but also in the lower correlation for PCDc than for PCD.

For macrophyte communities, both PCD and PCDc were most strongly correlated with water chemistry variables, and PCDc was also correlated with water color and the density of coarse woody debris (table 1). In contrast

to the fish communities, there was little evidence for phylogenetic effects through nonshared species; macrophyte PCDp was not correlated with any environmental variable once multiple comparisons were taken into account. Furthermore, many of the correlations for PCD were considerably lower than those for PCDc. This indicates that the environmental drivers are producing communities that differ more when communities are distinguished only by their shared species. For example, two communities in lakes with very different dissolved inorganic carbon (DIC) levels may have few species in common. Nonetheless, the nonshared species between each lake may be closely related, reducing the correlation for PCD and DIC relative to the correlation for PCDc and DIC.

In addition to these analyses using PCD, PCDc, and PCDp, two alternative approaches confirmed the contrast between fish communities that showed phylogenetic patterns and macrophyte communities that did not (app. B).

Comparisons of PCD with Two Other Metrics

We used the fish data to compare among PCD and existing metrics of phylogenetic community dissimilarity, Π_{ST} and UniFrac (fig. 3). There is considerable variability among the three metrics in values for pairs of lakes, especially for Π_{ST} and UniFrac, which are poorly correlated (fig. 3A–3C). Therefore, the three metrics are measuring different aspects of community structure. Nonetheless, the correlations between dissimilarity metrics and differences in environmental variables between lakes are related (fig. 3D–3F). All three metrics identified pH as the most important environmental variable for community structure.

In comparison to PCD, Π_{ST} and UniFrac have undesirable properties when applied to collections of communities that differ in size. To investigate the effect of community sizes, we randomly permuted fish species among lakes, thereby maintaining the prevalence of species (i.e., the proportion of communities in which they occur), and plotted the resulting pairwise values of each metric against the sum of species in both communities, $n_1 + n_2$ (fig. 4). We permuted fish species among lakes to remove the effects of environmental drivers (mainly pH) on the composition and size of communities. While PCD has constant mean and variance across values of $n_1 + n_2$ (fig. 4A), the variance of Π_{ST} and the mean of UniFrac decrease with increasing $n_1 + n_2$ (fig. 4B, 4C). Therefore, PCD is the only metric insensitive to community sizes.

To compare the performance of the metrics in greater detail, we simulated data sets under four different scenarios in which community composition is determined by a gradient in a single hypothetical environmental driver x (fig. 2). In the baseline case, with strong phylogenetic signal and random variation in community sizes (fig. 2C, 2D),
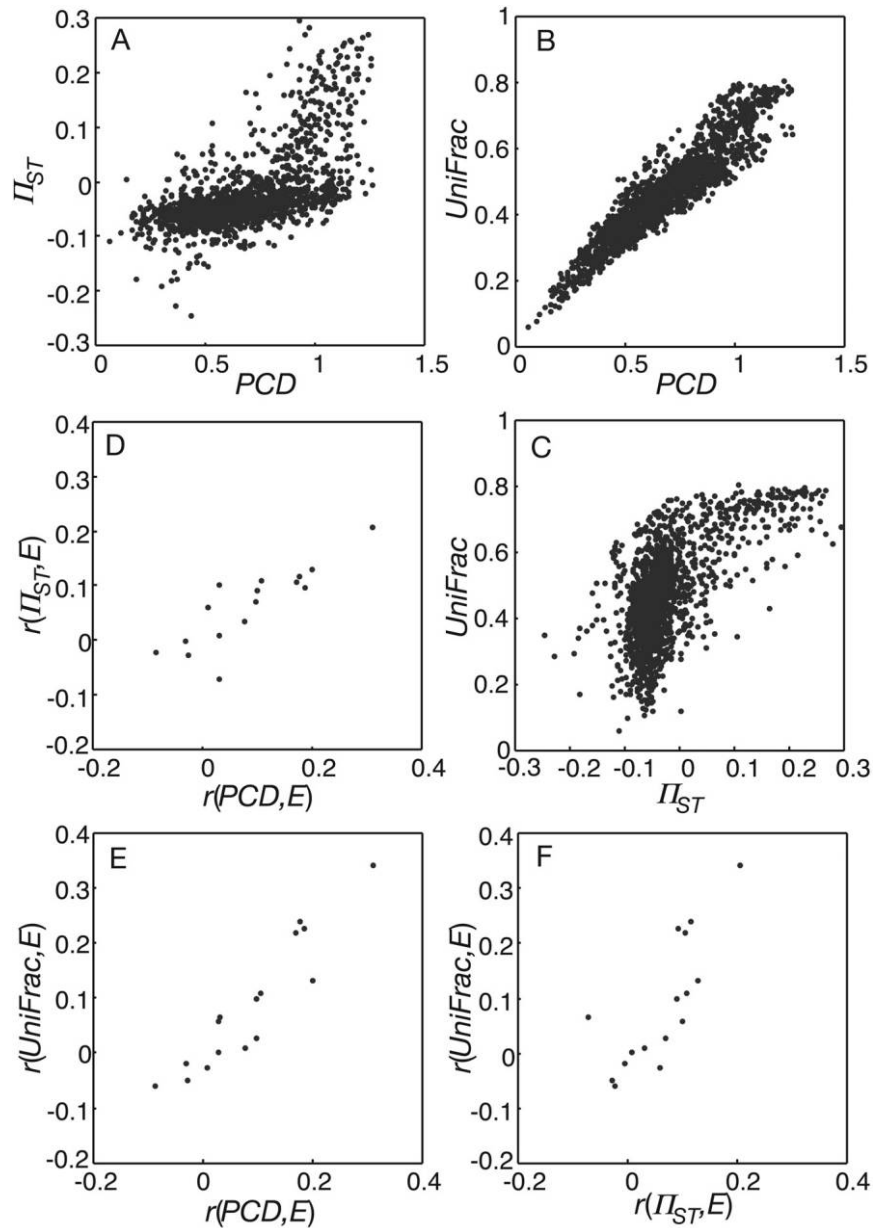
Figure 3: For fish communities, *A–C* show relationships between PCD, Π_{ST}, and UniFrac, with each point corresponding to a different lake pair. *D–F*, Relationships between the correlations *r* of each of the community dissimilarity metrics and the differences between lakes in the 16 environmental variables *E*.

PCD outperformed the other two metrics. The mean rank correlation between PCD and the pairwise differences in *x* between communities was higher than those for UniFrac, with the mean value for PCD (0.53) almost outside the 95% inclusion interval for values of UniFrac from the 1,000 simulations ("Baseline," table 2). For Π_{ST}, correlations were more variable than for PCD, as indicated by the 95% inclusion intervals; 2.5% of the simulations using

Π_{ST} had correlations of <0.17, whereas the corresponding value for PCD was 0.37. The poor performance of Π_{ST} is consistent with the pattern we illustrated with the fish data (fig. 4*B*); for smaller communities, estimates of Π_{ST} were highly variable. The poorer performance of UniFrac relative to PCD resulted at least in part from the effect of variation in community size that is independent of *x*. In the second scenario, with the random variation in com-
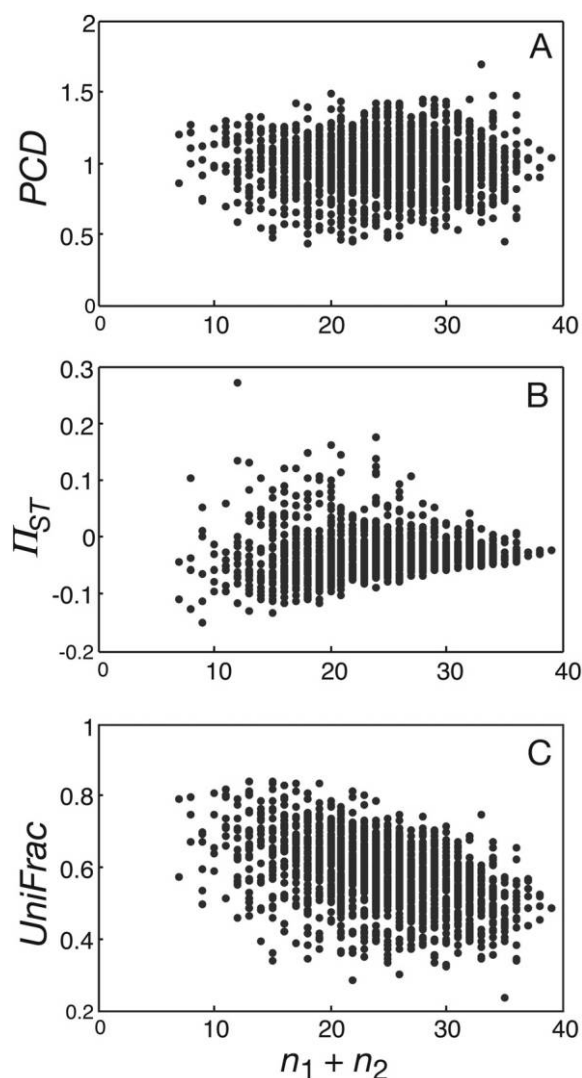
Figure 4: Relationships between PCD (*A*), Π_{ST} (*B*), and UniFrac (*C*) and the sum of the number of species in both fish communities, $n_1 + n_2$. To generate the null expectation for the effect of community size on the metrics of community structure, species were randomly permuted among lakes.

munity size removed ("No random variation in species numbers," table 2), the performance of UniFrac was similar to that of PCD.

The value of partitioning PCD into compositional and phylogenetic components can be seen when species' optimal environmental conditions x_{opt} are independent of phylogeny ("No phylogenetic signal," table 2). All three metrics identified the environmental driver, but Π_{ST} and UniFrac gave no indication that there is no phylogenetic signal in species turnover (cf. "Baseline" and "No phylogenetic signal" in table 2). In contrast, the decomposition

of PCD into PCDc and PCDp allows the identification of a role of phylogeny; in the baseline case, the mean of the rank correlations between PCDp and x was 0.23, and the 95% inclusion interval did not contain 0, whereas the mean correlation was -0.01 in the absence of phylogenetic effects (table 2).

The final case we considered is the same as the baseline except that the effect of environmental driver x on community composition was reduced by decreasing the sensitivities of each species (increasing σ; fig. 2*E*, 2*F*). This case illustrates the greater power of PCD to detect an environmental effect on community composition. For both Π_{ST} and UniFrac, 5% of the simulations (52 and 49 of 1,000, respectively) produced negative rank correlations between differences in x among communities and community dissimilarity, whereas this was the case in only 0.5% of simulations (5 of 1,000) for PCD.

To determine whether these properties of PCD improve its ability to reject the null hypothesis that the environmental driver has no effect on community composition, we used the simulation model to perform a power analysis. At each of nine values of σ, we simulated 1,000 data sets with 43 species distributed among 31 communities. The assumptions for these simulations are identical to those of the baseline case (fig. 2*C*, 2*D*; table 2), although we reduced the number of lakes to 31 to reduce the numerical intensity of the simulations. For each simulation data set, we performed the permutation test described previously to test the null hypothesis that the correlation between pairwise differences in x and pairwise community dissimilarities was 0, using $\alpha = 0.05$. When species are insensitive to x ($\sigma = \infty$), the power should equal 0.05 (i.e., α), and the power should increase as species become more sensitive to x (σ decreases).

For relatively insensitive species (large values of σ), PCD and Π_{ST} outperformed UniFrac, sometimes considerably (fig. 5). For example, for $\sigma = 6,000$, there is only a 30% chance of rejecting the null hypothesis when using UniFrac but a 50% chance when using PCD or Π_{ST}. For smaller values of σ (greater sensitivities of species to x), PCD outperformed Π_{ST}, although the difference was not large. Therefore, the high variability in the estimates of correlations observed in previous simulations (table 2) and its dependency on species number apparently did not greatly affect the power of Π_{ST} to detect environmental drivers of phylogenetic community composition.

Discussion

There is growing interest in incorporating phylogenetic information into assessments of community structure (Losos 1996; Warwick and Clarke 1998; Webb et al. 2002, 2006; Graham and Fine 2008; Cavender-Bares et al. 2009).

Table 2: Simulation results comparing the performance of phylogenetic community dissimilarity (PCD), Π_{ST}, and UniFrac at identifying correlations between an environmental driver and community composition

	Baseline	No random variation in species numbers	No phylogenetic signal	Weaker effect of environment
PCD	.53 (.37, .67)	.56 (.42, .67)	.54 (.43, .63)	.10 (.02, .20)
PCDc	.54 (.42, .65)	.55 (.43. .65)	.54 (.43, .63)	.11 (.04, .20)
PCDp	.23 (.03, .38)	.27 (.08, .43)	−.01 (−.11, .10)	.03 (−.06, .17)
Π_{ST}	.49 (.17, .78)	.57 (.24, .81)	.50 (.38, .60)	.12 (−.02, .31)
UniFrac	.43 (.31, .54)	.54 (.44, .64)	.43 (.34, .52)	.07 (−.01, .17)

Note: Inclusion intervals (95%) for the simulations are given in parentheses. PCDc = compositional component of PCD; PCDp = phylogenetic component of PCD.

The distribution of species among communities ultimately depends on traits that dictate their sensitivities to environmental variables. For broad, exploratory surveys, however, it is not practical to obtain detailed information about how sensitive all species are to all potentially important environmental variables. Phylogenetic information can be used as a possible surrogate. While we might not know exactly what traits are important in explaining the occurrence of species in a community, we know that related species likely share similar traits. Therefore, we might expect community structure to reflect phylogenetic patterns among species (Webb et al. 2002). Of course, phylogenetic information is not equivalent to information about species traits (Losos 2008), and analyses of large numbers of traits among numerous taxa (Freckleton et al. 2002; Blomberg et al. 2003) show a broad range of phylogenetic signal, that is, the degree to which variation in trait values among species can be explained by phylogenetic relationships. Nonetheless, the existence of phylogenetic differences among communities may still lead to hypotheses about the underlying drivers of community composition, and phylogenetic patterns of community composition are of interest in their own right.

Metrics of phylogenetic community similarity give tools for rapidly identifying environmental drivers of community structure. Analyses using PCD revealed strong effects of pH on fish community structure and of dissolved inorganic carbon (DIC), alkalinity, conductance, and pH on macrophyte community structure. A striking contrast between fish and macrophyte communities is the importance of phylogenetic relationships among species. For the fish communities, both nonphylogenetic and phylogenetic components of PCD (PCDc and PCDp, respectively) showed relationships with pH, indicating that communities with the same pH not only were more likely to share the same species but were also more likely to share closely related species (table 1). This is consistent with previous phylogenetic analyses of these fish communities, which show strong reductions in phylogenetic diversity (PSV) in lakes with low pH, reflecting the presence of the perciform

clade of fish, which are generally tolerant of low pH (Helmus et al. 2007). In contrast, there was no phylogenetic pattern in the structure of the macrophyte communities (table 1).

A broad survey such as the one we performed cannot reveal why macrophyte communities show no phylogenetic patterns or why fish communities do. Nonetheless, the analyses suggest where we might look in more detail to explain this contrast. Specifically, one hypothesis is that the absence of phylogenetic patterns in community structure is due to high movement rates of species among communities; even if there are environmental differences between communities, any effects that these might have to drive community structure are swamped by continuous immigration. This does not appear to be the case for mac-
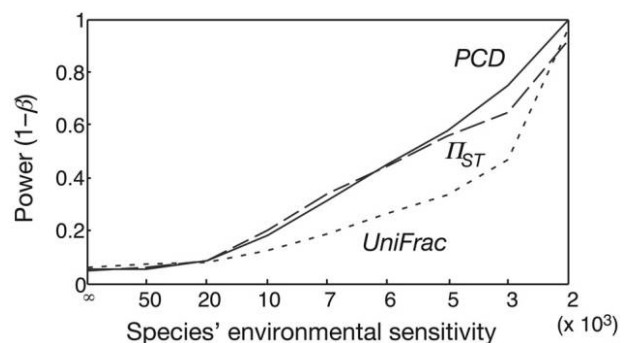

Figure 5: Power analysis of the ability of statistical tests based on PCD (*solid line*), Π_{ST} (*dashed line*), and UniFrac (*dotted line*) to reject the null hypothesis that an environmental driver x has no effect on community dissimilarities. At each of nine values of σ, we simulated 1,000 data sets with 43 species distributed among 31 lakes, and for each simulated data set we performed the permutation test to determine the statistical significance of the correlation between pairwise differences between communities in similarity and x. The power gives the probability of rejecting the null hypothesis at the $\alpha = 0.05$ level (one-tailed), calculated as $1 - \beta$, where β is the probability of committing a Type II error (accepting the null hypothesis when it is incorrect). Other assumptions of the model are the same as in the baseline case in table 2.

rophytes, however. Macrophytes show strong effects—stronger than those in fishes—of environmental factors on the composition (presence/absence) of species within lakes (table 1), indicating that environmental sorting processes within lakes are strong. Therefore, the absence of phylogenetic patterns in the macrophyte community similarities suggests that the sorting processes do not involve traits that themselves show strong phylogenetic signal among species. We do not know why this is true for macrophytes, while fishes apparently do have phylogenetically conserved traits that affect their presence/absence in lakes.

Methodologically, PCD has important advantages over existing metrics of phylogenetic community similarity. Although existing metrics of phylogenetic community structure, such as Π_{ST} and UniFrac, use phylogenetic information, they do not measure how much of the observed community structure can be attributed to phylogenetic information. The PCD metric naturally breaks down into a component reflecting nonphylogenetic community composition (whether the same species are shared among communities) and a component reflecting the phylogeny of nonshared species, PCDc and PCDp, respectively. This makes it possible, for example, to identify the contrast between fish and macrophyte communities in the importance of phylogeny. In principle, the same approach could be used for Π_{ST} and UniFrac, deriving composition-only versions by performing calculations assuming a star phylogeny (app. C), although this has not been investigated in detail.

A second advantage is that PCD has better statistical properties. In our simulations, PCD led to higher rank correlations between community dissimilarity and the differences in communities in a hypothetical environmental driver than either Π_{ST} or UniFrac. The poorer performance of Π_{ST} apparently stems from high variability in its values for small communities, and the poorer performance of UniFrac apparently stems from the fact that values of dissimilarity increase with smaller community sizes. In a power analysis to reject the null hypothesis that an environmental variable had no effect on community composition, PCD performed slightly better than Π_{ST} and much better than UniFrac. These comparisons of statistical properties are contingent on the particular simulation model that we used to test metric properties. Nonetheless, we constructed the simulation model to produce data having the key features shown by fish and macrophyte data sets, and it likely mimics the processes driving the structure of a broad range of real communities.

We have focused on using phylogenetic metrics of community similarity to identify single drivers of community structure. Our PCD and the other metrics can also be used with ordination techniques to give a composite picture of the role of multiple environmental drivers in driving com-

munity structure (Webb et al. 2008a; Faith et al. 2009). Ordination can be performed not only with PCD but also with its components PCDc and PCDp to separate compositional and phylogenetic patterns in community structure. We suspect that the statistical advantages we found for PCD in identifying single drivers will have corresponding advantages in ordination; the insensitivity of the mean and variance of PCD to community size will likely lead to greater precision and power to identify environmental effects on community structure.

Acknowledgments

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