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LETTER

Separating the determinants of phylogenetic community structure

Matthew R. Helmus,[1]***** **Kristina Savage,**[1] **Matthew W. Diebel,**[2] **Jeffrey T. Maxted,**[2] **and** **Anthony R. Ives**[1]

[1]*Department of Zoology, University of Wisconsin, Madison, WI 53706, USA*
[2]*Center for Limnology, University of Wisconsin, Madison, WI 53706, USA*
Correspondence: E-mail: mrhelmus@wisc.edu, mrhelmus@gmail.com

Abstract

The role of competition in forbidding similar species from co-occurring has long been debated. A difficulty in identifying this repulsion of similar species is that similar species share similar environmental requirements and hence show an attraction to communities where these requirements are met. To disentangle these opposing patterns, we use phylogenetic relatedness as an objective metric of species similarities. Studying 11 sunfishes (Centrarchidae) from 890 lakes, we first show no phylogenetic pattern in the raw community data. We then regressed sunfish presence/absence against seven environmental variables and show that lakes with similar water clarity and latitude likely contain closely related species. After statistically removing the environmental effects, phylogenetic repulsion was apparent, with closely related sunfishes less likely to co-occur. Thus, both phylogenetic attraction, driven by environmental filtering, and phylogenetic repulsion, possibly caused by competition, simultaneously occur and obscure one another in the overall phylogenetic structure of sunfish communities.

INTRODUCTION

Whether there are assembly rules that explain the composition of ecological communities has been vigorously, and sometimes acrimoniously, debated by ecologists (Gotelli & Graves 1996; Weiher & Keddy 1999). The most influential of these rules was proposed by Diamond: ecologically similar species exclude each other from the same communities through competition, leading to forbidden combinations of species (Diamond 1975). Despite considerable criticism of Diamond's original analyses and data set (Connor & Simberloff 1979; Harvey *et al.* 1983; Strong *et al.* 1984), recent analyses show empirical support for this assembly rule (Gotelli & McCabe 2002), although additional concerns about possible non-competitive processes leading to similar patterns have been raised (Ulrich 2004).

There are two general types of difficulties in testing an assembly rule involving competitive exclusion. First, statistical tests for assembly rules can be weak. Statistical tests require a metric that identify species having relatively low co-occurrences in communities; the statistical tests simultaneously identify these species and test whether these species co-occurrences represent statistically significant outliers under whatever null hypothesis is employed (Gotelli & McCabe 2002). An alternative approach is to form an *a priori* hypothesis about which species are likely to have low co-occurrence based on their similarity. There has been growing interest in searching for phylogenetic patterns in the composition of communities; because phylogenetically closely related species are more likely to be ecologically similar, ecological determinants of community composition should be reflected in phylogenetic patterns (Elton 1946; Losos 1996; Webb *et al.* 2002; Cavender-Bares *et al.* 2004). Applying this to Diamonzd's assembly rule, forbidden combinations of species should most likely be phylogenetically closely related. Of course, phylogenies only provide hypotheses about ecological similarity, phylogenetic similarity may not correlate with the trait(s) most important for coexistence and convergent evolution could override this hypothesized association. Nonetheless, phylogenies give objective, *a priori* hypotheses about species similarities that

can give an explicit probe into assembly rules and lead to stronger statistical tests.

A second difficulty in testing Diamond's assembly rule is that ecologically similar species might not only experience greater interspecific competition that limits co-occurrence, but might also share the same ecological requirements and therefore be more likely to co-occur in those communities where the requirements are met. In fish communities, for example, phylogenetically related species might share traits that confer tolerance to acidic conditions, leading to communities in acidic lakes made up of groups of phylogenetically related species (Helmus *et al.* 2007). Thus, the final composition of communities might reflect the combined effects of competitive interactions that limit co-occurrence of similar species and environmental filters that select for similar species.

Here, we address patterns of community structure that may arise when similar species are either more or less likely to co-occur, using phylogenetic relatedness as a measure of species similarity. In order to discuss the possible patterns that involve phylogenetic relatedness in the species composition of communities, we refine a lexicon already used to describe the possible patterns (Webb *et al.* 2002; Cavender-Bares & Wilczek 2003; Cavender-Bares *et al.* 2004). We define phylogenetic attraction as the pattern in which the species in a community are likely to contain greater phylogenetic relatedness than expected by chance, and we define phylogenetic repulsion as the opposite pattern (Cavender-Bares & Wilczek 2003). These definitions are contingent on exactly what is meant by 'chance', since there can be multiple null hypotheses that define specifically what makes a community random. Nonetheless, for a given null hypothesis these definitions can lead to explicit measures of phylogenetic attraction and repulsion. In the literature, phylogenetic attraction and repulsion are sometimes used synonymously with the terms phylogenetic underdispersion (or clustering) and phylogenetic overdispersion (e.g. Webb *et al.* 2002; Vamosi & Vamosi 2007). We make the distinction that communities are phylogenetically underdispersed when phylogenetic attraction dominates repulsion, or phylogenetically overdispersed when the reverse is true. Thus, both phylogenetic attraction and repulsion can occur simultaneously, but a set of communities cannot be both phylogenetically underdispersed and overdispersed.

Although our ultimate goal was to understand assembly rules, we do not think that this can be done using only the patterns of species presence/absence from communities; testing assembly rules must ultimately involve testing the hypothesized mechanisms that drive community composition. In the current literature, a dichotomy is often made between environmental filtering in which environmental factors select for phylogenetically related species in the same community, and competitive exclusion in which phyloge-

netically related species do not occur in the same communities (e.g. Webb *et al.* 2002; Horner-Devine & Bohannan 2006; Lovette & Hochachka 2006; Slingsby & Verboom 2006). Here, we use phylogenetic attraction and repulsion to refer to the patterns without any implied processes such as environmental filtering or competitive exclusion; and when we do infer a process, we make it explicit.

To separate the simultaneous patterns of phylogenetic attraction and repulsion, it is necessary to have more information about the communities than simply species composition. For example, to investigate whether there is phylogenetic attraction driven by related species that respond similarly to the same environmental factors, information is needed about the environment in which multiple communities reside. If the co-occurrence of related species is predicted by a specific environmental factor say pH, then this factor drives a component of phylogenetic attraction. Note that in contrast to the idea of environmental filtering, which is invoked to explain the presence of related species in the same communities, here we explicitly associate the presence/absence of species with specific, measured environmental variables. Not only does this make the role of specific environmental factors explicit, it also redirects attention from the composition of communities *per se* to the presence/absence of individual species among communities in different environments.

To investigate patterns of phylogenetic attraction and repulsion, we assembled data on the presence/absence of 11 sunfish species in 890 lakes in Wisconsin, USA. While we have data on all the fish species found in these lakes, we selected the sunfish family Centrarchidae because the majority of lakes in Wisconsin contain sunfishes, the geographic ranges of these species overlap in Wisconsin, a robust molecular phylogeny with fossil-calibrated branch lengths is available for sunfishes, and previous work has shown that phylogenetic relatedness is closely associated with ecologically important sunfish traits (Becker 1983; Wainwright 1996; Near *et al.* 2003, 2005; Collar *et al.* 2005). Similarly, while we focus only on the phylogenetic structure of a small pool of species, the methodology that we develop here should be applicable for any pool size given that the phylogeny and community data are reasonably good, that there is variation in environments among communities, and that there is enough species distribution data to calculate how most individual species respond to environmental variation.

To lay out the logic of our analyses, it is useful to outline our main results upfront. We begin with a standard null model analysis to look for phylogenetic structure using only data on the species composition of communities. We found that on average communities are neither phylogenetically overdispersed nor underdispersed. Then we performed logistic regression for the presence/absence of each species

from lakes against seven environmental variables, each of which has a statistically significant effect on the presence/absence of at least one species. The logistic regression coefficients from these analyses give the sensitivity of species presence/absence to each of the seven environmental variables. For two environmental variables, water clarity and latitude, closely related species had similar sensitivities, thereby implicating these environmental variables in driving phylogenetic attraction in community composition. We then investigated the co-occurrence of species after accounting for their shared responses to environmental variables; this revealed phylogenetic repulsion, with closely related species less likely to co-occur in lakes sharing the same environmental characteristics. In combination, these analyses demonstrate that phylogenetic attraction (driven by water clarity and latitude) and phylogenetic repulsion both occur, but they offset each other to mask any overall phylogenetic structure in the sunfish communities.

METHODS

Sunfish and environmental data sets

We analysed data giving the presence/absence of sunfish species for 890 lakes in Wisconsin, USA, from the United States Geological Survey Great Lakes Aquatic GAP project. This data set was assembled from fish surveys performed between 1965 and 2004 primarily by the Wisconsin Department of Natural Resources. Surveys were conducted during the ice-free season by electrofishing, netting or a combination of both, and were intended to assess whole-lake fish community composition. When a lake was sampled more than once, we used only the first survey date. All sampling was intensive enough to give accurate reports of the presence/absence of even uncommon species. No pattern was found between sunfish species richness or phylogenetic species variability (PSV; see description below) and sampling method or date. Thus, we assumed that the sampling was adequately uniform across the lakes for the purposes of our analyses.

We obtained environmental variables for the surveyed lakes from the Wisconsin Department of Natural Resources (K. Webster, unpublished data) including lake area, maximum depth, latitude, longitude, water conductivity, water clarity (Secchi depth measured in summer) and winterkill (a categorical variable of whether fish mortality occurs in a lake because of lake freezing). These environmental variables have been shown to affect fish community composition and correlate with fish species richness in Wisconsin lakes (Rahel 1984; Kratz et al. 1997; Jackson et al. 2001; Hrabik et al. 2005; Helmus et al. 2007).

We used the fossil-calibrated sunfish phylogeny of Near et al. (2005) to construct a phylogeny of the 11 species found

in Wisconsin (their Fig. 7). This phylogeny was converted into a phylogenetic covariance matrix $\mathbf{C}_{pool}$ describing the anticipated covariances between species in values of a single trait under 'Brownian motion' evolution (Felsenstein 1985; Garland et al. 1993). Although we do not assume that only a single trait dictates the co-occurrence of species in communities, this covariance matrix gives a way to translate a phylogeny into a statistical measure of phylogenetic relatedness (Garland & Ives 2000; Blomberg et al. 2003; Helmus et al. 2007; Ives et al. 2007).

Null model tests for phylogenetic community structure

We first tested for phylogenetic structure in the composition of sunfish communities without including environmental information, as is performed in many studies (e.g. Webb 2000; Slingsby & Verboom 2006; Swenson et al. 2006). We calculated PSV of each sunfish community containing at least two species (Helmus et al. 2007). We used this metric, as opposed to other metrics (e.g. Webb 2000; Hardy & Senterre 2007), because it has advantageous statistical properties when used in particular permutation tests for phylogenetic structure (Helmus et al. 2007). When PSV equals one, all of the species in the community are phylogenetically unrelated, indicating maximum PSV. As PSV approaches zero, average phylogenetic relatedness increases and PSV decreases.

We used permutation tests to determine whether the observed average PSV value across all lake communities, $\overline{PSV}_{obs}$, was different from that expected under two different null hypotheses. Null hypothesis 1 assumes that communities consist of random draws of species from the species pool of 11 sunfish. Therefore, there is no phylogenetic structure in either species prevalence (the number of lakes containing the species) or community composition (the co-occurrence of species after accounting for any differences in prevalence). Null hypothesis 2 assumes that communities are assembled by selecting species from the species pool in proportion to their prevalence among lakes. Null hypothesis 2 will only be rejected if phylogenetically related species are more or less likely to co-occur within lakes after accounting for differences in prevalence (Helmus et al. 2007). We permuted the sunfish presence/absence data under each null hypothesis to create 10 000 permutation data sets. For each permutation data set, we computed $\overline{PSV}$ to generate a null distribution for $\overline{PSV}_{obs}$. Note, this null model analysis, as well as all subsequent analyses, treat the phylogeny as fixed; however, if there are multiple phylogenetic hypotheses for a given data set then the analyses we describe can be performed for each tree and the conclusions of the analyses among trees be compared for similarity. Programs in R code to perform the null model analyses can be downloaded as

supplementary material and MATLAB code is available as supplementary material with Helmus *et al.* (2007).

Environmentally determined phylogenetic attraction

Phylogenetic attraction refers to the pattern in which phylogenetically related species are more likely to occur in the same community; this pattern may be driven by the propensity for closely related species to respond similarly to environmental variation. To identify environmental variables that affect the presence/absence of the 11 sunfish species, we performed logistic multiple regression with seven environmental variables (lake area, maximum depth, conductivity, water clarity, winterkill, latitude and longitude) as independent variables. The logistic regression had the form

$$\text{logit}(\boldsymbol{\theta}(\mathbf{x}_k)) = \mathbf{b}_0 + \mathbf{b}_1 x_{1,k} + \ldots + \mathbf{b}_j x_{j,k} \tag{1}$$

where $\boldsymbol{\theta}(\mathbf{x}_k)$ is a 11×1 vector of the probabilities that each of the 11 species occurs in lake $k (k = 1, \ldots, K)$, $x_{j,k}$ is the value of the jth environmental variable for lake $k (j = 1, \ldots, 7)$ and $\mathbf{b}_j$ is a 11×1 vector of regression coefficients for each of the 11 species in response to environmental variable j. For each of the environmental variables, we then asked whether closely related species are more likely to respond to environmental variation among lakes in the same way. Addressing this question identifies which, if any, of the seven environmental variables filter species according to phylogeny, thereby generating phylogenetic attraction. We treated the regression coefficients as species traits and tested for phylogenetic signal in the seven sets of coefficients. Because even non-statistically significant coefficients represent traits, we did not set them to zero, but instead performed tests for phylogenetic signal using the standard errors in the estimates of the coefficients as measurement error (Ives *et al.* 2007).

For each environmental variable j, we fit the model

$$\mathbf{b}_j = \beta_j \mathbf{1} + \boldsymbol{\varepsilon}_j + \boldsymbol{\eta}_j, \tag{2}$$

where β_j is the expected value of the logistic regression coefficient for $\mathbf{b}_j$, $\mathbf{1}$ is an 11×1 vector of ones, $\boldsymbol{\varepsilon}_j$ is a vector of error terms and $\boldsymbol{\eta}_j$ is the vector of estimated errors of the coefficients for x_j (i.e. measurement error). If closely related species respond in a similar manner to an environmental variable, the pattern of correlation in values of $\boldsymbol{\varepsilon}_j$ will reflect phylogenetic relatedness. Specifically, if $\mathbf{b}_j$ evolves under Brownian motion evolution, then the covariance matrix $E\{\boldsymbol{\varepsilon}_j \boldsymbol{\varepsilon}_j'\} = \sigma^2 \mathbf{C}_{\text{pool}}$, where the apostrophe denotes transpose, σ^2 scales the overall phylogenetically inherited variance (Garland & Ives 2000), and $\mathbf{C}_{\text{pool}}$ is the phylogenetic correlation matrix for the 11 species. In contrast, if there is no phylogenetic signal, values of $\mathbf{b}_j$ are independent among species, and $E\{\boldsymbol{\varepsilon}_j \boldsymbol{\varepsilon}_j'\} = \sigma^2 \mathbf{I}$, where $\mathbf{I}$ is the identity

matrix. We conducted a statistical test for phylogenetic signal by comparing the fit of the model given by eqn 2 using $\mathbf{C}_{\text{pool}}$ from the true phylogeny to the fit when assuming there is no phylogenetic signal. We fit the models using restricted maximum likelihood (REML), so the best-fitting model is that with the higher REML log likelihood (Ives *et al.* 2007). For those environmental variables for which the true phylogeny model fit the data better, we summarized the phylogenetic signal among the regression coefficients with the K^* metric developed by Blomberg *et al.* (2003) incorporating standard errors (Ives *et al.* 2007). A K^* value close to 1 implies that the observed phylogenetic signal in species regression coefficients is that expected under Brownian motion evolution.

Note that the methods we developed above have a similar purpose as the methods of Ackerly *et al.* (2006) and Silvertown *et al.* (2006) developed to measure phylogenetic signal in species' β niches (i.e. the habitats where a species is found). Our general methodology is given in much more detail in Ives *et al.* (2007) and programs written in MATLAB code to perform these analyses are available from T. Garland upon request (E-mail: tgarland@ucr.edu).

Phylogenetic repulsion

Phylogenetic repulsion refers to the pattern in which phylogenetically related species are less likely to occur in the same community. To compute the correlation in the presence/absence of species from a lake while factoring out the effect of environmental variables, we computed pairwise correlations between species h and i among the $K = 890$ lakes as

$$r_{h,i} = \frac{1}{K} \sum_{k=1}^{K} \frac{\left(Y_{h,k} - \theta_h(x_{\bullet,k})\right)\left(Y_{i,k} - \theta_i(x_{\bullet,k})\right)}{\left(\theta_h(x_{\bullet,k})\left(1 - \theta_h(x_{\bullet,k})\right)\theta_i(x_{\bullet,k})\left(1 - \theta_i(x_{\bullet,k})\right)\right)^{1/2}}, \tag{3}$$

where $Y_{h,k}$ is the presence/absence of species h for lake k, and $\theta_h(x_{\bullet,k})$ is the probability of occurrence estimated from logistic regression (eqn 2) using values of the environmental variables for lake k, $x_{\bullet,k}$. This formula uses the well known relationship that the variance of a binomial process with mean θ is $\theta(1-\theta)$. Because for each lake the expectation for the presence/absence of each species is computed using the given environmental variables, eqn 3 gives the correlation in species occurrences after accounting for the effects of these environmental variables. Conversely, if environmental variables are not included, values of θ_h are simply the prevalence of species h, and eqn 3 gives the simple correlation between species occurrences. In other words, eqn 3 can be considered the pairwise correlation between the residuals from the logistic regressions of species h and i. If instead we used

linear models with normal errors (e.g. if there were data on species abundances within each lake), then eqn 3 can be replaced with the simple pairwise correlation between the linear model residuals of species h and i.

To determine whether the presence/absence of species from lakes after factoring out the effect of environmental variables depended on their phylogenetic similarity, we estimated the strength of association (i.e. correlation) between $r_{h,i}$ and the phylogenetic relatedness among species given by the phylogenetic correlation matrix $\mathbf{C}_{\text{pool}}$. Then we computed $r_{h,i}$ without including the environmental variables and compared these without-environment values of $r_{h,i}$ to the with-environment values of $r_{h,i}$ to demonstrate the opposition between environmentally determined phylogenetic attraction and phylogenetic repulsion. Because three species occurred in very few lakes (11 or less), patterns of co-occurrences for these species provide little information; therefore, we analysed phylogenetic repulsion only for the remaining eight species that occurred in 42 or more lakes. For statistical inference, we performed permutation tests under null hypothesis 2 that lake communities are made up of species selected randomly but in proportion to their prevalence in the species pool, thus any phylogenetic pattern in the observed species prevalence does not affect these tests. For each of 10 000 permutation data sets, we performed logistic regressions (eqn 1) to compute $\theta_h(x_{\bullet,k})$ and $r_{h,i}$, and then computed the correlation between $r_{h,i}$ values and the phylogenetic relatedness contained in $\mathbf{C}_{\text{pool}}$. Programs in MATLAB code that perform these analyses can be downloaded as supplementary material.

RESULTS

Null model tests for phylogenetic community structure

The sunfish fauna of Wisconsin contains five pairs of closely related species, and in each pair there is one species of lower prevalence than the other species (Fig. 1). This pattern is statistically confirmed with our analysis using the metric of PSV that summarizes the degree of relatedness among species in a community. For the sunfish communities, the statistical test under null hypothesis 1 indicates that communities are composed of relatively unrelated species ($\overline{\text{PSV}}_{obs} = 0.8286$; $\overline{\text{PSV}}_{null1} = 0.7833$, $p_{null1} \ll 0.001$). Thus, under this null model the sunfish communities are phylogenetically overdispersed. However, the statistical test under null hypothesis 2 shows that the phylogenetic overdispersion in sunfish communities shown by null 1 can be explained solely by the phylogenetic pattern in species prevalence ($\overline{\text{PSV}}_{null2} = 0.8271$, $p_{null2} > 0.05$). Therefore, there is no evidence for either phylogenetic attraction or repulsion in the overall pattern of community composition.
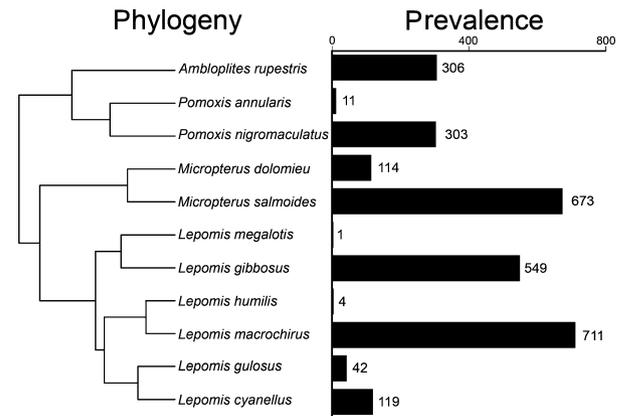

Figure 1 Phylogeny and prevalence of sunfish (Centrarchidae) species found in the lake communities of Wisconsin (890 lakes). Phylogeny adapted from Near *et al.* (2005).

Environmentally determined phylogenetic attraction

While all seven environmental variables explain statistically significant amounts of variation in the presence/absence for at least one species, only water clarity (Secchi depth) and latitude show evidence of phylogenetic signal (Table 1). This is not due to collinearity between these two variables: they are not correlated ($r = 0.03$). The K^* values for water clarity and latitude are close to 1, 1.24 and 0.91, respectively; thus, the sunfish phylogeny adequately describes the phylogenetic signal in how species' presence/absence is affected by these environmental variables (Blomberg *et al.* 2003; Ives *et al.* 2007).

Phylogenetic repulsion

When ignoring environmental variables, the correlations in species occurrences, $r_{h,i}$ (eqn 3), are not statistically associated with phylogenetic relatedness under null model 2 (Fig. 2a). This result is consistent with tests based on PSV that show that the sunfish phylogenetic composition is explained solely by differences among species prevalence. When environmental variables are included in the calculation of occurrence correlations, $r_{h,i}$, phylogenetic repulsion is evident, with the correlation between values of $r_{h,i}$ and the phylogenetic relatedness in $\mathbf{C}_{\text{pool}}$ equal to -0.40 (Fig. 2b); this correlation is statistically significant under null hypothesis 2 ($P < 0.02$). Although there is phylogenetic repulsion, with closely related species having lower occurrence correlations, the average occurrence correlation is 0.08, indicating that sunfishes overall are clustered among lakes (Fig. 2b).

The apparent increase in phylogenetic repulsion with the inclusion of environmental variables (Fig. 2b) is because there is a greater decrease in occurrence correlations $r_{h,i}$ for

Table 1 Tests for phylogenetic signal in the effects of seven environmental variables on the presence/absence of sunfish species

Environmental variable	Phylogenetic correlation, $\mathbf{C}_{\text{pool}}$			No phylogenetic correlation		
	β	σ^2	REML LL	β	σ^2	REML LL
Area	0.08	0.03	−5.72	0.05	0.03	−5.05
Maximum depth	0.14	0.08	−8.33	0.11	0.07	−7.38
Conductivity	0.08	0.02	−2.19	0.07	0.03	−2.18
Water clarity*	0.09	0.02	−2.89	0.11	0.02	−4.10
Winterkill	0.19	0.01	−2.99	0.18	0.02	−2.65
Latitude*	−0.29	0.27	−12.28	−0.42	0.31	−12.84
Longitude	−0.21	0.14	−9.08	−0.25	0.12	−8.48

Phylogenetic signal was assessed by fitting eqn 2 using either $\mathbf{C}_{\text{pool}}$ or assuming no phylogenetic correlation between species.
β, estimate of the logistic regression coefficient of an environmental variable; σ^2, estimated scalar of the overall phylogenetically inherited variance.
*Environmental variables for which the model using $\mathbf{C}_{\text{pool}}$ resulted in better fit (higher REML log likelihood).

closely related sunfishes than for less related sunfishes. Figure 2c shows the change in values of $r_{b,i}$ when environmental variables are included and shows greater decreases for closely related species ($P < 0.002$, null hypothesis 2). This gives strong evidence for phylogenetic repulsion. Thus, the phylogenetic attraction generated by common responses of closely related species to the same environmental factors mask the effect of phylogenetic repulsion of closely related species from lakes with the same environmental characteristics.

DISCUSSION

Our permutation analyses with a metric of phylogenetic relatedness, PSV, show no statistical evidence for sunfish phylogenetic community structure beyond that explained by the prevalence of species in the species pool (Fig. 1). Given our data set, we are not able to confidently explain the overdispersed biogeographic pattern in species prevalence (i.e. less related species are more prevalent), and more work needs to be performed on Centrarchidae speciation and biogeography (e.g. Near *et al.* 2003). Regardless, closely related sunfishes respond similarly to environmental variation in water clarity and latitude (Table 1), and this causes a pattern of phylogenetic attraction. After factoring out the effects of these environmental variables, an underlying pattern of phylogenetic repulsion emerges (Fig. 2). Thus, standard null model analyses that test for phylogenetic patterns in community composition may result in false negatives if other data, such as environmental variation across communities, are not taken into account.

Both water clarity and latitude are known to affect the distribution of sunfish species, and it is not surprising that they generate phylogenetic signals. Water clarity varies greatly across lakes (Peckham & Lillesand 2006); and, for example, the largemouth and smallmouth bass (*Micropterus salmoides* and *M. dolomieui*) occur more frequently in clear-

water lakes (Heimstra *et al.* 1969; Becker 1983). Lake latitude correlates with average water temperature, and species sensitivities to water temperature may have phylogenetic signal. For example, within the state of Wisconsin, warmouth (*Lepomis gulosus*) and green sunfish (*L. cyanellus*) have similar temperature preferences (Becker 1983). The other five environmental variables we tested did not show phylogenetic signal, but in logistic regression they all had statistically significant effects on the presence/absence of some species. The absence of a phylogenetic signal in these five variables might be due to the small number of species we investigated; Blomberg *et al.* (2003) found that statistical power for detecting phylogenetic signal dropped rapidly for analyses involving less than 20 species.

After removing the phylogenetic attraction caused by the environmental factors, we found phylogenetic repulsion – closely related species occurred together less often than unrelated species. What are the possible causes of this pattern? Phylogenetic repulsion is typically interpreted as evidence for competitive exclusion among ecologically similar species (e.g. Lovette & Hochachka 2006; Slingsby & Verboom 2006). An important aspect of sunfish ecology is differences in feeding morphology, and there is phylogenetic signal in sunfish feeding morphology (Wainwright 1996; Collar *et al.* 2005). For example, pumpkinseed (*Lepomis gibbosus*) and its sister species, redear sunfish (*L. microlophus*), are the only two sunfishes that have enlarged jaw muscles and bones that allows them to crush and eat snails (Wainwright 1996 and refs therein). No study has explicitly tested whether interspecific competition among sunfishes increases with phylogenetic relatedness, but much work shows that sunfishes compete (e.g. Werner & Hall 1976; Werner 1977; Werner *et al.* 1977; George & Hadley 1979; Mittelbach 1984, 1988; Arendt & Wilson 1999). For example, when green sunfish, bluegill (*Lepomis macrochirus*) and pumpkinseed occur singly within lakes, each forages on the same, energetically preferred prey that occur in vegetated
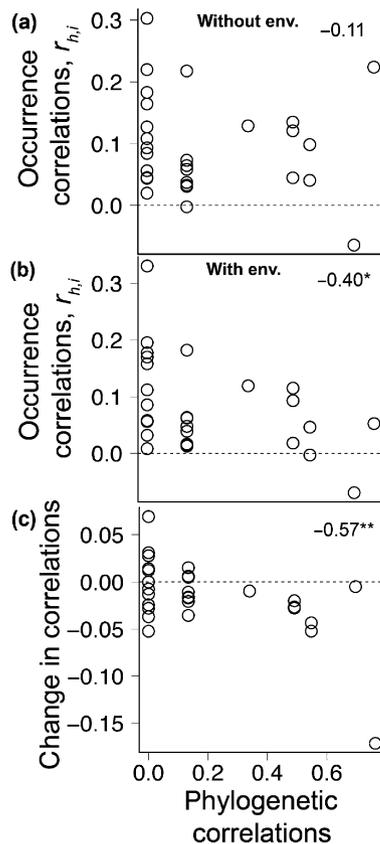
Figure 2 Sunfish species pairwise phylogenetic correlations from C_{pool} (phylogeny in Fig. 1) vs. the pairwise correlations of species occurrences, $r_{h,i}$ (eqn 3), computed (a) without- and (b) with-environmental variables. When including environmental variables (b), there is a stronger pattern of phylogenetic repulsion. This strong pattern occurs because the occurrence correlations between phylogenetically related species are more likely to decline once environmental variables are included. The changes in occurrence correlations when environmental variables included are given in (c). Associations shown in each panel are summarized by correlation coefficients, and statistical significance determined from permutation tests; * and ** indicate significant negative associations at the $P \leq 0.02$ and 0.002 levels (see *Methods*).

areas. When the three species occur in the same lake, only green sunfish feed on the optimal prey, while bluegill shift to feed on open-water prey (e.g. zooplankton) and pumpkinseed shift to feed on benthic prey (e.g. small mayflies, Werner & Hall 1976, 1977, 1979). Similarly, when largemouth bass and smallmouth bass co-occur, the two species spatially and temporally partition resources (Hodgson *et al.* 1997; Olson & Young 2003; Olson *et al.* 2003), yet when individuals are small, largemouth bass has been shown to out-compete smallmouth bass in tank competition studies (Winemiller & Taylor 1987). As there is ample evidence that sunfish species compete, and phylogenetic relatedness and ecological similarity are correlated, it is likely that compet-

itive exclusion plays at least some role in the phylogenetic repulsion observed in our sunfish communities.

Phylogenetic repulsion can also be driven by environmental factors if phylogenetically dissimilar species have become ecologically similar through evolutionary convergence (e.g. Cavender-Bares *et al.* 2004). Although we have no evidence for this possibility, it is difficult to discount, because it is impossible to identify all possible environmental variables that might affect sunfish community composition. Additionally, sunfish are sport fish that have been introduced into many of Wisconsin's lakes (Becker 1983) and this might somehow introduce phylogenetic patterns through the selection of species for introduction into specific lakes. Even after accounting for the two environmental variables that had phylogenetic signals (water clarity and latitude), unrelated species (with phylogenetic correlations of 0) tended to co-occur in the same lakes, leading to an average occurrence correlation of roughly 0.1 (Fig. 2b). This means that sunfishes tend to be found with other sunfishes regardless of phylogenetic relatedness. This pattern may exist if sunfishes are in general good dispersers (possibly with dispersal increased because of human introductions), if sunfishes generally facilitate sunfish coexistence, and/or if there are environmental variables that filter for sunfishes as a whole. This last point may be addressed by comparing the sunfish results to those using our methods on a larger species pool (e.g. all Perciformes or all fishes in the lakes) with, if available, additional environmental data. Consequently, using our methods on species pools that vary in phylogenetic scale is a possible way to infer species' β niches (Ackerly *et al.* 2006; Silvertown *et al.* 2006). Although the observational and experimental evidence that closely related sunfishes compete provides an argument for competition driving the phylogenetic repulsion we found (Fig. 2b); we cannot exclude other possible explanations involving unmeasured environmental variables or human interventions.

If we had only focused on the average relatedness of species in the sunfish communities (i.e. our PSV null hypothesis analyses), we would have concluded that there is no evidence for either phylogenetic attraction or phylogenetic repulsion. Instead, by taking a species perspective (i.e. regressing species presence/absence on environmental variables), we showed there to be evidence for both patterns. Thus, we have given an example in which communities simultaneously show phylogenetic attraction and repulsion, and in so doing we have presented a set of methods that can be used to separate these two opposing patterns in phylogenetic community structure.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

PSV Null Model R and Matlab Code (WinRAR ZIP archive)

Logistic Regression and Correlations Data and Matlab Code (WinRAR ZIP archive)

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01083.x

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