Hydrobiologia (2014) 734:69–79
DOI 10.1007/s10750-014-1870-0

PRIMARY RESEARCH PAPER

Broad-scale spatial patterns of canopy cover and pond morphology affect the structure of a Neotropical amphibian metacommunity

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Received: 22 July 2013 / Revised: 9 March 2014 / Accepted: 24 March 2014 / Published online: 9 April 2014

Abstract Spatial and environmental processes influence species composition at distinct scales. Previous studies suggested that the distribution of larval anurans at the landscape-scale is influenced by environmental gradients related to adult breeding site selection, such as pond canopy cover, but not by water chemistry. However, the combined effects of spatial, pond morphology, and water chemistry variables on metacommunity structure of larval anurans have not been analyzed yet. We used a partial redundancy analysis with variation partitioning to analyze the relative influence of pond morphology (e.g., depth, area, and aquatic vegetation), water chemistry, and spatial variables on a tadpole metacommunity from southeastern Brazil. We predict that pond morphology and canopy cover will influence the metacommunity at broad spatial scales, while water chemistry would play a larger role at finer scales. We found that broad-scale spatial patterns of pond canopy cover and pond morphology strongly influenced metacommunity structure, with water chemistry being not significant. Additionally, species composition was spatially autocorrelated at short distances. We suggest that the reproductive behavior of adult anurans is

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Electronic supplementary material The online version of this article (doi:10.1007/s10750-014-1870-0) contains supplementary material, which is available to authorized users.

Handling editor: Lee B. Kats

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driving tadpole metacommunity dynamics, since pond morphology, but not water chemistry affects breeding site selection by adults. Our results contribute to the understanding of amphibian species diversity in tropical wetlands.

Keywords Brazilian Atlantic Rainforest · Spatial dynamics · Species diversity · Habitat selection · Spatial scale

Introduction

Both environmental and spatial processes influence species diversity in ecological communities. The metacommunity concept is a multiscale approach useful to analyze the interplay between these environmental and spatial processes that regulate species composition and distribution at local and regional scales. The metacommunity concept has also advanced our understanding of how dispersal and patch heterogeneity influence species abundance and distribution in a set of local communities (Leibold et al., 2004).

Spatial patterns in metacommunities may arise from neutral- and niche-based mechanisms (Leibold et al., 2004; Diniz-Filho et al., 2012). Spatial distribution of species under niche-based mechanisms is driven by their distinct demographic characteristics as a result of differential responses to the environment (stabilizing mechanisms; Chesson, 2000). According to this view, individuals occupy sites along environmental gradients in order to maximize their fitness. Conversely, under neutral dynamics species are ecologically equivalent and have the same chance to give birth, die, migrate, and speciate (equalizing mechanisms; Chesson, 2000), and thus their abundance is dictated solely by stochastic demographic fluctuations. Consequently, species distribution would be random, but spatially autocorrelated, due to dispersal limitation of organisms (Leibold et al., 2004). Nonetheless, discerning the scale at which spatial processes influence ecological patterns remains a challenge for ecologists (Levin, 1992; Landeiro et al., 2011).

The joint influence of environmental and spatial processes on metacommunity structure has been largely studied on theoretical grounds (e.g., Leibold & McPeek, 2006). As a result, empirical studies on the effects of environmental and spatial processes on metacommunity structure of freshwater organisms are scarce (Logue et al., 2011). For instance, recent experiments with aquatic microorganisms found interacting effects of local environmental factors and dispersal on species richness and composition (Altermatt et al., 2011). Pond organisms with complex life cycles, such as anuran amphibians, are a useful model system to test metacommunity theory, since they are subjected to different spatial and environmental processes at the adult and larval stages. Most amphibians are dispersal-limited organisms that require wet environments to live and reproduce (reviewed in Smith & Green, 2005; Wells, 2007). Additionally, several anurans exhibit a marked philopatric behavior, breeding in the same pond in which they emerged as juveniles (Semlitsch, 2008). This complex habitat selection behavior coupled with specific environmental requirements may act as an endogenous ecological process (McIntire & Fajardo, 2009; Legendre & Legendre, 2012), creating spatial autocorrelation in species composition, i.e., ponds close to each other would have a similar species composition than farther ponds. Moreover, adults are the life stage that disperse and effectively connect breeding sites by oviposition (Wells, 2007; Semlitsch, 2008). As a result, both the spatial arrangement of water bodies and their surroundings play a role in the distribution of pond-breeding anurans and their larvae.

The dynamics of the terrestrial ecosystem surrounding ponds affect freshwater metacommunities. One aspect of the terrestrial ecosystem that strongly influences the aquatic ecosystem is pond canopy cover, which is a key gradient affecting the distribution of several freshwater organisms, from invertebrates (McCauley et al., 2008; Hoverman et al., 2011) to amphibians (Skelly et al., 1999; Werner et al., 2007). Canopy cover alters light availability and leaf litter input into ponds (Stoler & Relyea, 2010), and consequently primary productivity and decomposition (Skelly et al., 2002). As a result, larval fitness is lower in less productive, closed-canopy ponds (Skelly et al., 2002; Schiesari, 2006). Besides primary productivity, studies conducted in eastern North America show that canopy cover may affect other water chemistry variables that influence larval development, such as temperature, conductivity, and dissolved oxygen (Werner & Glennenmeier, 1999; Stoler & Relyea, 2010). As a result, the colonization of closed-canopy ponds involves a trade-off, since a few generalist species can tolerate it (Skelly et al., 1999; Werner et al., 2007), but experience lower exploitative competition and predation on the other hand (Schiesari, 2006). Nonetheless, the effects of canopy cover on anuran species seem to depend on life history strategies (e.g., larval period length; Skelly et al., 2002), on the leaf litter species (Stoler & Relyea, 2010), and on the composition of the regional species pool.

On the other hand, the influence of water chemistry on freshwater communities has been rarely investigated at the metacommunity scale (e.g., Hecnar & M'Closkey, 1996; Hájek et al., 2011). Several water chemistry variables, such as conductivity, pH, and dissolved oxygen modulate tadpole survival, development, and time to metamorphosis (reviewed in Ultsch et al., 1999). Hence, water chemistry represents the influence of within-pond environment on tadpole abundance, as expected under the species sorting perspective.

Taken together, the aforementioned environmental variables seem to differentially affect adult anurans and their larvae. On the one hand, the distribution of adult anurans seems to be more influenced by spatial processes and landscape attributes of the terrestrial ecosystem (Resetarits et al., 2005; Binckley & Resetarits, 2007; Wells, 2007). Whereas larval development, growth, and abundance might be directly influenced by pond water chemistry (Ultsch et al., 1999), although any metacommunity-scale process on adults will probably affect the distribution of their larvae. However, to the best of our knowledge, empirical studies have not tested the combined effects of spatial structure, water chemistry, and pond morphology on amphibian species composition, especially in diverse, tropical environments (see Logue et al., 2011). In particular, the characteristic complex life cycle of amphibians has the potential to simultaneously test whether different perspectives in metacommunity theory could explain community assembly.

Therefore, we hypothesized that water chemistry, and canopy cover and pond morphology variables represent two distinct mechanisms that would affect differently the metacommunity dynamics of adults and their larvae. Following McIntire & Fajardo (2009), we argued that pond morphology and canopy cover would be proxies for the effect of adult breeding site selection at the metacommunity scale, while water chemistry would represent the effects of pond environment, by influencing tadpole development and survival. Given that anurans are strongly dispersal-limited organisms and are distributed in patchy environments (ponds), it is likely that they would conform to the patch dynamics perspective. Concurrently, species sorting might also play a role, given the tendency of adult amphibians to track environmental characteristics related to breeding sites. As a result, we expect that pond morphology and canopy cover influence species composition at broad scales, while water chemistry would be more significant at finer spatial scales.

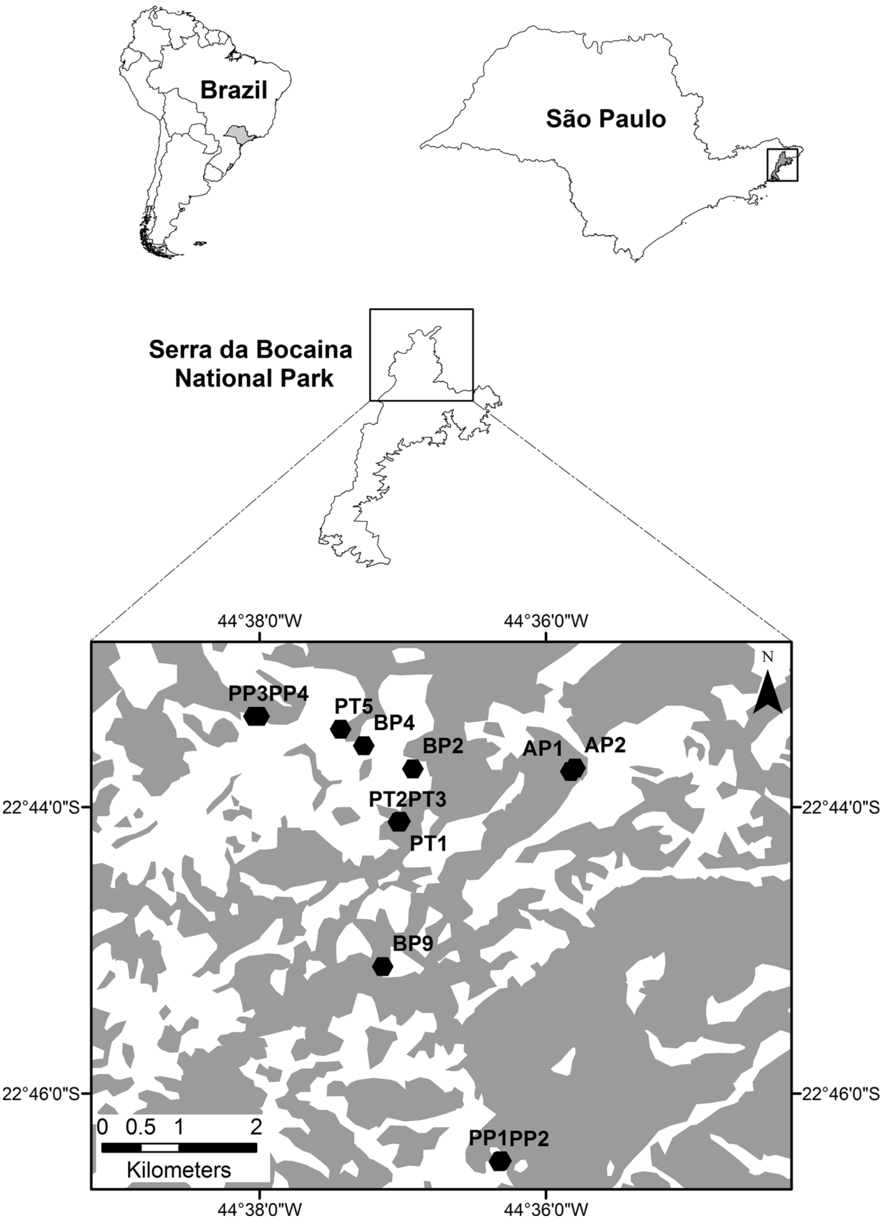
Materials and methods

Study area and sampling

This study was carried out in the Serra da Bocaina National Park (22°40′ to 23°20′S; 44°24′ to 44°54′W), at the border between the states of São Paulo and Rio de Janeiro, southeastern Brazil (Fig. 1). Samplings were conducted on the Bocaina highlands (1,500 m a.s.l.), in São José do Barreiro, São Paulo, and extended over an area of approximately 11 km^2 (ponds were 2.15 km apart in mean, maximum 6 km). The climate in this region is of the type Cwb (humid subtropical highland; Peel et al., 2007), with moderated temperatures, dry winters (between April and September) and warm summers (from October to March). The annual rainfall varies between 400 and 2,100 mm, with mean annual temperature of 22° C. The breeding season for the majority of adult anurans is during the rainy season (Garey, unpub. data). Thus, we sampled ponds in this period in order to maximize the chance of collecting most of the species.

We sampled tadpoles using a hand dipnet in 13 water bodies with different morphologies (e.g., area, depth, and aquatic vegetation) and varying degrees of canopy cover, monthly between August 2008 and January 2009. All ponds were sampled within a 1-week period each month. All ponds were fishless, and 3 out of 13 held water during only 3 months, all others were permanent ponds. Hydroperiod seems to be the main driver of the community structure of several freshwater taxa (Wellborn et al., 1996). However, since most of our ponds were permanent, we could not evaluate the role of this variable in our study system. Blind sweeps were made along the entire margins of water bodies, with effort proportional to surface area (Skelly & Richardson, 2010). Tadpoles were fixed in the field with 10% formalin. In

Fig. 1 Map showing the location of the study area and the spatial distribution of sampled ponds in the Serra da Bocaina National Park, southeastern Brazil. *Gray areas* represent primary and secondary forest; *white areas* represent open areas



addition, adult anurans were acoustically monitored monthly to record the species present in each water body, which helped in tadpole identification. When identification was not possible based on original descriptions, we reared tadpoles in aquaria until metamorphosis, feeding them with commercial fish food.

Prior to tadpole sampling, we recorded two sets of pond characteristics (Table S1): (i) water chemistry variables, namely: conductivity (mS/cm), dissolved oxygen (mg/l), pH, temperature (°C), and turbidity (NTU) using a Horiba U-10 multiparameter water quality checker; and (ii) pond morphology variables: surface area (m^2), maximum depth (m), and aquatic vegetation (%). We estimated aquatic vegetation visually by dividing pond surface into quadrants; the percentage of aquatic vegetation was used as a proxy for habitat structural complexity, varying from 0% (low complexity) to 100% (high complexity). We also recorded pond canopy cover (%) using a spherical densitometer (Forestry Suppliers, Jackson, MS, USA); measurements were taken in four directions (N, S, E, W), and the center of the pond. Pond morphology variables were measured only once at the peak of the rainy season, whereas water chemistry was measured monthly during the sampling period (Table S1). Prior to analyses, we standardized environmental variables to zero mean and unit variance to account for their different scales of measurement. Standardizations were implemented in *vegan* package (Oksanen et al., 2011) in R version 2.13.2 (R Core Team, 2011).

Spatial variables

We used distance-based Moran's Eigenvector Maps (dbMEMs; Dray et al., 2012; Legendre & Legendre, 2012) to describe spatial structures. dbMEMs (formerly called Principal Coordinates of Neighbor Matrices—PCNMs) are a class of flexible, multiscale ordination methods that produce orthogonal eigenvectors used to represent spatial relationships among sampling sites in uni- and multivariate response data (Dray et al., 2012). dbMEMs can also be divided into submodels corresponding to different spatial scales. By concentrating most of the variation, the first eigenvectors usually describe broad spatial structures, i.e., that encompass the spatial variation in the whole sampled area, while the last eigenvectors (with lower eigenvalues) describe fine spatial structures, which capture variation at the scale of sampling sites (Dray et al., 2012; Legendre & Legendre, 2012). We computed dbMEM eigenvectors from a truncated geodesic distance matrix obtained with R package *fields* (Furrer et al., 2011). The longest distance (2.887 km) connecting two ponds in a minimum spanning tree (Fig. S1) was used as a threshold to truncate the distance matrix. All ponds separated by distances lower than the threshold distance were connected, whereas those more distant than the threshold are disconnected. This procedure produced 7 dbMEMs. Analysis was conducted using R package *PCNM* (Legendre et al., 2010). Further, we implemented a forward selection procedure with double-stopping criteria (Legendre & Legendre, 2012) in R package *packfor* (Dray, 2009) to only select dbMEMs that significantly explained the variance in the species composition matrix. This procedure recovered 5 dbMEM (accumulated $R^2_{adj} = 0.414$; Fig. S2, S3). dbMEMs 1 and 2 were arbitrarily classified as broad-scale variables, dbMEM 4 as medium scale, and dbMEMs 5 and 7 as fine-scale variables (Fig. S2). dbMEMs 1 and 2 had positive spatial autocorrelation (Moran's $I = 0.291$ and 0.084, respectively), while the dbMEMs 4, 5, and 7 had negative autocorrelation (Moran's $I = -0.218$, -0.068, and -0.033, respectively). All the five selected dbMEMs were used as spatial variables in the following analysis, since excluding those with negative Moran's I seems not to change overall results (see Legendre & Legendre, 2012).

Data analyses

For all subsequent analyses, we transformed the total counts of species using the Hellinger transformation (Legendre & Legendre, 2012) to homogenize variation among species abundances. None environmental variable had a variation inflation factor higher than 3 (Zuur et al., 2010). Thus, all were included in the further analysis. We employed a variation partitioning approach to disentangle species response to environmental (pond morphology, canopy cover, and water chemistry) and spatial variables (dbMEMs) driving metacommunity structure (Legendre & Legendre, 2012). Despite some recent criticism (Gilbert & Bennett, 2010; Smith & Lundholm, 2010; but see Diniz-Filho et al., 2012), this analytical technique remains useful to separate variation in species composition explained by environmental gradients, spatial autocorrelation, and spatially structured environmental gradients (i.e., variance in species composition explained by both spatial and environmental variables). We determined the exclusive and shared effects of water chemistry, pond morphology, and pond spatial network on species composition using a partial redundancy analysis (pRDA; Legendre & Legendre, 2012), with adjusted canonical R^2 values (Legendre & Legendre, 2012). Since we sampled ponds repeatedly, we used each pond and month as factors in the pRDA and then performed a randomization stratified within ponds (Lepš & Šmilauer, 2003), with 999 Monte Carlo randomizations to determine significance. We also computed a Mantel correlogram to quantify the pattern in spatial autocorrelation of community similarity, calculated as Bray–Curtis distance, and also correlograms, with the same minimum spanning tree used to calculate dbMEMs, to analyze the spatial patterns of individual environmental variables. Analyses were

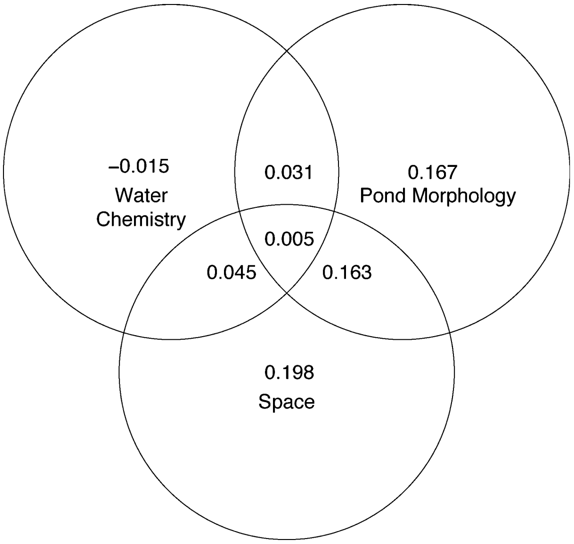


Fig. 2 Result of variation partition with partial redundancy analysis showing the pure and shared influences of spatial variables, water chemistry, and pond morphology on tadpole species composition. *Numbers* represent adjusted canonical R^2 values

implemented in R packages *vegan* (Oksanen et al., 2011) and *spdep* (Bivand, 2012). To identify the environmental variables related to each spatial model, we regressed each dbMEM (explanatory variables) against the detrended pond morphology and water chemistry (predictor variables; Borcard et al., 2004). Linearity was checked visually, using Q–Q plots.

Results

We recorded tadpoles of 15 amphibian species belonging to five families. The most abundant species were *Rhinella icterica* (3,532 individuals), *Hypsiboas* sp. (aff. *polytaenius*) with 2,339 individuals, and *Scinax* sp. (aff. *hayii*) with 2,318 individuals. The mean species richness per pond was 2.8 (±1.45 SD; range 2–9). *Chiasmocleis mantiqueira* and *Scinax* sp. (aff. *obtriangulatus*) were represented by only two individuals and were not included in further analysis, since they could affect pRDA.

Table 1 Correlations (loadings) of pond morphology and water chemistry variables with the first two RDA axes

	RDA1 (31%)	RDA2 (28%)
Temperature	0.314	−0.013
pH	−0.157	0.052
Dissolved oxigen	−0.140	−0.224
Turbidity	−0.304	0.051
Conductivity	0.183	0.101
Pond canopy cover	0.003	−0.320
Floating vegetation	−0.327	0.305
Depth	−0.228	−0.068
Area	−0.156	−0.012

Values in parenthesis are the relative eigenvalues of each axis

Both environmental variables and the spatial distribution of ponds affected metacommunity structure. Pond morphology and canopy cover accounted for 16.7% of the variation in species composition ($P = 0.005$), whereas water chemistry did not explain a significant proportion of it ($R^2_{\text{adj}} = 0.00$; $P = 0.75$; Fig. 2). Pond canopy cover and aquatic vegetation were the two environmental variables that mainly influenced species composition (Table 1; Fig. 3). The spatial component alone explained about 20% ($P = 0.005$) of the variation in species composition. Residual variation represented 40%. Furthermore, it is noteworthy that nearly all variation (16 %) in pond morphology and canopy cover were spatially structured (Fig. 2).

Species composition showed significant, positive spatial autocorrelation in the first two distance classes (between 0.01 and 1.63 km) and negative autocorrelation in the third and fourth distance classes (between 2.43 and 3.24 km; Fig. S4). Ponds separated by 2.43 km (upper limit of the third distance class) differ in composition, probably due to contrasting values at short distances of canopy cover, area, depth, and floating vegetation (Fig. S5). Water depth was related to all spatial variables (Table 2). This suggests that the variation in water depth is not related to any particular spatial scale, which hinders its interpretation in a spatial context. Floating vegetation, canopy cover, dissolved oxygen, conductivity, and area were related to one or two broad-scale dbMEMs (cf. Table 2; Fig. S2). For example, canopy cover, conductivity, and floating vegetation were negatively related to dbMEM 2. This indicates that there is a spatial gradient in these variables, in which they increase from south to north of the sampled area, since dbMEM 2 differentiates ponds in the north from those in the south (Fig. S2). Canopy cover seems also to vary significantly at the fine scale (dbMEM 7; Table 2). Temperature, pH, and turbidity were not significantly related to any spatial variable (Table 2; Fig. S5). Thus, the strong induced spatial dependence of pond morphology and canopy

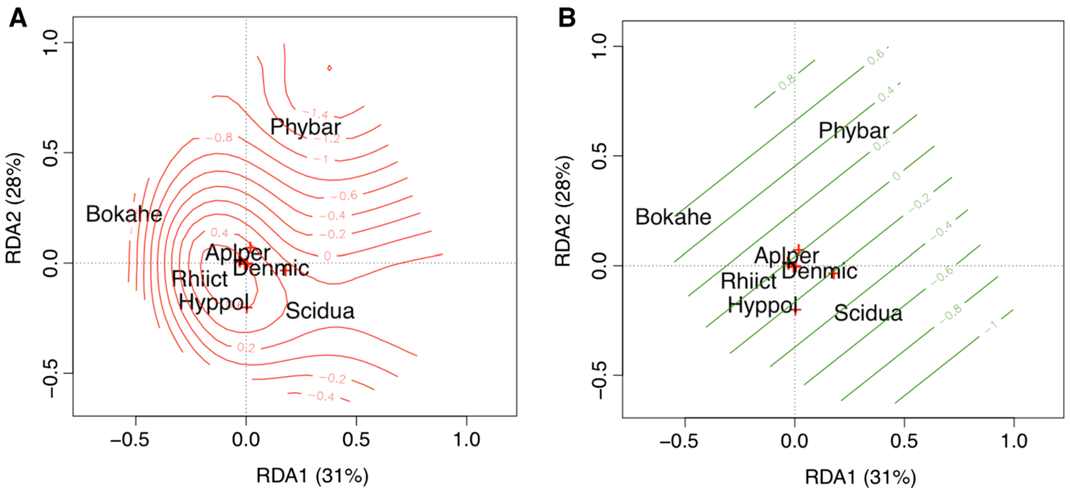


Fig. 3 Biplot of the redundancy analysis showing the major influence of **A** pond canopy cover and **B** aquatic vegetation on Hellinger-transformed data of tadpole species abundance. Isolines represent the fitted smooth surface for each environmental variable, obtained with function *ordisurf* in R package *vegan*. Only species with high scores are shown. Aplper, *Aplastodiscus perviridis*; Bokahe, *Bokermannohyla ahenea*; Denmic, *Dendropsophus microps*; Hyppol, *Hypsiboas* sp. (aff. *polytaenius*); *Phybar*, *Physalaemus barrioi*; *Rhiict*, *Rhinella icterica*; Scidua, *Scinax* sp. (aff. *duartei*)

Table 2 Standardized regression coeficients for environmental variables used to predict each spatial variable in the linear model

	dbMEM 1	dbMEM 2	dbMEM 4	dbMEM 5	dbMEM 7
Temperature	−0.170	0.007	−0.164	0.104	−0.352
pH	−0.118	0.032	0.035	0.218	0.131
Dissolved oxygen	**−0.195***	0.033	−0.136	0.177	−0.248
Turbidity	−0.100	0.054	−0.061	0.122	−0.118
Conductivity	0.138	**−0.317****	**−0.191***	0.010	0.016
Floating vegetation	**0.254***	**−0.577****	0.259	−0.274	−0.020
Canopy cover	0.176	**−0.565****	0.175	0.046	**−0.433***
Depth	**−0.542****	**−0.281****	**−0.570****	**−0.435***	**0.436***
Area	**1.037****	−0.251	**−0.233***	0.282	−0.180
R^2	**0.85****	**0.71****	**0.79****	0.36	**0.48***

All values in bold are significant at the 0.05 level

* $P < 0.05$; ** $P < 0.01$

cover ($R^2_{adj} = 0.163$; Fig. 2) is directly influencing the spatial dynamics of amphibian species. Taken together, these results suggest that species sorting and patch dynamics related to adult breeding site selection are shaping the metacommunity structure.

Discussion

We found that both the pure spatial and environmental components related to pond morphology and canopy cover accounted for a large and significant fraction of the variation in species composition. More importantly, the gradients of canopy cover and pond morphology were spatially structured. These results point to a combination of different metacommunity processes, in which both patch dynamics and species sorting play key roles. Additionally, the induced spatial dependence of variables from the surrounding terrestrial ecosystem (e.g., canopy cover) and pond morphology, which represent the effect of adult breeding site selection, suggest that the landscape-scale distribution of anuran larvae is essentially influenced by behavioral decisions of adults in response to spatially structured environmental gradients.

The broad-scale spatial pattern, which represents the scale of the sampled area, of pond morphology variables and canopy cover influenced tadpole metacommunity dynamics. This is supported by our results showing that canopy cover and pond morphology are related to broad-scale dbMEMs, while most of water chemistry variables did not show a spatial pattern. Those variables are known to influence breeding site selection by adults (Resetarits et al., 2005; Binckley & Resetarits, 2007). Canopy cover was lower in the northernmost ponds of our study area. As a result, open-canopy specialist species were more abundant in ponds of that region (except *D. minutus* and *B. ahenea*, which occur more widely, but are less abundant elsewhere). Canopy cover is a key gradient determining amphibian distribution in wetlands (Skelly et al., 1999; Werner et al., 2007), by influencing larval growth and development (Skelly et al., 2002; Schiesari, 2006; Stoler & Relyea, 2010). This preference for open- versus closed-canopy ponds allows species to coexist locally (Chesson, 2000; Chase et al., 2005), by maximizing the fitness of individuals from species with distinct life history strategies in each of those contrasting environments. Additionally, pond depth and area had a strong spatial dependence and also influenced species composition. Deeper and larger ponds have more physical space and resource diversity, allowing more species to breed. Furthermore, a taller water column allows the colonization of larvae that occupy different microhabitats (e.g., nektonic, benthic). These results support the idea that stabilizing niche differences (Chesson, 2000) related to environmental requirements for adult reproduction, which varied at the metacommunity scale, is a key mechanism structuring this metacommunity.

We also found that the pure spatial component (~20%) seems to play a larger role in shaping species composition, compared to pond morphology variables alone (16%). The high variation accounted for by the pure spatial component can be attributed either to unmeasured environmental variables or pure spatial processes, such as dispersal limitation (Landeiro et al., 2011; Legendre and Legendre, 2012). Dispersal ability varies among species in a metacommunity, and populations of some species may be more isolated than others. Dispersal in adult anurans is usually restricted to the surroundings of one breeding site or a cluster of nearby ponds (Semlitsch, 2008). As a consequence, it is difficult to assign a single mechanism (e.g., dispersal limitation, philopatry) to the pure spatial component in our study. Future studies should use a recent analysis (Diniz-Filho et al., 2012) to tease apart these two processes. Despite that limitation, previous studies, using microsatellite markers as an indirect way to estimate dispersal in anurans (Newman & Squire, 2001 and references therein), did not find population differentiation at the scale of 2 km. These data agree with our results about spatial autocorrelation in species composition, since we also did not find a differentiation in species composition in ponds separated by 2.43 km. The spatial autocorrelation in species composition at short distances seems to be driven by the induced spatial dependence of canopy cover and pond morphology variables, such as aquatic vegetation, depth, and area. Indeed, several niche-based processes predict dispersal limitation, especially when associated with spatially heterogeneous environments, demographic stochasticity, or strong, asymmetric competition (Chesson, 2000; Chase et al., 2005). Thus, despite the lack of data for dispersal ability, these results suggest that both dispersal limitation and species response to spatially structured environmental gradients (Shurin et al., 2009) could be involved in determining the dynamics of this larval metacommunity.

Contrary to our initial predictions, water chemistry variables did not influence tadpole species composition. This result is in agreement with previous studies (Hecnar & M'Closkey, 1996; Brodman et al., 2003) that analyzed the effects of water chemistry on broad-scale amphibian distribution. The development and survival of tadpoles is strongly influenced by water chemistry (reviewed in Ultsch et al., 1999) and pond drying, which affect water chemistry (Wellborn et al., 1996). Adult anurans seem to select pond to oviposit according to the presence of conspecifics and fish (Resetarits et al., 2005). Therefore, tadpole survival and development are affected by water chemistry, but its effects on the distribution of species between ponds could be weakened by variables that influence adult habitat selection behavior. Additionally, water chemistry variables seemed not to vary in a wide range at the landscape-scale in our study area. Furthermore, phenotypic plasticity (Miner et al., 2005) could play a role in mediating species coexistence and their response to water chemistry in our system. The high adaptive plasticity of tadpoles in response not only to predators (Relyea, 2004), but also to local environmental variables, food availability, and pond drying (Newman, 1992) may be a possible mechanism responsible for the lack of influence of water chemistry on species composition.

In summary, we have shown that the induced spatial dependence of pond morphology and canopy cover strongly influenced the metacommunity structure of tadpoles. These findings posit a strong role for adult behavior in determining larval ecology. Our results should be useful to explain the distribution of other organisms with similar complex life cycles, whose biomass export play a key role in linking aquatic and terrestrial ecosystems (Earl et al., 2011). The effect of the surrounding terrestrial landscape in determining community assembly of freshwater organisms deserves further investigation. For example, understanding how the spatial dynamics of terrestrial landscape and species composition modulate aquatic communities may contribute to studies modeling the flux of species and subsides, trophic interactions, and metaecosystem dynamics (Massol et al., 2011). Future studies should also evaluate how different dispersal abilities and philopatry generate spatial patterns in anuran metacommunities at multiple scales. In addition, metacommunity simulations in an environmentally homogeneous domain could evaluate how philopatric behavior and neutral dynamics create spatial patterns.

Acknowledgments We are indebted to M. Almeida Neto, F. Altermatt, L. M. Bini, J. W. Fox, V. L. Landeiro, G. F. Livingston, T. F. Rangel, and T. Siqueira for providing useful insights to this manuscript. A. Bispo and B. Vilela helped with the map. IBAMA provided collecting permits (#14474) and the staff of the Serra da Bocaina National Park kindly provided logistical support and housing. This paper is part of DBP master's-thesis at the graduate program in Biologia Animal, supported by fellowships from FAPESP (#2008/55744-6) and CAPES-DS. We greatly acknowledge the input received from L.C. Schiesari and L. Casatti as members of DBP's examining committee. MVG and TG-S were supported by FAPESP doctoral fellowships (#2008/50575-1, 2008/58979-4, respectively). DCRF thanks FAPESP (2010/52321-7) and CNPq (563075/2010-4). IAM was supported by a Jovem Pesquisador Grant from FAPESP (01/13341-3 and 06/56007-0). During the final preparation of the manuscript, DBP was supported by a CAPES-DS and CAPES-PDSE doctoral fellowships. We also thank all those who helped in the field and lab work. Voucher specimens are housed at the tadpole collection of DZSJRP-UNESP.

Note added in proof *Hypsiboas* sp. (aff. *polytaenius*) was formally described as *Hypsiboas bandeirantes,* Caramaschi and Cruz, 2013.

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