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Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions

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Abstract A number of studies at large scales have pointed out that abiotic factors and recolonization dynamics appear to be more important than biotic interactions in structuring stream-fish assemblages. In contrast, experimental and field studies at small scales show the importance of competition among stream fishes. However, given the highly variable nature of stream systems over time, competition may not be intense enough to generate large-scale complementary distributions via competitive exclusion. Complementary distribution is a recurrent pattern observed in fish communities across stream gradients, though it is not clear which instances of this pattern are due to competitive interactions and which to individual species' requirements. In this study, I introduce a series of null models developed to provide a more robust evaluation of species associations by facilitating the distinction between different processes that may shape species distributions and community assembly. These null models were applied to test whether conspicuous patterns in species co-occurrences are more consistent with their differences in habitat use, morphological features and/or phylogenetic constraints, or with species interactions in fish communities in the streams of a watershed in eastern Brazil. I concluded that patterns in species co-occurrences within the studied system are driven by common species-habitat relationships and species interactions may not play a significant role in structuring these communities. I suggest that large-scale studies, where adequate designs and robust analytical tools are applied, can contribute substantially to understanding the importance of different types of processes in structuring stream-fish communities.

Keywords Stream fish communities · Habitat affinities · Species distribution · Competition · Null models

Introduction

Patterns of species co-occurrence in space and time have been widely investigated by ecologists in order to provide insight about mechanisms determining species distributions and the structure of communities. Analysis of non-random patterns in species co-occurrence can help to identify the abiotic and biotic filters affecting local faunas. Brown (1987) separated these filters as “capacity rules” (i.e., species attributes and habitat features) and “allocation rules” (i.e., species interactions) in the organization of communities. Because of high environmental variability in streams, ecologists debate whether the relative importance of habitat, behavioral, morphological, and physiological adaptations exceeds that of species interactions, such as competition (Grossman et al. 1998). A number of studies showing significant community-environment association have pointed out that abiotic factors and recolonization dynamics appear to be more important in structuring stream-fish assemblages than biotic interactions (e.g., Harrel 1978; Schlosser 1982; Poff and Allan 1995; Taylor 1997). In contrast, experimental and field studies at small scales show the importance of local competition among stream fishes (e.g., Rodriguez 1995; Resetarits 1997; see Jackson et al. 2001 for a review). However, given the highly variable nature of stream systems over time, competition may not be intense enough to generate complementary distributions via competitive exclusion at larger spatial scales. Complementary distribution is a recurrent pattern observed in fish communities across stream gradients (Gilliam et al. 1993; Taylor et al. 1993; Winston 1995; Taylor 1996), though it is not clear whether this pattern is due to competitive interactions (allocation rules) or to individual species requirements (capacity rules).

Null models have been widely used to investigate patterns in species distributions and co-occurrences (e.g.,

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Caswell 1976; Connor and Simberloff 1979; Jackson et al. 1992; Cook and Quinn 1995; Gotelli and Graves 1996; Weiher and Keddy 1999; Peres-Neto et al. 2001). Although null models are commonly used for assessing the influence of species associations in determining community composition, a number of factors other than biotic interactions can produce similar non-random patterns in species distributions. Similarities or differences in species dispersal abilities or habitat requirements may lead to patterns similar to those produced by competition or facilitation (Schluter 1984; Bradley and Bradley 1985; Peres-Neto et al. 2001). Allopatric speciation with subsequent contact (Wiley and Mayden 1985) can generate patterns of association equivalent to those caused by competition if species differentially adapt to distinct habitats. Spatial distribution of sampling units (e.g., sites, fragments, islands) and the limited dispersal abilities of some species may produce spurious positive associations in nearby sites or negative associations in distant sites. Phylogenetic constraints or plasticity of species' ecology may also influence species co-occurrences (Webb 2000; Silvertown et al. 2001). For these reasons, once a particular species co-occurrence pattern is detected, it is important to investigate further whether this pattern could have arisen for ecological reasons (e.g., morphological and habitat constraints) other than species interactions. This kind of framework can help to distinguish between competing hypotheses that may be invoked to explain the same pattern (Weiher et al. 1998) or to disentangle their relative power of explanation (Peres-Neto et al. 2001). Large-scale studies, where adequate designs and robust analytical tools are applied, can contribute substantially in understanding the importance of different types of local processes (e.g., competition) in structuring stream-fish communities at larger scales (e.g., complementary distribution). Arguably, given that experimental data alone cannot address the extent to which particular local mechanisms are influential at macroecological scales (Bennet 1990; Maurer 1999), null models and experimentation should be regarded as complementary tools in the search for mechanisms structuring ecological communities (see Kelt and Brown 2001; Gotelli and McCabe 2002).

Small, independent hydrographic basins in eastern Brazil provide convenient systems for measuring the relative roles of species-level traits versus the potential role of species interactions in shaping patterns in the co-occurrence of fish species. First, sampling protocols may be established to gather distributional data from large portions of the watershed. Therefore, important features such as species distribution, habitat corridors for dispersion, local abundance, isolation, and habitat affinities can be estimated with relatively good accuracy. Second, populations in these systems can disperse only within basins. As a consequence, population density and range of distribution within basins depend largely on the abiotic and biotic characteristics of the system. In this study, I examine fish communities in streams of an eastern Brazilian watershed using a series of null models to test

whether conspicuous patterns in species co-occurrence are more consistent with the species' differences in habitat use, morphological features, and phylogenetic constraints, or with their interactions.

Materials and methods

Study area

The eastern region of Brazil has the highest density of small streams (Menezes 1972) and endemic fish taxa (Bohlke et al. 1978) in South America. Its fauna has more than 285 species, the majority of which are endemic (Bizerril 1994). Most river systems in eastern Brazil are found along the Serra do Mar, a relatively high altitude mountain range (2,400 m) along the Brazilian coast (10–28°S). The area is characterized by steep rocky slopes, which, combined with a tropical rainy climate, have formed a large number of small watersheds that flow parallel to each other towards the Atlantic Ocean. I collected fish distribution data and environmental attributes from a typical system in this area, the River Macacu (70 km long), composed of relatively small and pristine streams.

Fish sampling procedures

Fifty-three sites were sampled throughout the Macacu watershed. Sites were situated between 42°33'W and 42°47'W, and 22°22'S and 22°37'S. Sites were chosen in order to measure all types of habitat available in the system and were positioned according to accessibility throughout the entire watershed (see Peres-Neto 2002 for geographical positioning of all sites). Sites varied between 50 and 70 m in length and between 2 and 8 m in width, and were sampled intensively using electrofishing with pulsed current. Since my interest was only in the presence or absence of species, only one pass was conducted throughout the reach in a zigzag movement against the current, removing all the fishes encountered. Individuals were identified in the field when possible and released into the stream. For all species, a few individuals were also preserved for morphological measures.

Local environmental characteristics

Nine habitat variables were measured at each site. Stream cross-sectional depth was measured every 50 cm, and at 5 m intervals longitudinally. Current velocity was recorded in the middle of the water column at the same points where depth was recorded, using a digital flow probe. The average current was recorded for each point for a period of 10 s. For depth and current, the averages of all points were used to summarize the site. Substrate coarseness was visually estimated in a cross section by the percentage composition of sand (<2 mm), gravel (2–60 mm), rubble (60–150 mm) and boulder (>150 mm) every 5 m. Because width varied along the site section, the weighted average by width for each substrate category was then used as an overall measure per site. Irregularity was measured as the coefficient of variation for width taken every 5 m along the sampled site. Area was calculated every 5 m by interpolating linear distances between section widths to form a tetragon: total area was estimated as the sum of these independent areas along the length of the sampling site. Elevation was acquired from topographic maps. Three additional variables were based on coefficients of variation for depth, current velocity, and sediment. Latitudinal and longitudinal geographic positions for each site were acquired using a GPS.

Site suitability descriptors

Accounting for spatial autocorrelation

Ecologists are increasingly aware of the problems imposed by spatial processes when assessing relationships between distributional patterns and local environmental characteristics. The problem relates to the fact that common spatial processes that influence both stream-fish distribution and environmental factors in similar ways may generate apparent species-environment concordance. Probably the most common approach used for partitioning out the common effects due to spatial processes is to use trend surface polynomial regression (e.g., Borcard et al. 1992; Legendre and Legendre 1998, and references therein). However, in stream systems, nearest neighbor sites on the basis of geographic coordinates are not necessarily nearest neighbors in the stream network. Here I suggest a different approach based on watercourse distances between sites. The approach is similar to trend surface regressions, in that each habitat variable is regressed separately on spatial predictors. The difference relates to the way in which spatial predictors were estimated. First, a pairwise watercourse distance matrix between all sites was calculated. Next, a principal coordinate analysis (PCoA; see Legendre and Legendre 1998 for a review) was applied in order to obtain a Euclidean representation in a Cartesian coordinate system of the distance matrix that can be used as spatial descriptors.

Specific environmental affinities

In order to construct a set of environmental descriptors for each species, while partitioning out the variance related to other common spatial processes, I adopted the following approach:

1. Perform a separate multiple regression for each environmental variable on all spatial predictors, computing the matrix of residuals $X_{\text{env.space}}$. The first five principal coordinates were used as spatial predictors as they provided the set in which residuals were most independent from space (Peres-Neto 2002). Together, these five axes accounted for 99.0% of the total spatial variation.
2. Build species-habitat models by modeling species presence-absence as a function of $X_{\text{env.space}}$ using linear discriminant analysis (LDA). The results from the LDA produced a site-by-species matrix containing probability estimates for species occurrence at each site (see Peres-Neto et al. 2001 for more details).

Morphological descriptors

Seventeen morphometric landmarks positioned in the left lateral view (Fig. 1) were digitized in three dimensions using a Microscribe-3D digitizer (Immersion Corporation). For each species, 15 adult specimens varying in size were digitized three times, resulting in 45 configurations of landmarks within a species. Configurations were superimposed by the generalized least-squares Procrustes method (Rohlf and Slice 1990; Peres-Neto and Jackson 2001a). This procedure allowed the computation of an average configuration for each species. The 25 average configurations were superimposed using the generalized orthogonal resistant fit (Rohlf and Slice 1990). This latter technique provides a better fit in the presence of anomalous landmarks and/or when species are quite different in morphology, which is the case of this study.

Differences in shape were recorded as residuals from the average configuration using the resistant fit. The 51 residuals (one x,y,z triplet for each of the 17 landmarks) for each species were then analyzed by a principal component analysis (PCA) using a variance-covariance matrix (Walker 1996). A randomization test for eigenvalues (Peres-Neto 2002) indicated that the first three axes summarized the interpretable sources of shape variation among landmarks and these were therefore retained as shape descriptors.

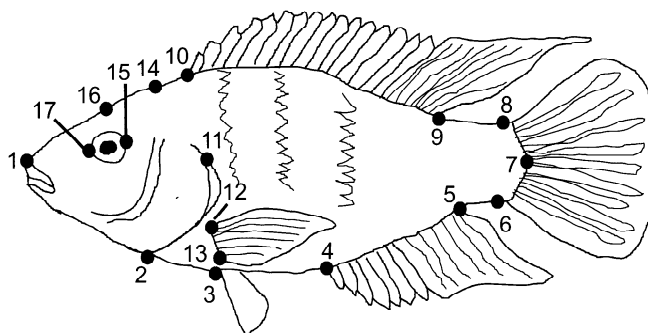


Fig. 1 The 17 landmarks used in geometric morphometric analysis

The scores from these axes were then used to summarize differences in shape.

Knowing that estimates of adult body size in fishes are problematic due to indeterminate growth, and interindividual and interpopulation differences (Gotelli and Taylor 1999), I have characterized size based on the “average” adult individual amongst the ones measured for each species. Size was estimated as the scaling factor used to scale the “average” individual to a common size in the Procrustean fit (Peres-Neto and Jackson 2001a).

Phylogenetic descriptors

Phylogenetic relationships were assessed by a composite topology based on osteological characters and molecular data. Partial cladograms constructed using maximum-parsimony methods were extracted from Buckup (1998), Montoya-Burgos et al. (1998), de Pinna (1998), Schaefer (1998), Bizerril (unpublished data) and Bockman (unpublished data). For simplicity, the cladogram is presented at the genus level (Fig. 2).

Species co-occurrence descriptors

Many indices summarize patterns in species co-occurrences, and I have chosen two indices that reflect either negative or positive associations between species.

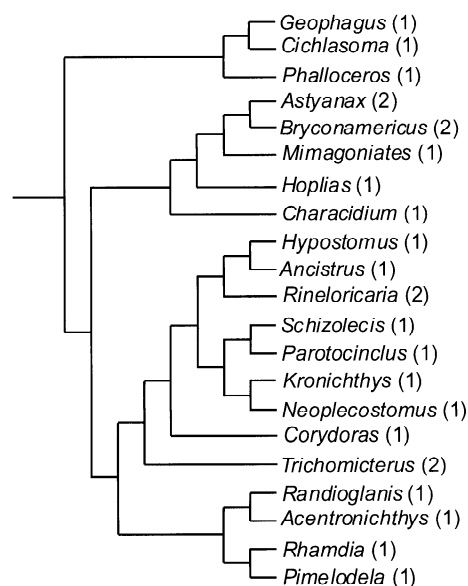


Fig. 2 Composite cladogram of taxa analyzed from the river Macacu. Number of species per genus is indicated in parentheses

1. The C-score statistic (Stone and Roberts 1992; Gotelli 2000) calculates the number of checkerboard units for all species-pair combinations (i.e., the number of sites for which species A is present and species B is absent and vice-versa). Increasing C-scores indicate an increasing degree of mutual exclusivity between species.
2. The T-score statistic (Stone and Roberts 1992) calculates the degree of togetherness by counting the number of sites where species A and B are both either present or both absent. A high T-score indicates positive co-occurrence between species.

Null models

Here I assess the degree to which environment, morphology or phylogeny influenced coexistence positively (e.g., common species-environment relationships) or negatively (e.g., different environmental requirements). For instance, did morphologically similar species tend to co-occur in the same or different sites? In the case of overdispersion (Weiher et al. 1998), species having similar trait values will tend to occupy different sites and competitive interactions may then be evoked as the process determining species co-occurrences. In the case of underdispersion (Weiher et al. 1998), species having similar trait values will tend to occupy the same sites, and abiotic filters may be then evoked as the process determining species co-occurrences. In order to assess these two possibilities, I applied two types of null model. The first one contrasted unconstrained with environmentally-constrained null models (Peres-Neto et al. 2001) in order to evaluate the extent to which positive and negative species associations may be due to similarities or differences in habitat requirements. The second type was based on niche overlap null models (Gotelli and Graves 1996; Gotelli and Ellison 2002) to assess to what extent species co-occurrences were limited by their morphologies and/or phylogenetic constraints.

Unconstrained versus environmentally constrained null models

Here two randomization approaches were applied. The first (i.e., unconstrained version) randomizes the incidence values (1/0) fixing the sum of rows (i.e., species occurrences are maintained constant). The second approach (i.e., environmentally-constrained version; Peres-Neto et al. 2001) takes into account species-environment relationships so that species are reassigned to sites during the generation of "null communities" depending on the how suitable sites are in terms of environment. I refer to this algorithm as Ct-RA1. The first step involved a single-species approach to estimate the probability of species presence or absence at each study site based on the local environmental characteristics. Here, I used the species-by-site probability estimates from the LDA above (i.e., specific environmental affinities section). This matrix contained site-occurrence probabilities for each species at each site. A high predicted probability indicates that a site contains suitable environmental conditions for species occurrence, whereas a low probability suggests a lack of suitable environmental conditions. Species are then randomized across sites based on these probabilities (see Peres-Neto 2002 for more details). In addition, I considered situations where the probability of species occurrence is low (i.e., less than 0.5), although the species is observed to be present (i.e., poor prediction by the model). Using these probabilities during the generation of "null communities" would identify these sites as unfavorable although the species is present. Therefore, I used a second algorithm Ct-RA2 that assigns a probability of 1.0 to all sites in the species-specific probability matrix where the species is actually present in the observed incidence matrix. Therefore, for Ct-RA2 only the probabilities from the species-habitat models for empty sites are used. In both protocols I maintain fixed species frequencies, so that the number of sites occupied by any species in each random matrix is the same as in the observed matrix. Note, however, that site frequencies were allowed to vary. For each of the three null models (i.e., unconstrained, Ct-RA1 and Ct-RA2) the

appropriate randomization approach was repeated a large number of times and at each time the index measuring species co-occurrence (C_{rnd} or T_{rnd}) is calculated and recorded. The observed value (C_{obs} or T_{obs}) is then contrasted to the null distribution of random values and the probability of rejection is estimated. The test is one-tailed and the probability is calculated as: (number of C_{rnd} or T_{rnd} equal to or larger than C_{obs} or $T_{\text{obs}}+1$)/(number of randomizations+1), where 1 represents the observed value for the index being evaluated and is also included as a value of the randomized distribution. For all analyses, we used 999 random permutations. Both the entire incidence matrix (i.e., average across all species-pair combinations) and species-pair associations were examined. Given that only species frequencies were kept constant while number of species per site was allowed to vary at each permutation, the probability values for the entire matrix for the C-score and T-score statistics can be different. However, if the sum of both rows and columns (i.e., species occurrences and site richness are maintained constant), then the probabilities of both indexes based on the entire matrix are exactly the same. For the constrained approach it is not possible to maintain both sums constant, hence I decided also to keep only the sum of rows constant for the unconstrained null model so that differences between the outcomes of the two models could be evaluated on a more equal basis. More details on the analytical procedures and rationales behind environmentally-constrained null models are provided in Peres-Neto et al. (2001).

In the case where species-habitat associations are extremely poor, the unconstrained and constrained null models would provide similar results (Peres-Neto et al. 2001). However, I also tested whether species co-occurrences may or may be not attributed to their responses to environmental gradients. First, a species pairwise matrix based on the Euclidean distances between the estimated site probabilities (i.e., from the LDA) was calculated. Note that, because these predictions retain only the variation in species distribution related to habitat descriptors, this pairwise matrix measures environmental affinities between species. A Procrustean randomization test (PROTEST; Peres-Neto and Jackson 2001a) was then used to test whether species differences or commonalities in terms of distribution (i.e., the species pairwise matrices containing the C-scores and T-scores) are associated with their habitat affinities (i.e., matrix containing distances in site probabilities). A PCoA was conducted on each of these matrices and the first five eigenvectors were used in the test (see Peres-Neto and Jackson 2001a for additional details). The test indicated that both negative and positive species co-occurrences are significantly associated with their variation in habitat preferences ($P < 0.001$ for both tests). Thus, it is expected that the constrained null model should indicate that a number of species associations can be explained by their differences in habitat use.

Morphological and phylogenetic overlap null models

The rationale behind these null models was that if a community is structured by competition, then species within an assemblage should be more different morphologically or phylogenetically than expected from assemblages that are comprised of random samples drawn from a pool of potential colonizers (e.g., Scheibe 1987; Juliano and Lawton 1990; Arita 1997; Weiher et al. 1998; Gotelli and Graves 1996; Lockwood et al. 1999). Alternatively, if morphological constraints limit the types of habitats in which particular species can live, species within communities should be more similar than expected by chance. The most common protocol for assessing this hypothesis is as follows. First, species packing within communities is assessed, usually by calculating the mean distance to each species' nearest neighbor (MNND) based on the matrix of interest (i.e., phylogeny, shape and size) of an assemblage of species (Ricklefs and Miles 1994; Shepherd and Kelt 1999; Peres-Neto and Jackson 2001b). Next, the observed MNND for the community in question is contrasted against a null distribution generated by randomly drawing sets of species from the pool equal in number to the real community. The likelihood that the observed MNND is different (larger or

smaller) from values expected under the null hypothesis can be estimated as the proportion of permuted sets that are equal to or smaller (or larger) than the observed.

The basic information for the class of null models described above is a pairwise distance matrix expressing species morphological or phylogenetic relationships. Species scores on the three retained shape axes and size were used to calculate two separate pairwise (shape and size) Euclidean distances between species. In the case of shape descriptors, I used scores scaled by their eigenvalues to weight axes by their respective variation (Peres-Neto and Jackson 2001b). A phylogenetic distance matrix based on the cladogram depicted in Fig. 2 was used. The probability of rejection of the null model for any particular site was calculated as follows:

1. calculate the mean of the Euclidean distances for the species in a site j to their nearest neighbors (i.e., most similar species) in the community ($MNND_{obs,j}$);
2. randomly choose the same number of species as found at site j and calculate their $MNND_{md,j}$; and (3) repeat this previous step 999 times saving each $MNND_{md,j}$. For negative interactions, the probability of rejection was assessed as (number of $MNND_{md,j}$ equal to or smaller than $MNND_{obs,j}+1$)/1000. For positive interactions, the probability of rejection was assessed as (number of $MNND_{md,j}$ equal to or larger than $MNND_{obs,j}+1$)/1000. The addition of one in both numerator and denominator included the observed value as a possible outcome under chance as well.

I applied four different models for selecting species by chance that maintained different properties of species (dispersion and colonization abilities) and sites (quality) as follows:

1. all sites were assumed to have equal probability of colonization;
2. species were assumed to have dispersal abilities equal to the number of sites occupied (i.e., species occurrence is maintained constant);
3. species occurrence and site richness was maintained; and
4. sites were environmentally constrained, as described in Peres-Neto et al. (2001).

I also applied the same four null models using the average for all species (i.e., all nearest neighbors for a given species) in sites rather than just the nearest neighbor species.

Results

Only species occurring at more than 5% of the sites were examined in all analyses. Initially, 27 species out of 35 met this criterion. However, two species, *Synbranchius marmoratus* and *Gymnotus pantherinus*, were not included in the analysis, as they do not show some homologous morphological characters with the other species. Thus, in total, 25 species in 21 genera were considered (Fig. 2). It is interesting to observe that there is a maximum of two species within each genus, and that most genera are represented by only one species.

Unconstrained versus environmentally constrained null models

Based on the entire incidence matrix, the unconstrained and constrained null models exhibited significant positive associations, but not negative ones ($C=79.7$, $P=1.000$ for all null models; $T=110.0$, $P<0.0001$ for all null models). Examining species-pair associations revealed that the number of significant associations, both positive and

negative, was reduced dramatically by the constrained null model when compared to the unconstrained version (Table 1). Thus, most negative and positive co-occurrence patterns may be explained by specific differences or similarities in habitat use rather than interspecific interactions.

Morphological and phylogenetic overlap null models

Table 2 shows the results for the morphological and phylogenetic null models. It is apparent that morphology or phylogeny did not constrain which sites each species inhabits. For illustrative purposes, I ran the same null models, but based on the environmental differences between species (Table 2, under environment). As expected, species having similar habitat use tended to inhabit the same sites. Note that results for null model 4, which represents the environmentally constrained version, were non-significant, indicating that, in fact, the constrained procedure removed common species-habitat relationships from the previous null models.

Discussion

The results of this study provide strong evidence that contemporary patterns of species co-occurrences within the Macacu River system are driven mainly by common species-habitat relationships, and that species interactions currently do not play a major role in structuring stream-fish communities. This conclusion was reached by interpreting the results of a variety of null models used to assess whether ecological attributes at the level of species distribution, habitat use, morphology, and phylogeny are consistent with the outcomes of species interactions. In all cases, there was no strong evidence indicating that species interactions produce complementary distributions or facilitation. Note that I assumed that habitat affinities and morphology are species-level traits not

Table 1 Summary results from the null models. The number of rejections for species pair-wise comparisons for different significance levels is presented. For instance, for an $\alpha=0.05$, 25 species-pairs out of a total of 300 pairs (i.e., 25 species) were negatively associated (C-score) according to the unconstrained null model. See methods for a description of Ct-RA1 and Ct-RA2

Unconstrained null models		Environmentally constrained null models	
		Ct-RA1	Ct-RA2
<i>C</i> -score			
0.01	14	1	1
0.05	25	8	8
0.10	34	12	12
<i>T</i> -score			
0.01	23	2	2
0.05	49	11	10
0.10	71	23	22

Table 2 Results of the phylogenetic and morphological null models based on sites. The reported values are the number of sites out of 53 where the null hypothesis was rejected. Null model types and test directionality (i.e., larger than and smaller than) are explained at the end of the Materials and methods section. *Null model 1* All sites have equal probability of colonization, *null model 2* species were assumed to have dispersal abilities equal to the number of sites occupied, *null model 3* species occurrence and site richness were maintained, and *null model 4* sites were environmentally constrained

	Null model			
	1	2	3	4
Phylogeny				
Larger than:				
Nearest neighbor	4	3	3	10
All neighbors	4	6	5	1
Smaller than:				
Nearest neighbor	2	2	2	1
All neighbors	1	4	3	3
Shape				
Larger than:				
Nearest neighbor	1	1	0	3
All neighbors	3	3	4	0
Smaller than:				
Nearest neighbor	2	1	2	0
All neighbors	1	1	2	0
Size				
Larger than:				
Nearest neighbor	0	0	0	2
All neighbors	1	1	1	3
Smaller than:				
Nearest neighbor	0	0	0	1
All neighbors	3	3	4	0
Environment				
Smaller than:				
All neighbors	19	21	18	0

determined by recent species interactions. Thus, both species-specific evolutionary constraints on these traits or distant-past interactions were given the same consideration as they cannot be disentangled by the framework applied in the present study. I also assumed that morphology and phylogeny characterize important ecological aspects that are perhaps not fully depicted by habitat affinities.

It is important to reiterate that the null models applied here assessed whether complementary patterns in species distribution of stream fishes are consistent with species interactions via exclusion. The results presented here, however, do not preclude that competition or facilitation may be important at other levels of habitat selection, such as microhabitat selection or in affecting local densities. Gotelli et al. (1997) suggested that patterns associated with negative co-occurrence might be classified either as ecological segregation, habitat segregation, or geographic segregation. In the first case, a number of species have similar habitat requirements, but do not seem to co-occur less often than expected by chance (*sensu* Gotelli et al. 1997), as indicated by the environmentally constrained

null model. Therefore, species do not appear to be segregated ecologically. However, the results obtained here may indicate that species interactions are also not important at other levels of species segregation. For instance, in the second case, species are habitat-segregated as indicated by the contrast between the unconstrained and environmentally constrained null models. However, this segregation is also consistent with the results of independent evolution of habitat affinities and therefore may not be the result of competitive interactions (Brooks and McLennan 1993). Finally, species in the system are not isolated to particular fractions of the watershed (Peres-Neto 2002), so geographic segregation may be also rejected. The low number of positive or negative interactions detected using the environmentally constrained null models may be explained by either elevated type I error rates, due to the number of tests being conducted (Peres-Neto 1999), or by differences or similarities in habitat requirements not captured by the variables used in the present study. Note that given that interactions between pair of species may depend on other pairs, these corrections may be not the most appropriate. In addition, even though the environmentally constrained null model can detect negative associations in cases considered non-significant by the unconstrained version (Peres-Neto et al. 2001), this did not occur for any species pair tested here (Table 1).

Temporal variation in flow regime, whether by flooding or drought, is considered the most important source of natural disturbance in stream systems (Jackson et al. 2001). Streams in the Macacu River are subject to heavy rain (1,500 mm year⁻¹), especially during November–January, and to severe tropical storms (>120 mm in a day), to frequent floods increasing flow three-fold in a few hours, and to drought (Peres-Neto 1995; Mazzoni and Lobón-Cerviá 2000). Temporal variation in species composition is also common in streams of the Serra do Mar system (e.g., Mazzoni and Lobón-Cerviá 2000), including the River Macacu (Peres-Neto 1995). I have shown elsewhere (Peres-Neto 2002) that, although there is substantial evidence of habitat specialization, colonization-extinction dynamics may play an even more important role in determining local community composition in this system. Thus, species distributions may be determined through differential adaptations to unpredictable habitat changes (Grossman et al. 1982, 1998), downplaying even further the putative role of competition. My results suggest, however, that such adaptations are not related to morphology or phylogeny, as indicated by the overlap null models (Table 2): thus, these adaptations deserve further discussion.

Recently, Taylor and Warren (2001) showed strong evidence that stream fish indeed present differential capacities to cope with environmental variability. Two of their conclusions are important for my study: species with high local abundances were better colonizers and less prone to extinction; and extinction and colonization rates were independent of species body size. Looking at the results from their Table 1, I find these rates also did not

seem phylogenetically or morphologically related. Regarding species abundances, there was an extremely strong association between average species abundance and number of sites occupied in my study ($r=0.87$, $P<0.0001$). Assuming that the species in the Macacu River have extinctions and colonization rates that are a function of the number of sites occupied, I did not find any significant association between the latter and size ($R^2=0.017$, $P=0.408$), shape ($R^2=0.126$, $P=0.504$) or phylogeny ($R^2=0.106$, $P=0.438$). This finding suggests that there is no direct association between colonization capacity and/or extinction likelihood on the one hand and these species-level traits on the other.

One main goal of this study was to assess whether species interactions, mainly competition, could account for complementary patterns in species distributions in stream landscapes. I am aware of only two studies that have attempted a similar goal. Winston (1995) used null models to test whether morphologically and phylogenetically similar species would co-occur more than expected by chance. He concluded that competition was a major force in explaining the distribution of a monophyletic group of North American cyprinids. However, Winston (1995) did not take into account differences in habitat affinities between species, as was done here. His study spanned more than 500 km, thus encompassing very heterogeneous habitats with high beta diversity (Winston 1995). Environmentally constrained null models may have accounted for a large number of the negative species-pair associations found in his study. The second study was conducted by Taylor (1996), where he assessed experimentally whether local competition could be responsible for species distribution on a regional scale. Although his experiments controlled for habitat differences, he found support for competitive interactions only in a few species pairs, which could not account for the patterns of complementary distribution found across his system.

The importance of competition in determining complementary distribution at broad spatial scales in stream-fish communities seems small, though it is shown to be important at small scales by experimental evidence in the literature. Due to the environmental variability in stream systems, there are strong arguments for accepting that species adaptations may play a more important role than competition. The net increase of species richness along gradients of high to low environmental variability (Gilliam et al. 1993), and the fact that many populations undergo substantial periodic reductions in size over time, have been used to argue that competition is a less important factor in shaping stream community structure than in more stable systems (Jackson et al. 2001). Also, populations in variable environments could be stable but at densities below where competition becomes important.

Most freshwater fish ecologists now accept the idea that scale is important when considering the various processes structuring local stream-fish communities (e.g., Angermeier and Winston 1998; see Jackson et al. 2001 for a review). Several studies at small spatial scales show the presence of competition among stream fishes (e.g.,

Resetařits 1997). However, the accumulation and interpretation of evidence from numerous isolated, small-scale studies does not provide a suitable basis for extrapolation to large-scale patterns (Bennett 1990; Underwood and Petraitis 1993). Natural experiments, like the one conducted here, can accommodate not only larger numbers of species, large spatial and long time scales, and a greater number of treatment levels and combinations, but they can also be used to control for confounding effects that could mimic the results of competition, such as differences in habitat optimums (e.g., Taylor 1996). Natural experiments where adequate designs and robust analytical tools are applied can contribute substantially to understanding the importance of different types of processes in structuring stream-fish communities. Where appropriate, subsequent experiments at small scales may elucidate whether the putative process is reasonable at smaller scales so that the power of explanation at larger scales is reinforced.

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References

- Angermeier PL, Winston MR (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79:911–927
- Arita HT (1997) Species composition and morphological structure of the bat fauna of Yucatan, Mexico. *J Anim Ecol* 66:83–97
- Bennet WA (1990) Scale of investigation and the detection of competition: an example from the house sparrow and house finch introductions in North America. *Am Nat* 135:725–747
- Bizerril CRSF (1994) Análise taxonômica e biogeográfica da ictiofauna de água doce do Leste Brasileiro. *Acta Biol Leopoldensia* 16:51–80
- Bohlke JE, Weitzman SHL, Menezes NA (1978) Estado atual da sistemática dos peixes de água doce da América do Sul. *Acta Amazon* 8:657–677
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial components of ecological variation. *Ecology* 73:1045–1055
- Bradley RA, Bradley DW (1985) Do non-random patterns of species in niche space imply competition? *Oikos* 45:443–446
- Brooks DR, McLennan DA (1993) Historical ecology: examining phylogenetic components of community evolution. In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp 267–280
- Brown JH (1987) Variation in desert rodent guilds: patterns, processes, scale. In: Giller JHR, Giller PS (eds) *Organization of communities: past and present*. Blackwell, Oxford, pp 185–203
- Buckup PA (1998) Relationships of the Characidiinae and phylogeny of Characiform fishes (Teleostei: Ostariophysi). In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (eds) *Phylogeny and classification of neotropical fishes*. EDIPUCRS, Porto Alegre, pp 123–144
- Caswell H (1976) Community structure: a neutral model analysis. *Ecol Monogr* 46:327–354

- Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition? *Ecology* 60:1132–1140
- Cook R, Quinn JF (1995) The importance of colonization in nested species subsets. *Oecologia* 102:413–424
- Gilliam JF, Fraser DF, Alkins-Koo M (1993) Structure of a tropical stream fish community: a role for biotic interactions. *Ecology* 74:1856–1870
- Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621
- Gotelli NJ, Ellison AM (2002) Assembly rule for New England ant assemblages. *Oikos* 99:591–599
- Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press, Washington, DC
- Gotelli NJ, McCabe DL (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules. *Ecology* 83:2091–2096
- Gotelli NJ, Taylor CM (1999) Testing macroecology models with stream-fish assemblages. *Evol Ecol Res* 1:847–858
- Gotelli NJ, Buckley NJ, Wiens JA (1997) Co-occurrence of Australian birds: Diamond's assembly rules revisited. *Oikos* 80:311–324
- Grossman GD, Moyle PB, Whitaker JO (1982) Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage—a test of community theory. *Am Nat* 120:423–454
- Grossman GD, Ratajczak RE, Crawford M, Freeman FC (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol Monogr* 68:395–420
- Harrel HL (1978) Response of the Devil's River (Texas) fish community to flooding. *Copeia* 1978:60–68
- Jackson DA, Somers KM, Harvey HH (1992) Null models and fish communities: evidence of nonrandom patterns. *Am Nat* 139:930–951
- Jackson DA, Peres-Neto PR, Olden JD (2001) What controls who is where in freshwater fish communities—the roles of biotic, abiotic and spatial factors? *Can J Fish Aquat Sci* 58:157–170
- Juliano SA, Lawton JH (1990) The relationship between competition and morphology. I. Morphological patterns on co-occurring dysticid beetles. *J Anim Ecol* 59:403–419
- Kelt DA, Brown JH (2001) Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In: Weiher E, Keddy P (eds) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 75–107
- Legendre P, Legendre L (1998) Numerical ecology. 2nd English edn. Elsevier, Amsterdam
- Lockwood JL, Moulton MP, Balent KL (1999) Introduced avifaunas as natural experiments in community assembly. In: Weiher E, Keddy P (eds) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 108–129
- Maurer BA (1999) Untangling ecological complexity: the macroscopic perspective. University of Chicago Press, Chicago
- Mazzoni R, Lobón-Cerviá J (2000) Longitudinal structure, density and production rates of a neotropical stream fish assemblage: the river Ubatuba in the Serra do Mar, southeast Brazil. *Ecography* 23:588–602
- Menezes NA (1972) Distribuição e origem da fauna de peixes de água doce das grandes bacias fluviais do Brasil. Comissão Internacional da Bacia Paraná/Uruguai. Faculdade de Saúde Pública USP e Instituto de Pesca, São Paulo, pp 79–108
- Monteiro LR, Reis SF (1999) Princípios de morfometria geométrica. Holos, São Paulo
- Montoya-Burgos J-I, Muller S, Weber C, Pawlowski J (1998) Phylogenetic relationships of the Loricariidae (Siluriformes) based on mitochondrial rRNA gene sequences. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (eds) *Phylogeny and classification of neotropical fishes*. EDIPUCRS, Porto Alegre, pp 363–374
- Moyle PB, Senanayake FR (1984) Resource partitioning among the fishes of rainforest streams in Sri Lanka. *J Zool (Lond)* 202:195–223
- Peres-Neto PR (1995) Estrutura de comunidades de peixes ao longo de um gradiente lótico de um rio costeiro do Leste Brasileiro (Rio Macacu, RJ). Master dissertation. Universidade Federal do Rio de Janeiro
- Peres-Neto PR (1999) How many statistical test are too many? The problem of conducting multiple inferences revisited. *Mar Ecol Prog Ser* 176:303–306
- Peres-Neto PR (2002) The distribution of fishes across stream and landscapes analytical approaches and ecological patterns. Doctoral thesis, Department of Zoology, University of Toronto
- Peres-Neto PR, Jackson DA (2001a) How well do multivariate data sets match? The robustness and flexibility of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129:169–178
- Peres-Neto PR, Jackson DA (2001b) The importance of scaling of multivariate analysis in ecological studies. *Écoscience* 8:522–526
- Peres-Neto PR, Olden JD, Jackson DA (2001) Environmentally constrained null models: site suitability as occupancy criterion. *Oikos* 93:110–120
- Pinna MCC de (1998) Phylogenetic relationships of neotropical Siluriformes: historical overview and synthesis of hypotheses. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (eds) *Phylogeny and classification of neotropical fishes*. EDIPUCRS, Porto Alegre, pp 279–330
- Poff NL, Allen JD (1995) Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* 76:606–627
- Reseratis WJ (1997) Interspecific competition and qualitative competitive asymmetry between two benthic stream fish. *Oikos* 78:429–439
- Ricklefs RE, Miles DB (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright PC, Reilly SM (eds) *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, pp 13–41
- Rodriguez MA (1995) Habitat-specific estimates of competition in stream salmonids—a field-test of the isodar model of habitat selection. *Evol Ecol* 9:169–184
- Rohlf FJ, Slice DE (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39:40–59
- Schaefer SA (1998) Conflict and resolution: impact of new taxa on phylogenetic studies of the neotropical Cascudinhos (Siluriformes: Loricariidae). In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (eds) *Phylogeny and classification of neotropical fishes*. EDIPUCRS, Porto Alegre, pp 375–400
- Scheibe JS (1987) Climate, competition, and the structure of temperate zone lizard communities. *Ecology* 68:1424–1436
- Schlösser IJ (1982) Fish community structure and function along two habitat gradients in a headwater stream. *Ecol Monogr* 52:395–414
- Schlösser IJ (1987) A conceptual framework for fish communities in small warmwater streams. In: Matthews WJ, Heins DC (eds) *Community and evolutionary ecology of North American stream fishes*. Oklahoma University Press, Oklahoma, pp 17–24
- Schluter DA (1984) A variance test for detecting species associations, with some example applications. *Ecology* 65:998–1005
- Shepherd UL, Kelt DA (1999) Mammalian species richness and morphological complexity along an elevational gradient in the arid south-west. *J Biogeogr* 26:843–855
- Siegel AF, Benson RH (1982) A robust comparison of biological shapes. *Biometrics* 38:341–350
- Silvertown J, Dodd M, Gowing D (2001) Phylogeny and the niche structure of meadow plant communities. *J Ecol* 89:428–435
- Slice DE (1994) GRF-ND: generalized rotational fitting on n-dimensional landmark data. Department of Ecology and Evolution, State University of New York, Stony Brook

- Stone L, Roberts (1992) Competitive exclusion, or species aggregation? An aid in deciding. *Oecologia* 91:419–424
- Taylor CM (1996) Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshw Biol* 36:385–396
- Taylor CM (1997) Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110:560–566
- Taylor CM, Warren ML (2001) Dynamics in species composition of stream fish assemblages: Environmental variability and nested subsets. *Ecology* 82:2320–2330
- Taylor CM, Winston MR, Matthews WJ (1993) Fish species-environment and abundance relationships in a Great Plains river system. *Ecography* 16:16–23
- Townsend CR (1989) The patch dynamics concept of stream community ecology. *J N Am Benth Soc* 8:36–50
- Underwood AJ, Petraitis PS (1993) Structure of intertidal assemblages in different locations: how can local processes be compared? In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp 39–51
- Walker JA (1996) Principal components of body shape variation within an endemic radiation of Threespine stickleback. In: Marcus LF, Corti M, Loy A, Naylor G, Slice DE (eds) *Advances in morphometrics*. NATO ASI series A: life sciences, vol 284. Plenum, New York, pp 321–334
- Webb CO (2000) Exploring the phylogenetic structure of ecological communities: an example for rainforest trees. *Am Nat* 156:145–155
- Weiher E, Keddy P (1999) Introduction: the scope and goals of research on assembly rules. In: Weiher E, Keddy P (eds) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 1–20
- Weiher E, Clarke GD, Keddy PA (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322
- Wikramanayake ED (1990) Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. *Ecology* 71:1756–1764
- Wiley EO, Mayden RL (1985) Species and speciation in phylogenetic systematics, with examples from North American fish fauna. *Annu Mo Bot Gardens* 72:596–635
- Winston MR (1995) Co-occurrence of morphologically similar species of stream fishes. *Am Nat* 145:527–545
- Wood BM, Bain MB (1995) Morphology and microhabitat use in stream fish. *Can J Fish Aquat Sci* 52:1487–1498