1   Broad-scale spatial patterns of canopy cover and pond morphology affect the structure of a

2   Neotropical amphibian metacommunity

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24   **Abstract**

25   Spatial and environmental processes influence species composition at distinct scales. Previous

26   studies suggested that the landscape-scale distribution of larval anurans is influenced by

27   environmental gradients related to adult breeding site selection, such as pond canopy cover, but

28   not water chemistry. However, the combined effects of spatial, pond morphology, and water

29   chemistry variables on metacommunity structure of larval anurans have not been analyzed. We

30   used a partial redundancy analysis with variation partitioning to analyze the relative influence of

31   pond morphology (e.g., depth, area, and aquatic vegetation), water chemistry, and spatial

32   variables on a tadpole metacommunity from southeastern Brazil. We predict that the

33   metacommunity will be spatially structured at broad spatial scales, while environmental

34   variables, mainly related to adult habitat selection, would play a larger role at fine spatial scales.

35   We found that broad-scale spatial patterns of pond canopy cover and pond morphology strongly

36   influenced metacommunity structure. Additionally, species composition was spatially

37   autocorrelated at short distances. We suggest that the reproductive behavior of adult anurans is

38   driving tadpole metacommunity dynamics, since pond morphology, but not water chemistry

39   affects breeding site selection by adults. Our results contribute to the understanding of amphibian

40   species diversity in tropical environments.

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42   **Keywords** Brazilian Atlantic Rainforest; spatial dynamics; species diversity; habitat selection;

43   spatial scale.

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47 **Introduction**

48 A main goal of ecology is to find causal explanations for patterns of distribution and relative

49 abundance of species (Vellend 2010). Traditionally, environmental gradients have been deemed

50 as major determinants of species distribution. However, spatial gradients may also influence the

51 assembly of ecological communities, for example as surrogates for dispersal ability (Beisner et

52 al., 2006; McIntire & Fajardo, 2009; Landeiro et al., 2011). Accordingly, spatial dynamics have

53 continuously been incorporated into community ecology through several frameworks (*e.g.*,

54 Leibold et al., 2004). The primary framework is metacommunity theory, which has advanced our

55 understanding of how dispersal and patch heterogeneity influence species abundance and

56 distribution in a set of local communities (Leibold et al., 2004). In addition, the metacommunity

57 concept represents a multiscale approach to test the joint effects of environmental and spatial

58 processes on species diversity.

59   Recent studies (Logue et al., 2011; Winegardner et al., 2012) have claimed for an

60 integrated view of the metacommunity perspectives (Leibold et al., 2004). The assumptions and

61 predictions of these perspectives differ depending on the amount of dispersal rate and patch

62 heterogeneity at play in the metacommunity. For instance, the mass effect perspective predicts

63 that species composition varies with both space and environment, when environment is spatially

64 structured (Chase et al., 2005). However, species sorting also modulates organismal responses to

65 environmental heterogeneity (Leibold et al., 2004), especially when organisms track

66 environmental characteristics related to their fitness, such as breeding site selection (Resetarits et

67 al., 2005). Nonetheless, data from a number of empirical studies have conformed usually to more

68 than one perspective (Cottenie, 2005; Logue et al., 2011).

69   Spatial patterns in metacommunities may arise from neutral- and niche-based

70   mechanisms. Spatial distribution of species under niche-based mechanisms is driven by their

71   distinct demographic characteristics as a result of differential responses to the environment

72   (stabilizing mechanisms; Chesson, 2000). According to this view, individuals occupy sites along

73   environmental gradients in order to maximize their fitness. Conversely, under neutral dynamics

74   species are ecologically equivalent (equalizing mechanisms) and have the same chance to give

75   birth, die, migrate, and speciate (equalizing mechanisms; Chesson, 2000), and thus their

76   abundance is dictated solely by stochastic demographic fluctuations. Consequently, species

77   distribution would be random, but spatially autocorrelated, due to dispersal limitation of

78   organisms (equalizing mechanisms; Leibold et al., 2004). Nonetheless, discerning the scale at

79   which spatial processes influence ecological patterns remains a challenge for ecologists (Levin,

80   1992; Landeiro et al., 2011).

81   The joint influence of environmental and spatial processes on metacommunity structure

82   has been largely studied on theoretical grounds (Leibold & McPeek, 2006). As a result, empirical

83   studies on the effects of environmental and spatial processes on metacommunity structure of

84   freshwater organisms are scarce, especially in tropical environments (Logue et al., 2011). For

85   instance, recent experiments with aquatic microorganisms found interacting effects of local

86   environmental factors and dispersal on species composition and diversity (Cadotte, 2006;

87   Altermatt et al., 2011). Pond organisms with complex life cycles, such as anuran amphibians, are

88   a useful model system to test metacommunity theory, since they are subjected to different spatial

89   and environmental processes at the adult and larval stages. Most amphibians are dispersal-

90   limited organisms that require wet environments to live and reproduce (reviewed in Smith &

91   Green, 2005; Wells, 2007). Additionally, several anuran amphibians exhibit a marked philopatric

92   behavior, breeding in the same pond in which they emerged as juveniles (Semlitsch, 2008),

93   which reinforces the potential effects of both environmental and spatial processes on anuran

94   metacommunity structure. This complex habitat selection behavior coupled with specific

95   environmental requirements may act as an endogenous ecological process (McIntire & Fajardo,

96   2009; Legendre & Legendre, 2012), creating spatial autocorrelation in species composition.

97   Moreover, adults are the life stage that disperse and effectively connect breeding sites by

98   oviposition (Wells, 2007; Semlitsch, 2008). As a result, both the spatial arrangement of water

99   bodies and their surroundings may play a role in the distribution of pond-breeding anurans and

100   their larvae.

101   The dynamics of the terrestrial ecosystem surrounding ponds strongly also affects

102   freshwater metacommunities. One aspect of the terrestrial ecosystem that strongly influences the

103   aquatic ecosystem is pond canopy cover, which is a key gradient affecting the distribution of

104   several freshwater organisms, from odonate larvae (McCauley et al., 2008), to tadpoles (Skelly et

105   al., 1999; Werner et al., 2007), to snails (Hovermann et al., 2011). Canopy cover alters light

106   availability and leaf litter input into ponds, and consequently primary productivity and

107   decomposition (Werner et al., 2007). As a result, larval fitness is lower in less productive,

108   closed-canopy ponds (Schiesari, 2006). Besides primary productivity, canopy cover may affect

109   other water chemistry variables that influence larval development, such as temperature,

110   conductivity, and dissolved oxygen (Werner & Glennenmeier, 1992). Consequently, few species

111   tolerate and colonize closed-canopy ponds, but those that do benefit from lower exploitative

112   competition (Schiesari, 2006).

113   On the other hand, the influence of water chemistry on freshwater communities has been

114   rarely investigated at the metacommunity scale (*e.g.*, Hecnar & M'Closkey, 1996; Hajek et al.,

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115   2011). Several water chemistry variables modulate tadpole survival, development, and time to

116   metamorphosis. Conductivity is often correlated with dissolved ions and solids, mineral particles,

117   disturbance or eutrophication that affect osmoregulation and larval development (Welch &

118   MacMahon, 2005). Low pH disrupts the Ca:Na ratio, directly influencing survival. Temperature

119   and dissolved oxygen affect metabolic rates and directly influence time to metamorphosis and

120   larval fitness (reviewed in Ultsch et al., 1999). Turbidity is related to the trophic status of ponds

121   (Scheffer et al., 1993). Hence, water chemistry may represent the influence of local environment

122   on tadpole relative abundance, as expected under the species sorting perspective.

123   Taken together, the aforementioned environmental variables seem to differentially affect

124   adult anurans and their larvae. On the one hand, the distribution of adult anurans seems to be

125   more influenced by spatial processes and landscape attributes of the terrestrial ecosystem

126   (Resetarits et al., 2005; Binckley & Resetarits, 2007; Wells 2007). On the other hand, larval

127   development, growth, and abundance might be directly influenced by local water chemistry

128   (Ultsch et al., 1999), although any metacommunity-scale process on adults will probably affect

129   their larvae. However, to the best of our knowledge, empirical studies have not tested the

130   combined effects of spatial structure, water chemistry, and pond morphology on amphibian

131   species composition, especially in diverse, tropical environments (see also Logue et al., 2011). In

132   particular, the complex life cycle characteristic of amphibians has the potential to simultaneously

133   test whether different perspectives in metacommunity theory could explain community

134   assembly.

135   Therefore, we hypothesized that these two sets of environmental variables represent

136   alternative mechanisms driving metacommunity dynamics. Following McIntire & Fajardo

137   (2009), we argued that pond morphology and canopy cover could be proxies for the effect of

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138   adult breeding site selection at the metacommunity scale, while water chemistry represented the

139   local effects of pond environment, by influencing tadpole development and survival. In this

140   framework, closed-canopy ponds are harsh environments, acting as a sink, whereas open-canopy

141   ponds are more favorable, source environments. Therefore, we hypothesize that a mass effect

142   may be involved in maintaining populations in closed-canopy ponds, which disperse from open-

143   canopy. Concurrently, species sorting may also play a role in amphibian metacommunities, given

144   the low dispersal ability of adults, and their tendency to track environmental characteristics

145   related to breeding sites. As a result, we expect that pond morphology and canopy cover

146   influence species composition at broad scales, while water chemistry would be more significant

147   at fine spatial scales.

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149   **Material and methods**

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151   Study area and sampling

152   This study was carried out in the Serra da Bocaina National Park (22º 40' to 23° 20' S; 44° 24' to

153   44° 54' W), at the border between the states of São Paulo and Rio de Janeiro, southeastern Brazil

154   (Fig. 1). Our samples were collected on the Bocaina highlands (1,500 m a.s.l.), in São José do

155   Barreiro, São Paulo, and extended over an area of approximately 11 Km^2 (ponds were 2.15 Km

156   apart in mean, maximum 6 Km). The climate in this region is of the type Cwb (humid

157   subtropical highland) according to the Köppen-Geiger classification (Peel et al., 2007), with

158   moderated temperatures, dry winters (between April and September) and warm summers (from

159   October to March). The annual rainfall varies between 400 and 2100 mm, with mean annual

160   temperature of 22º C. The breeding season for the majority of adult anurans is during the rainy

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161 season (M.V. Garey, unpub. data). Thus, we sampled ponds in this period in order to maximize

162 the chance of collecting most of species.

163 We sampled tadpoles using a hand dipnet in 13 water bodies with different morphologies

164 (e.g., area, depth, and aquatic vegetation) and varying degrees of canopy cover, monthly between

165 August 2008 and January 2009. All ponds were sampled within a one-week period each month.

166 All ponds were fishless, and 3 out of 13 held water during only three months, all others were

167 permanent ponds. Blind sweeps were made along the entire margins of water bodies, with effort

168 proportional to surface area (Skelly & Richardson, 2010). Tadpoles were fixed in the field with

169 10% formalin. In addition, adult anurans were acoustically monitored monthly to record the

170 species present in each water body, which would help in tadpole identification.

171 Prior to tadpole sampling, we recorded two sets of pond characteristics: (i) water

172 chemistry variables, namely: conductivity (mS/cm), dissolved oxygen (mg/l), pH, temperature

173 (ºC), and turbidity (NTU) using a Horiba U-10 multiparameter water quality checker; (ii) pond

174 morphology variables: surface area (m^2), maximum depth (m), and aquatic vegetation (%). We

175 estimated aquatic vegetation visually by dividing pond surface into quadrants; the percentage of

176 aquatic vegetation was used as a proxy for habitat structural complexity, varying from 0 (low

177 complexity) to 100% (high complexity). We also recorded pond canopy cover (%) using a

178 spherical densitometer (Forestry Suppliers, Jackson, MS, U.S.A.); measurements were taken in

179 four directions (N, S, E, W), and the center of the pond. Pond morphology variables were

180 measured only once at the peak of the rainy season, whereas water chemistry was measured

181 during all sampling period. Prior to analyses, we standardized environmental variables to zero

182 mean and unit variance to account for their different scales of measurement. Calculations were

183 implemented in *vegan* package (Oksanen et al., 2011) in R version 2.13.2 (R Core Team, 2011).

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185   Spatial variables

186   We used distance-based Moran's Eigenvector Maps (dbMEM; Dray et al., 2012; Legendre &

187   Legendre, 2012) to describe spatial structures. We computed dbMEM eigenvectors from a

188   truncated geodesic distance matrix obtained with R package *fields* (Furrer et al., 2011). The

189   longest distance (2.887 Km) connecting two ponds in a minimum spanning tree of sampling sites

190   (Fig. S1) was used as a threshold to truncate the distance matrix. This procedure produced 7

191   dbMEMs. Analysis was conducted using R package *PCNM* (Legendre et al., 2010). By

192   concentrating most of the variation, the first eigenvectors usually describe broad spatial

193   structures, while last eigenvectors describe fine spatial structures (Dray et al., 2012; Legendre &

194   Legendre, 2012). Further, we implemented a forward selection procedure with double-stopping

195   criteria (Legendre & Legendre, 2012) in R package *packfor* (Dray, 2009) to only select dbMEMs

196   that significantly explained the variance in the species composition matrix. This procedure

197   recovered 5 dbMEM (accumulated $R^2_{adj} = 0.414$; Fig. S2-S3). dbMEM 1 and 2 were arbitrarily

198   classified as broad-scale variables, dbMEM 4 as medium scale, and dbMEM 5 and 7 as fine-

199   scale variables (Fig. S2). The first two dbMEMs modeled positive spatial autocorrelation

200   (Moran's $I = 0.291$ and 0.084, respectively), while the last three modeled negative

201   autocorrelation (Moran's $I = -0.218$, -0.068, and -0.033, respectively). All eigenvectors were

202   used as spatial variables in the following analysis, since excluding those with negative Moran's I

203   seems not to change overall results (see Legendre & Legendre, 2012).

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207   Data analyses

208   For all subsequent analyses, we transformed the total counts of species using the Hellinger

209   transformation (Legendre & Legendre, 2012) to homogenize variation among species

210   abundances. None environmental variable had a Variation Inflation Factor higher than 3. Thus,

211   all were included in the further analysis. We employed a variation partitioning approach to

212   disentangle species response to environmental (pond morphology, canopy cover, and water

213   chemistry) and spatial variables (dbMEMs) driving metacommunity structure (Cottenie, 2005;

214   Legendre & Legendre, 2012). Despite some recent criticism (Gilbert & Bennett, 2010; Smith &

215   Lundholm, 2010; but see Diniz-Filho et al., 2012), this analytical technique remains useful to

216   separate variation in species composition generated by environmental gradients, spatial

217   autocorrelation, and spatially structured environmental gradients (shared variance). We

218   determined the pure and shared effects of water chemistry, pond morphology, and pond spatial

219   network (dbMEM) on species composition using a partial Redundancy Analysis (pRDA;

220   Legendre & Legendre, 2012), with adjusted canonical R^2 values (Legendre & Legendre, 2012).

221   Since we sampled ponds repeatedly, we used each pond and month as factors in the pRDA and

222   then performed a randomization stratified within ponds (Lepš & Šmilauer, 2003), with 999

223   Monte Carlo randomizations to determine significance. We also built a Mantel correlogram to

224   investigate the spatial pattern of species composition and also correlograms to analyze the spatial

225   patterns of environmental variables. Analyses were implemented in R packages *vegan* (Oksanen

226   et al., 2011) and *spdep* (Bivand, 2012). To identify the environmental variables related to each

227   spatial model, we regressed each dbMEMs (explanatory variables) against pond morphology and

228   water chemistry (predictor variables; Borcard et al., 2004). Linearity was checked visually.

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Results

We recorded tadpoles of 15 amphibian species belonging to 5 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 ($\pm$ 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.

Both environmental variables and spatial distribution of ponds affected metacommunity structure. Pond morphology and canopy cover accounted for 16 % (P = 0.005), whereas water chemistry did not explain a significant proportion of the variation in species composition (R^2_{adj} = 0.00; P = 0.75; Fig. 2). Pond canopy cover and aquatic vegetation were the two variables that mainly influenced species composition (Table 1; Fig. 3). The pure spatial component explained about 20 % (P = 0.005) of the variation in species composition. Residual variation represented 40 %. Furthermore, it is noteworthy that 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 of canopy cover, area, depth, and aquatic vegetation at short distances (Fig. S5). Water depth was the most important variable, explaining all spatial variables. Other variables were related to one or two broad-scale dbMEMs. Temperature, pH, and turbidity were not significantly related to any

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253   spatial variable (Table 2). Thus, the strong induced spatial dependence of pond morphology and

254   canopy cover (R^2_{adj}=0.16; Fig. 2), but not water chemistry (R^2_{adj}=0.04; Fig. 2) are directly

255   influencing the spatial dynamics of amphibian species. Taken together, these results suggest that

256   species sorting and mass effects related to adult breeding site selection are shaping

257   metacommunity structure.

258

259   **Discussion**

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261   We found that both the pure spatial and environmental component related to pond morphology

262   and canopy cover accounted for large and significant fractions of the variation in species

263   composition. More importantly, the gradients of pond canopy cover and morphology were

264   spatially structured. These results point to a combination of different metacommunity processes,

265   in which both mass effects and species sorting are playing key roles in metacommunity

266   dynamics. Additionally, the induced spatial dependence of variables from the surrounding

267   terrestrial ecosystem (i.e., pond morphology and canopy cover), which we hypothesized to

268   represent the effects of adult breeding site selection, suggest that spatial dynamics of anuran

269   larvae is essentially determined by behavioral decisions of adults in response to spatially

270   structured environmental gradients.

271   All of the variation in species composition accounted for by pond morphology and

272   canopy cover was spatially structured. We hypothesized that canopy cover and other pond

273   morphology variables represented the effects of the surrounding terrestrial landscape on adult

274   habitat selection (Resetarits et al., 2005; Binckley & Resetarits, 2007). In this sense, tadpole

275   metacommunity structure seems to be essentially determined by environmental characteristics

276   that vary at the metacommunity scale (i.e., pond morphology), in contrast to local, pond water

277   chemistry variables. Furthermore, we also showed that the pure spatial processes (~ 20%) seem

278   to play a larger role in shaping species composition, compared to pond morphology variables

279   alone (16%). The high variation accounted for by the pure spatial component can be attributed

280   either to unmeasured environmental variables or pure spatial processes, such as dispersal

281   limitation (Landeiro et al., 2011; Legendre and Legendre, 2012). Indeed, several niche-based

282   processes predict dispersal limitation, especially when associated with spatially heterogeneous

283   environments, demographic stochasticity, or strong, asymmetric competition (Chesson, 2000;

284   Chase et al., 2005).

285   The broad-scale spatial pattern of pond morphology variables and canopy cover seems to

286   influence tadpole metacommunity dynamics. These variables are also known to influence

287   breeding site selection by adults (Resetarits et al., 2005; Binckley & Resetarits, 2007; Skelly et

288   al., 1999; Werner & Glennemeier, 1999). An experimental study (Binckley & Resetarits, 2007)

289   showed that treefrogs actively selected open-canopy ponds and deposited significantly more eggs

290   in these ponds than in closed-canopy ponds. Additionally, treefrogs and aquatic beetles

291   discriminated between fish and fishless ponds for oviposition sites. In our study area, canopy

292   cover was lower in the northernmost ponds (Table 2). As a result, species inhabiting open-

293   canopy ponds are more abundant in that region (except *D. minutus* and *B. ahenea*, which occur

294   more widely, but are less abundant elsewhere). These results support the idea that stabilizing

295   niche differences (Chesson, 2000) related to different environmental requirements for adult

296   reproduction as key mechanisms structuring this metacommunity.

297   Contrary to our initial prediction about within-pond community structure, water

298   chemistry variables do not seem to influence tadpole species composition. This result is in

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299   agreement with previous studies on amphibians (Hecnar & M'Closkey, 1996; Brodman et al.,

300   2003). Other abiotic (e.g., pond canopy cover, productivity, hydroperiod) and biotic variables

301   (e.g., presence of fish) may be more important than water chemistry in determining pond

302   colonization by adults and survival of tadpoles. Additionally, water chemistry variables seemed

303   not to vary in a wide range at the landscape-scale in our study area. Phenotypic plasticity

304   mediates species coexistence in ecological communities and also their response to environmental

305   variation (Miner et al., 2005). The high adaptive plasticity of tadpoles in response not only to

306   predators (Relyea and Werner, 2000), but also to local environmental variables, food availability,

307   and pond drying (Newman, 1992) is a possible mechanism responsible for the lack of influence

308   of water chemistry on species composition.

309   The spatial autocorrelation in species composition at short distances seems to be driven

310   by the induced spatial dependence of pond morphology variables, such as aquatic vegetation,

311   depth, area, and canopy cover. However, it is difficult to tease apart if species composition is

312   spatially autocorrelated due to dispersal limitation or due to species response to spatially

313   structured environmental variables, or even a combination of both (Shurin et al., 2009). Dispersal

314   ability varies among species in a metacommunity and populations of some species may be more

315   isolated than others. Dispersal in adults is usually restricted to the surroundings of one breeding

316   site or a cluster of ponds nearby (Semlitsch, 2008). As a consequence, it is still difficult to assign

317   a single mechanism (e.g., dispersal limitation, philopatry) to the pure spatial component. Despite

318   that limitation, previous studies using microsatellite markers as an indirect way to estimate

319   dispersal in anurans (Newman & Squire, 2001 and references therein) did not find population

320   differentiation at the scale of 2 km. These data agree with our results about spatial

321   autocorrelation in species composition, since we also did not find a differentiation in species

322   composition of ponds separated by 2.43 Km. Thus, despite the lack of data for dispersal ability,

323   these results could suggest that both dispersal limitation and responses to spatially structured

324   environmental variables can be involved in the dynamics of this larval metacommunity.

325   In summary, we have shown that the induced spatial dependence of pond morphology

326   and canopy cover strongly influenced the tadpole metacommunity structure. These findings posit

327   strong role for adult behavior in determining larval ecology. It might be possible to extrapolate

328   our results to explain the distribution of other organisms with similar complex life cycles that

329   represent an important link between aquatic and terrestrial ecosystems and play a key role in

330   biomass export (Earl et al., 2011). The effect of the surrounding terrestrial landscape in

331   determining species assembly in the adjacent, aquatic ecosystem deserves further investigation in

332   other freshwater organisms. For example, understanding how the spatial dynamics of terrestrial

333   landscape and species composition modulate aquatic communities may contribute to studies

334   modeling the flux of species and subsides, trophic interactions, and metaecosystem dynamics

335   (Massol et al., 2011). Future studies should also integrate the effects of broad- and fine-spatial

336   scales on amphibian species with different dispersal abilities. In addition, metacommunity

337   simulations in an environmentally homogeneous domain could evaluate how philopatric

338   behavior and neutral dynamics create spatial patterns.

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340   **Acknowledgments**

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475

476   Figure legends

477

478   Fig. 1. Map showing the location of the study area and the spatial distribution of sampled ponds

479   in the Serra da Bocaina National Park, southeastern Brazil. Gray areas represent primary or

480   secondary forest; white areas represent open areas.

481

482   Fig. 2. Result of variation partition with partial Redundancy Analysis showing the pure and

483   shared influences of spatial variables, water chemistry, and pond morphology on tadpole species

484   composition. Numbers represent adjusted canonical R^2 values.

485

486   Fig. 3. Biplot of the Redundancy analysis showing the major influence of A) pond canopy cover

487   and B) aquatic vegetation on Hellinger-transformed data of tadpole species abundance. Isolines

488   represent the fited smooth surface for each environmental variable, obtained with function

489   *ordisurf* in R package *vegan*. Only species with high scores are shown. Aplper=*Aplastodiscus*

490   *perviridis*, Bokahe=*Bokermannohyla ahenea*, Denmic= *Dendropsophus microps*,

491   Hyppol=*Hypsiboas* sp. (aff. *polytaenius*), Phybar=*Physalaemus barrioi*, Rhiict=*Rhinella*

492   *icterica*, Scidua=*Scinax* sp. (aff. *duartei*).

−0.015
Water
Chemistry

0.031

0.167
Pond Morphology

0.005

0.045

0.163

0.198
Space

A

RDA2 (28%)

Phybar

Bokahe

Aplder
Denmic
Rhlict
Hyppol   Scidua

RDA1 (31%)

B

RDA2 (28%)

Phybar

Bokahe

Aplder
Denmic
Rhlict
Hyppol   Scidua

RDA1 (31%)