

# 1 Predator phylogenetic diversity decreases 2 predation rate via antagonistic interactions

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## 12 **Abstract**

13 **Background:** Predator assemblages can differ substantially in their top- down effects on  
14 community composition and ecosystem function, but few studies have sought to explain  
15 this variation in terms of the phylogenetic distance between predators. The effect of a local  
16 predator assemblage will depend on three things – which predators tend to co-occur, how  
17 similar their prey preferences are, and how they interact with each other and the whole  
18 community. Phylogenetic distance between predators may correlate with each of these  
19 processes, either because related predators are more likely to share the same traits, and  
20 therefore have similar habitat and prey preferences, or because predators are more likely to  
21 compete, and therefore diverge in habitat and prey preferences. Therefore, the phylogenetic  
22 structure of predator assemblages could provide a unifying framework for predicting how  
23 predators will impact their prey - and therefore any ecosystem functions mediated by their  
24 prey.

25 **Methods:** We examined the effects of predators on macroinvertebrate food webs found  
26 in bromeliads, combining field observations, laboratory feeding trials and a manipulative  
27 experiment. We determined whether the phylogenetic distance between predators could  
28 explain: the co-observed occurrence of predator species among bromeliads, overlap in prey  
29 preferences under no-choice conditions, and effects of predator composition on prey survival,  
30 prey composition and ecosystem processes.

31 **Results:** We found that phylogenetic distance does not predict either the co-occurrence  
32 of predator species nor the overlap in their prey preferences. However, our manipulative  
33 experiment showed that prey mortality decreased as the phylogenetic distance between

34 predator species increased, reflecting antagonistic interactions among more distant predators.  
35 These effects of phylogenetic distance on prey mortality did not translate into effects on  
36 ecosystem function, as measured by rates of detrital decomposition and nitrogen cycling.  
37 **Discussion:** We conclude that the effects of predator phylogenetic diversity on the  
38 bromeliad food web are primarily determined by antagonistic predator-predator interac-  
39 tions, rather than habitat distribution or diet overlap. This study illustrates the potential  
40 of a phylogenetic community approach to understanding food webs dynamics.

## 41 **Introduction**

42 Predators can have strong top-down effects, both on community structure and ecosystem  
43 processes (Estes et al. 2011). The combined effect of predator species on communities is often  
44 stronger or weaker than that predicted from a study of those same species in isolation (Sih  
45 et al. 1998; Ives et al. 2005). These non-additive effects occur when predators interact with  
46 each other directly, or via their shared prey species. For example, predators feed directly on  
47 each other (intra-guild predation), consume the same prey (resource competition) or modify  
48 the behaviour of prey or other predator species (Sih et al. 1998; Nyström et al. 2001;  
49 Griswold and Lounibos 2006). These non-additive effects can be positive or negative. For  
50 example, prey may have an induced defense against one predator which increases (negative  
51 non-additive effect) or decreases (positive non-additive effect) the likelihood of consumption  
52 by a second predator. While there are many possible mechanisms underlying the effect of  
53 predator composition, we lack a means of predicting *a priori* the strength and direction of  
54 this effect on community structure and ecosystem function.

55 The phylogenetic relationships among predators could provide a framework for combining  
56 different approaches to studying predator-predator interactions, thus helping us make predic-  
57 tions about combined effects of predators. A phylogenetic approach to species interactions  
58 extends the measurement of species diversity to include the evolutionary relationships be-  
59 tween species. Relatedness may be a proxy for ecological similarity; very similar species may  
60 compete strongly, and/or may interfere with each other while very different species may  
61 not be able to occur in the same patch. This approach was first used to interpret observa-  
62 tions of community structure, as ecologists interpreted nonrandom phylogenetic structure  
63 (i.e.~under- or over- dispersion) as evidence for processes, such as habitat filtering or com-  
64 petition, which structure communities (Webb et al. 2002; Cavender-Bares et al. 2009).  
65 Recently, this approach has been applied to manipulative experiments. For example, the  
66 phylogenetic diversity of plant communities is a better predictor of productivity than ei-  
67 ther species richness or diversity (Cadotte et al. 2008; e.g. Cadotte et al. 2009; Godoy  
68 et al. 2014). In all cases, an implicit assumption is that increased phylogenetic distance  
69 is associated with increased ecological dissimilarity – either in the form of differences in  
70 species niches, interactions, or functional traits. When this is true, high phylogenetic diver-  
71 sity should lead to complementarity in resource use between species, resulting in increased  
72 ecosystem functioning (Srivastava et al. 2012).

73 Phylogenetic diversity may be a better predictor of species effects on ecosystem functioning  
74 than species identity alone. For example, studies of plants (Cadotte et al. 2008) have shown  
75 that ecosystem function is positively related to the phylogenetic diversity of plants. Although  
76 there have been many studies taking a phylogenetic approach to community ecology and

77 although predators have large effects on many communities, the phylogenetic diversity of  
78 local predator assemblages has rarely been measured (Bersier and Kehrli 2008; Naisbit et  
79 al. 2011). Many studies of phylogeny and predator traits focus on whole clades, rather than  
80 local assemblages (e.g. *Anolis* lizards (Knouft et al. 2006), warblers (Böhning-Gaese et al.  
81 2003), tree boas (Henderson et al. 2013) and wasps (Budriene and Budrys 2004)), making  
82 it difficult to connect these results to predator effects at the scale of a local community.  
83 These clade specific studies often find weak evidence for phylogenetic signal in ecologically  
84 relevant traits. In contrast, studies at the level of the whole biosphere (Bersier and Kehrli  
85 2008; Gómez et al. 2010) demonstrate that related organisms often have similar interspecific  
86 interactions, i.e. related predators often consume similar prey. At the local scale, only a few  
87 studies have examined how phylogeny may shape food webs (Rezende et al. 2009; Cagnolo et  
88 al. 2011); these observational studies found that models containing both relatedness (either  
89 from taxonomic rank or phylogenetic trees) and body size were better at predicting which  
90 predator-prey interactions occurred than models with body size alone. As observational  
91 studies, however, they cannot isolate if it is differences in predator distribution or diet that  
92 leads to a phylogenetic signal in predator-prey interactions, nor how these interactions affect  
93 the whole community.

94 Can phylogeny help us predict how predators will impact community composition and ecosys-  
95 tem functioning? Within a local community, the effect of predator species diversity will  
96 depend on three factors: how predators are distributed among habitats, how they interact  
97 with their prey, and how they interact with each other. To the extent that phylogenetic  
98 relationships are correlated with these three factors, they enable us to predict the impact of

99 predator diversity on communities. For instance, phylogeny could constrain predator species  
100 co-occurrence if more distant relatives have more distinct fundamental niches, whereas close  
101 relatives are too similar to co-exist (Webb et al. 2002; Emerson and Gillespie 2008). When  
102 predators do co-occur, phylogeny may correlate with their feeding behavior, such that closely  
103 related predators consume similar prey. For example, diet overlap (shared prey species be-  
104 tween predators) will depend on the feeding traits and nutritional requirements of predators  
105 – both of which may be phylogenetically conserved. If this is the case, then predator as-  
106 semblages with higher phylogenetic diversity will show a greater range of prey consumed  
107 and therefore stronger top- down effects (Finke and Snyder 2008). In some cases, predator  
108 diets may extend to include other predators, leading to direct negative interactions such  
109 as intraguild predation, which may also have a phylogenetic signal (Pfennig 2000). To our  
110 knowledge, the relationship of phylogeny to predator distribution, diet, and intraguild inter-  
111 actions has never been investigated in a single study.

112 We tested for the effects of phylogenetic distance on the distribution, diet and interactions  
113 of predators living in a natural mesocosm: water reservoirs found inside bromeliad leaves.  
114 Bromeliads (Bromeliaceae) are flowering plants abundant in the Neotropics. Within this  
115 aquatic food web, damselfly larvae (e.g. *Leptagrion* spp., Odonata:Coenagrionidae) are  
116 important predators that dramatically reduce insect colonization (Hammill et al. 2015)  
117 and emergence (Starzomski et al. 2010), and increase nutrient cycling (Ngai and Srivas-  
118 tava 2006). In addition to damselfly larvae, other predators are also found in bromeliads,  
119 including large predaceous fly larvae (Diptera: Tabanidae) and predatory leeches (Hiru-  
120 dinae:Arhynchobdellida) (see Frank et al. (2009)). Many bromeliads contain water and

121 trapped, terrestrial detritus which supplies nutrients for the bromeliad (Reich et al. 2003).  
122 The small size of these habitats permits direct manipulations of entire food webs, manipula-  
123 tions which would be difficult in most natural systems. Predators have been shown to have  
124 large top-down effects on ecosystem functions in bromeliads, including nitrogen uptake by  
125 the plant (Ngai and Srivastava 2006), detrital decomposition, and CO<sub>2</sub> flux (Atwood et al.  
126 2013; Atwood et al. 2014).

127 We tested for a relationship between the distribution, diet and ecosystem effect of predators  
128 and their phylogenetic distance using observations, lab feeding trials, and manipulative field  
129 experiments, respectively. We observed the distribution of predators between bromeliads by  
130 dissecting a sample of natural bromeliads. We quantified diet preferences in a series of no-  
131 choice feeding trials. We measured ecosystem-level effects with a manipulative experiment:  
132 we added predators to standardized bromeliad communities, adding either a single predator  
133 species or a pair of species of varying phylogenetic distance. In each approach, we test the  
134 hypothesis that the phylogenetic distance between predators determines the net impact of  
135 predator assemblages on the bromeliad community:

136 1. *Distributional similarity*: We predict that closely related predators occur in the same  
137 habitat patch more frequently than less related predators. Alternatively, closely related  
138 species may never co-occur because of competitive exclusion.

139 2. *Diet similarity*: We predicted that closely related predators will eat similar prey at  
140 similar rates. Alternatively, closely related species may have evolved different diets to  
141 facilitate coexistence.

142 3. *Ecosystem-level effects*: We tested two sets of hypotheses about direct and indirect

143 effects of predator combinations on ecosystems, predicting:

144 (a) Closely related predators will have similar individual effects on the community.

145 This will occur if related predators have similar trophic interactions (e.g. predation  
146 rate, diet similarity). Our single-species treatments allow us to assess the effect  
147 of each predator both on prey survival and on ecosystem functions.

148 (b) Predator assemblages with higher phylogenetic diversity will have synergistic  
149 (greater than additive) effects on prey consumption and associated ecosystem

150 functions. This will occur if phylogenetic distance correlates with increasing trait  
151 difference, and if this trait difference in turn results in niche complementarity.

152 However, at the extreme, different predators may consume each other, thus creat-  
153 ing antagonistic (less than additive) effects on prey consumption. By comparing  
154 treatments with pairs of predators to treatments that received each predator alone,  
155 we are able to estimate additive and non-additive effects.

## 156 **Methods**

### 157 **Study Design**

158 We used three empirical approaches to test the hypotheses outlined above. To test hypothesis  
159 1 (distribution) we sampled bromeliads for predator species. To test hypothesis 2 (diet  
160 similarity), we conducted a series of laboratory feeding trials. Finally, we tested hypothesis  
161 3 (similarity of community effect and interaction) with a field experiment in which predators  
162 were added to bromeliads containing standardized communities of prey. This experiment



163 included both single species treatments and two species treatments; the latter were chosen  
164 to create the widest possible range of phylogenetic diversity.

165 We included phylogenetic information in our analyses of all three datasets. We obtained this  
166 phylogenetic information first from classification alone. Next we added information about  
167 the age of each node from “timetree.org”, an online database of published molecular time  
168 estimates (Hedges et al. 2006). The timetree online database collects information from  
169 multiple independent phylogenetic studies. These studies provide independent estimates  
170 of the age of the most recent common ancestor for two lineages. Lineages that diverged  
171 a long time ago have been dated by multiple studies; for such nodes we used the median  
172 age. All internal nodes were dated by at least one study, however data was unavailable  
173 for the youngest nodes (i.e. tips) of the tree. For these nodes, either a lack of taxonomic  
174 information (e.g. Tabanidae) or a lack of phylogenetic study (e.g. *Leptagrion*) prevented more  
175 information from being included. These branches were left unresolved (i.e., as polytomies)  
176 and were all assigned identical, arbitrary and short branch lengths (15 Mya). The result is a  
177 phylogeny that closely resembles the qualitative, taxonomy-based tree with which we began.  
178 Because the node ages between our major predators (leeches, tabanids and odonata) are so  
179 deep, variation among studies in the estimated age of these nodes was minor compared to  
180 the differences between them Our final tree is available at [https://dx.doi.org/10.6084/m9.](https://dx.doi.org/10.6084/m9.figshare.3980349.v1)  
181 [figshare.3980349.v1](https://dx.doi.org/10.6084/m9.figshare.3980349.v1).

182 We conducted all three experiments in Parque Estadual da Ilha do Cardoso (25° 03' S, 47°  
183 53' W), a 22.5 ha island off the south coast of São Paulo state, Brazil. We worked in a coastal  
184 forest (*restinga*) with an understory dominated by *Quesnelia arvensis* Mez. (Bromeliaceae).

185 *Q. arvensis* is a large terrestrial bromeliad that catches and holds rainwater (phytotelmata),  
186 accumulating up to 2.8 L of rainwater in a single plant. Our observational survey found  
187 more than 47 species of macroinvertebrates in these aquatic communities (Romero and Sri-  
188 vastava 2010), in 25 bromeliads of various sizes. This diversity encompasses multiple trophic  
189 and functional groups. Filter feeders were entirely mosquito larvae (Diptera:Culicidae);  
190 detritivores include shredders (Diptera:Tipulidae, Trichoptera:Calamoceratidae), scrapers  
191 (Coleoptera:Scirtidae), and collectors (All Diptera:Chironomidae, Syrphidae, Psychodidae).  
192 All these species are prey for a diverse predator assemblage dominated by at least three  
193 species of damselfly larvae (*Leptagrion* spp., Odonata:Coenagrionidae), two species of horse-  
194 fly larvae (Diptera:Tabanidae), and two species of leech (Arhynchobdellida). A lower per-  
195 centage of predator biomass was composed of Dytiscid larvae (Coleoptera), midge larvae  
196 (Diptera: Ceratopogonidae) and chironomid larvae (Diptera: Tanypodinae).

## 197 **Data collection**

### 198 **Distributional similarity**

199 We asked whether closely related predators were found in the same bromeliads. In 2008, each  
200 bromeliad was dissected and washed to remove invertebrates. We passed this water through  
201 two sieves (150 and 850  $\mu\text{m}$ ), which removed particulate organic matter without losing any  
202 invertebrates. All invertebrates were counted and identified to the lowest taxonomic level  
203 possible. The body length of all individuals was measured when possible for small and  
204 medium-sized taxa ( $< 1\text{cm}$  final instar) and always for large-bodied taxa ( $> 1\text{ cm}$  final

205 instar).

## 206 **Diet Similarity**

207 To test whether related predators eat similar prey, we fed prey to predators in laboratory  
208 feeding trials. We conducted 314 feeding trials of 10 predator taxa and 14 prey taxa between  
209 March and April 2011. We included all potential predator-prey pairs present in the experi-  
210 ment (described below), and attempted to perform all other combinations whenever possible.  
211 However, due to the rarity of some taxa, many predator-prey pairs were not possible to as-  
212 semble in the field; we tested 56 pairwise combinations. Most trials were replicated at least  
213 five times, but the number of replicates ranged from 1 to 11. To conduct the trials, we placed  
214 predators together with prey in a 50ml vial, with a stick for substrate. The only exception  
215 was the tabanid larvae, which we placed between two vertical surfaces to imitate the narrow  
216 space found in bromeliad leaf axils (their preferred microhabitat, necessary for successful  
217 feeding). Generally our trials contained a single predator and a single prey individual, ex-  
218 cept in the case of very small prey (*Elpidium* sp.) or predators (*Monopelopia* sp.), in which  
219 case we increased the density. We recorded whether prey was consumed after 24 hours. All  
220 feeding trial data is available at <https://dx.doi.org/10.6084/m9.figshare.3978783.v1>

## 221 **Community effect experiment**

222 Our third hypothesis had two parts: (a) how do predator species differ in their individual  
223 effects on the invertebrate community composition (the number of surviving prey species)  
224 and ecosystem processes (rates of detritus consumption and nitrogen cycling) and (b) do

225 predator combinations show non-additive effects on community and ecosystem processes,  
226 and do these non-additive effects increase or decrease with phylogenetic distance?

227 We tested effects of both single and multiple predator species on community responses with  
228 a manipulative experiment where identical prey communities were exposed to treatments of  
229 either a single predator, or pairs of predators representing increasing phylogenetic diversity.  
230 In this experiment we focused on the four most abundant large predators found in the com-  
231 munity: *Leptagrion andromache* and *Leptagrion elongatum* (Odonata: Coenagrionidae), a  
232 predatory Tabanid fly (Diptera:Tabanidae:*Stibasoma* sp.) and a predatory leech. We com-  
233 bined these species in eight treatments: predator-free control (no predators), each of the four  
234 predator species alone (3a) and pairs of predator species chosen to maximize variation in  
235 phylogenetic distance (3b). Specifically, these pairs were: two congeneric damselflies (*Lep-  
236 tagrion andromache* and *Leptagrion elongatum*), two insects (*L. elongatum* and *Stibasoma*),  
237 and two invertebrates (*L. elongatum* and a predatory leech). We used five replicate bromeli-  
238 ads for each of these 8 treatments (8 treatments, n=5). This experiment, therefore, allows  
239 the estimation of the effect of each predator species (single-species treatments), as well as  
240 the detection of non-additive effects in predator combinations.

241 We created bromeliad communities that were as similar as possible to each other, and also  
242 to the average composition of a bromeliad. In February 2011 we collected bromeliads with  
243 a volume between 90 and 200ml, thoroughly washed the plants to remove organisms and  
244 detritus, and soaked them for 12 hours in a tub of water. We then hung all bromeliads for  
245 48 hours to dry. This procedure was intended to remove all existing macroinvertebrates; one  
246 bromeliad dissected afterwards contained no insects (a similar technique was used by Romero

247 and Srivastava (2010)). We simulated natural detritus inputs from the canopy by adding  
248 a standard mass of dried leaves of the species *Plinia cauliflora* (Jabuticaba, Myrtaceae; a  
249 common Brazilian tree;  $1.5\text{g bromeliad}^{-1} \pm 0.02$ , mean  $\pm$  sd). In order to track the effects  
250 of detrital decomposition on bromeliad N cycling, we enriched these leaves with  $^{15}\text{N}$  by  
251 fertilizing five plants with  $40\text{ml pot}^{-1} \text{ day}^{-1}$  of  $5\text{g L}^{-1}$  ammonium sulphate containing 10%  
252 atom excess of  $^{15}\text{N}$ . After 21 days we then collected *P. cauliflora* leaves, air-dried until  
253 constant weight, and then soaked them for three days. This procedure removes excess  
254 nutrients from the artificial fertilization. Because some of our prey species consume fine  
255 detritus, not coarse, we also added a standard amount of dried fine detritus to our bromeliads  
256 ( $0.23\text{g bromeliad}^{-1} \pm 0.02$ ). This fine detritus originated from detrital material between 150  
257 and 850 micrometers in size obtained from unmanipulated bromeliads and oven-dried.

258 Each bromeliad was stocked with a representative insect community (See supplementary  
259 material). The densities of each prey taxon were calculated from the observational dataset  
260 (Hypothesis 1), using data from bromeliads of similar size to those in our experiment. We  
261 ran this experiment in two temporal blocks for logistical reasons: three complete replicates  
262 of all treatments were set up on 20 February 2011, and two on 08 March 2011. We first  
263 placed the prey species into the bromeliad, allowed two days for the prey to adjust, then  
264 added predators. After 26 days from the beginning of each block, we added the same  
265 prey community a second time to simulate the continuous oviposition that characterizes the  
266 system. We concluded the experiment 43 days from the first addition of prey (20 April  
267 2011). Throughout the experiment, all bromeliads were enclosed with a mesh cage topped  
268 with a malaise trap and checked daily for emergence of adults. At the end of the experiment

269 we completely dissected our bromeliads, collecting all invertebrates and detritus remaining  
270 inside.

271 We used a substitutive design, maintaining the same predator metabolic capacity in all repli-  
272 cates (see below). In a substitutive experiment, all experimental units receive the same  
273 “amount” of predators – usually standardized by abundance – and only species composition  
274 varies. However, when species differ substantially in body size - as in this experiment - abun-  
275 dance does not standardize the their effects on the community. We chose to standardize  
276 using metabolic capacity instead (after Srivastava (2009)). Integrating the allometric rela-  
277 tionship between body size and feeding rate (Brown et al. 2004; Wilby et al. 2005) over  
278 all individuals of a species allows estimates of “metabolic capacity”, or the potential energy  
279 requirements of a species (Srivastava and Bell 2009). Metabolic capacity is equal to indi-  
280 vidual body mass raised to the power of 0.69 (an invertebrate-specific exponent determined  
281 by Peters (1986) for invertebrates and confirmed by Chown et al, (2007)); this reflects the  
282 nonlinear relationship between feeding rate and body size across many invertebrate taxa.

283 To quantify the effect of predators on ecosystem function, at the end of the experiment  
284 we measured five community and ecosystem response variables: decomposition of coarse  
285 detritus, production of fine particulate organic matter (FPOM), bromeliad growth, uptake  
286 of detrital nitrogen into bromeliad tissue, and survival of invertebrate prey (emerged adults  
287 + surviving larvae). We measured decomposition by passing the bromeliad water through a  
288 850  $\mu\text{m}$  sieve, collecting the retained detritus and determining the mass of this detritus after  
289 oven-drying it at approximately 70°C. We measured the production of FPOM by taking the  
290 remaining liquid and filtering it on pre-weighed coffee filters, which were then dried and

291 reweighed. We measured bromeliad growth as the average increase in length of five leaves  
292 per plant. We tracked the uptake of labeled detrital nitrogen by analyzing the isotopic  
293 composition of the three innermost (closest to meristem) bromeliad leaves at the end of  
294 the experiment. These analyses were performed at the Stable Isotope Facility laboratory  
295 (UC Davis, CA, USA) using continuous flow isotope ratio mass spectrometer (20-20 mass  
296 spectrometer; PDZ Europa, Sandbach, England) after sample combustion to N<sub>2</sub> at 1000°C  
297 by an on-line elemental analyzer (PDZ Europa ANCA GSL). Finally, we quantified the  
298 species composition and survivorship of invertebrate prey by combining counts of emerging  
299 adult insects and surviving larvae. All experimental data is available at [https://dx.doi.org/](https://dx.doi.org/10.6084/m9.figshare.3983964)  
300 [10.6084/m9.figshare.3983964](https://dx.doi.org/10.6084/m9.figshare.3983964).

## 301 **Data analysis**

302 We quantified the effect of phylogenetic distance on each of distributional (Hypothesis 1)  
303 and diet (Hypothesis 2) similarity. First, we calculated phylogenetic distance between each  
304 pair of species. We then evaluated both distributional and diet similarity between predators  
305 using Pianka's index of niche overlap (Pianka 1974):

$$306 \quad O_{kl} = \frac{\sum_i^n p_{il}p_{ik}}{\sqrt{\sum_i^n p_{il}^2 \sum_i^n p_{ik}^2}}$$

307 For each pair of predators,  $p_{ik}$  and  $p_{il}$  represent the preference of predator  $k$  or  $l$  for resource  
308 or habitat  $i$ . The value  $O_{kl}$  represents similarity (in our case, in either distribution or diet)  
309 and ranges from 0 (complete dissimilarity) to 1 (complete similarity). The  $n$  resources  
310 represent the different habitats surveyed for Hypothesis 1 (distributional similarity), or the

311 different prey species assayed for Hypothesis 2 (diet similarity). Preference ( $p_{ik}$ ) represents  
312 the proportion of a predator's total metabolic capacity found in a particular bromeliad  
313 (Hypothesis 1); or the proportion of feeding trials in which it ate a particular prey (Hypothesis  
314 2). We then compared these effects via a Mantel test, to check for overall correlation between  
315 the phylogenetic distance matrix and dissimilarity in either predator distribution or diet  
316 preferences.

317 We divided the analysis of the manipulative experiment into three parts: quantifying the  
318 effect of phylogenetic distance on prey community similarity, on community and ecosystem  
319 responses, and on non-additive effects of predator combinations. First, we compared the four  
320 treatments with single predator species by calculating the similarity in species composition  
321 (Pianka's index) between surviving prey communities and relating this to the phylogenetic  
322 distance between predators with a linear regression. If predator feeding choices are phyloge-  
323 netically conserved, then diet similarity will decline with increasing phylogenetic distance.

324 Second, we measured five community and ecosystem responses, testing in turn the effect of  
325 predator presence, number, species identity, and finally phylogenetic diversity. To test for an  
326 effect of predator presence, we compared the control treatment (predators absent) with the  
327 mean responses of all seven treatments that did contain predators. To test for an effect of  
328 predator species number (one or two predators), we compared the means of all single-species  
329 treatments with the means of all two-species treatments. To test for an effect of predator  
330 identity, we compared all four single-species treatments. Finally, to test for an effect of  
331 predator combinations we compared all two-species treatments (3 pairs total). We analyzed  
332 each of these of these orthogonal comparisons with one-way ANOVA.



333 In our third and final analysis, we quantified the non-additive effect of predator species on our  
334 responses. We calculated this effect as the difference between the response in bromeliads with  
335 both predator species (n=5) and the mean response in bromeliads with either one of these  
336 two predator species (n=5 for each predator species). We generated bootstrap confidence  
337 intervals for these non-additive effects; confidence intervals that do not overlap zero indicate  
338 a significant non-additive effect of a predator combination. We used R version 3.2.0 (R  
339 Core Team 2015) for all calculations, and two packages: *picante* (Kembel et al. 2010) for  
340 calculating phylogenetic distances matrices, and *vegan* (Oksanen et al. 2015) for distance  
341 metrics. All the code documenting our analyses is archived at [http://dx.doi.org/10.5281/](http://dx.doi.org/10.5281/zenodo.16805)  
342 [zenodo.16805](http://dx.doi.org/10.5281/zenodo.16805)

## 343 **Results**

### 344 **Hypothesis 1: similarity in distribution**

345 We did not find any significant relationship between the co-occurrence of a pair of predators in  
346 bromeliads (measured as Pianka's index of niche overlap) and the phylogenetic distance be-  
347 tween the two predators. A Mantel test found no evidence of correlation between differences  
348 among predators in habitat use, and phylogenetic distance (correlation -0.18,  $p = 0.82$ , 999  
349 permutations). This indicates that all 14 predator species have roughly similar habitat distri-  
350 butions – indeed, we often found multiple predator species co-occurring in the same bromeli-  
351 ads (mean  $4.45 \pm 2.8$  predator species per plant). We were able to sample a wide range  
352 of phylogenetic relatedness, including two groups of congenics – two species of *Bezzia* sp.

353 (Diptera:Ceratopogonidae) and three species of *Leptagrion* sp. (Odonata:Coenagrionidae).  
354 There were also two groups of confamilials – three species of Tabanidae and two species of  
355 Empididae, all Diptera. Deeper divisions were also present: three families of Diptera were  
356 represented by a single predator species each (Dolichopodidae, Corethrellidae and Chirono-  
357 midae) and the deepest taxonomic divide was between all insects present and the predatory  
358 leeches (Arhynchobdellida:Hirudinidae).

### 359 **Hypothesis 2: Similarity in diet**

360 Overall, predators were remarkably similar in their diets, reflecting the broad generalist  
361 diets of most predators (Fig. 1b). Although diet similarity appears to decline slightly  
362 with phylogenetic distance between predators, this effect disappears once we correct for  
363 non-independence of predator pairs with a Mantel test (correlation -0.27,  $p = 0.88$ , 999  
364 permutations).

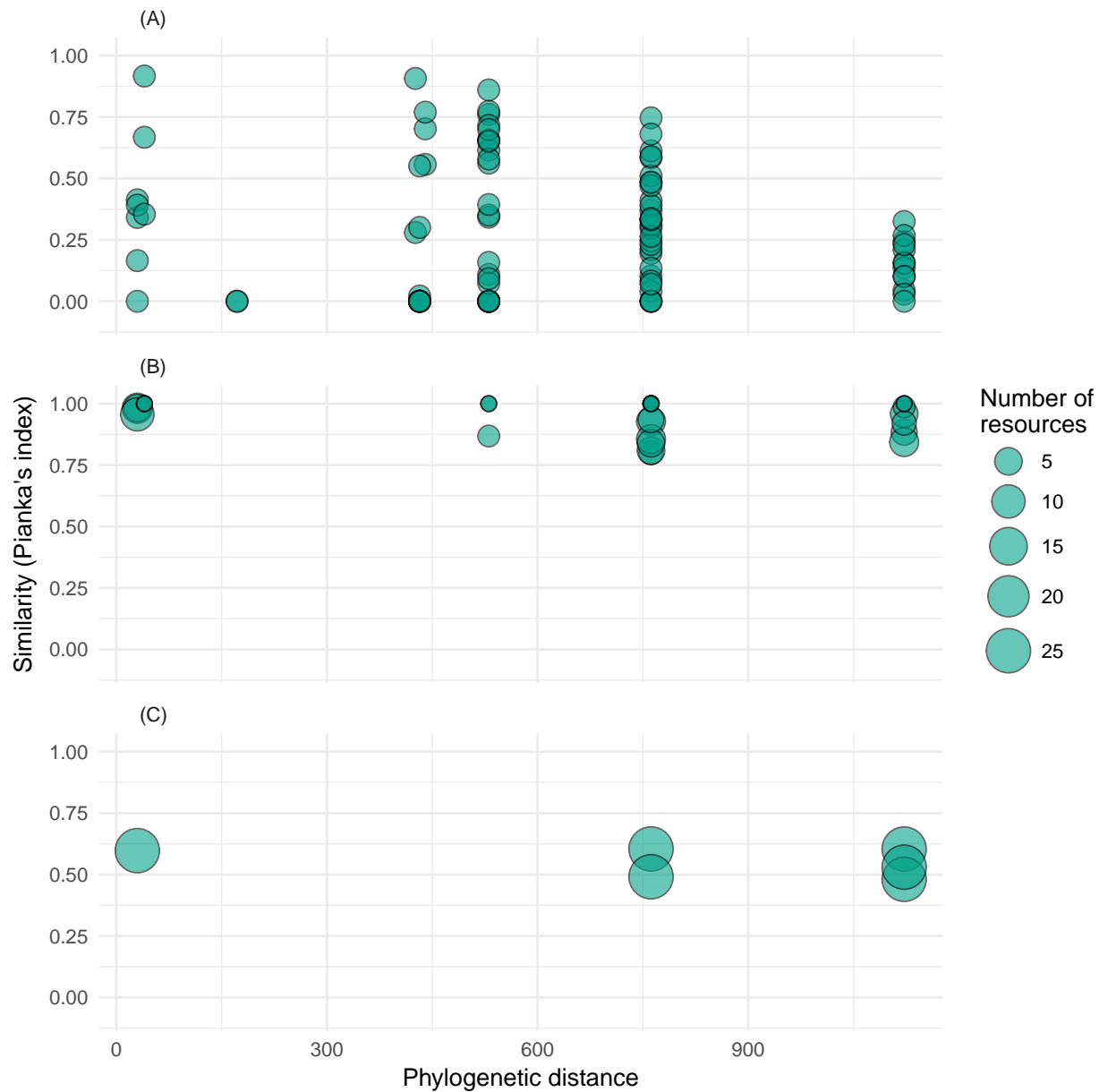
### 365 **Hypothesis 3: similarity in top-down effects**

366 We analyzed our five univariate response variables from the manipulative experiment by di-  
367 viding them into four separate and orthogonal tests: predator presence, predator number,  
368 predator species identity, and increasing predator phylogenetic diversity. Across all four  
369 tests, we saw the strongest responses in terms of total prey survivorship (Table 1). Prey sur-  
370 vivorship was halved when predators were present (Figure 2a, Table 1). Although predator  
371 species differed in their individual effects on the composition of the surviving prey com-  
372 munity, this difference was unrelated to the phylogenetic distance between predator species

373 (Fig 1c,  $F_{1,4}=0.71$ ,  $p=0.45$ , distance measured as Bray-Curtis dissimilarity). Although single  
374 predator species had similar effects on prey survivorship (Figure 2c, Table 1), combinations  
375 of predators with higher phylogenetic diversity showed a significant increase in total prey  
376 survivorship (Fig 2d). That is, more phylogenetically diverse pairs of predators caused less  
377 prey mortality. Interestingly, these antagonistic effects on prey survivorship did not result  
378 in a change in the processing of detritus (measured either as reduction in coarse detritus or  
379 production of fine detritus), bromeliad growth or nitrogen cycling (Table 1).

380 We tested for non-additive effects of predator phylogenetic diversity with bootstrap confi-  
381 dence intervals. When we compared the actual effects of predator combinations with those  
382 expected from the mean of each single-species treatment, we found that predator pairs with  
383 the greatest phylogenetic diversity had the highest prey survival (Table 1). Whereas effects  
384 of *L. andromache* and *L. elongatum* in combination were quite similar to the effect of either  
385 alone, when *L. elongatum* was placed in the same plant as either a *Stibasoma* larva or leeches,  
386 on average five more prey individuals (18% of total prey community) survived till the end  
387 of the experiment (Fig 3; Tabanid,  $p = 0.016$ , Leech,  $p = 0.016$ ). Once again, this effect on  
388 invertebrate density did not in turn create a significant difference in the ecosystem function  
389 variables.

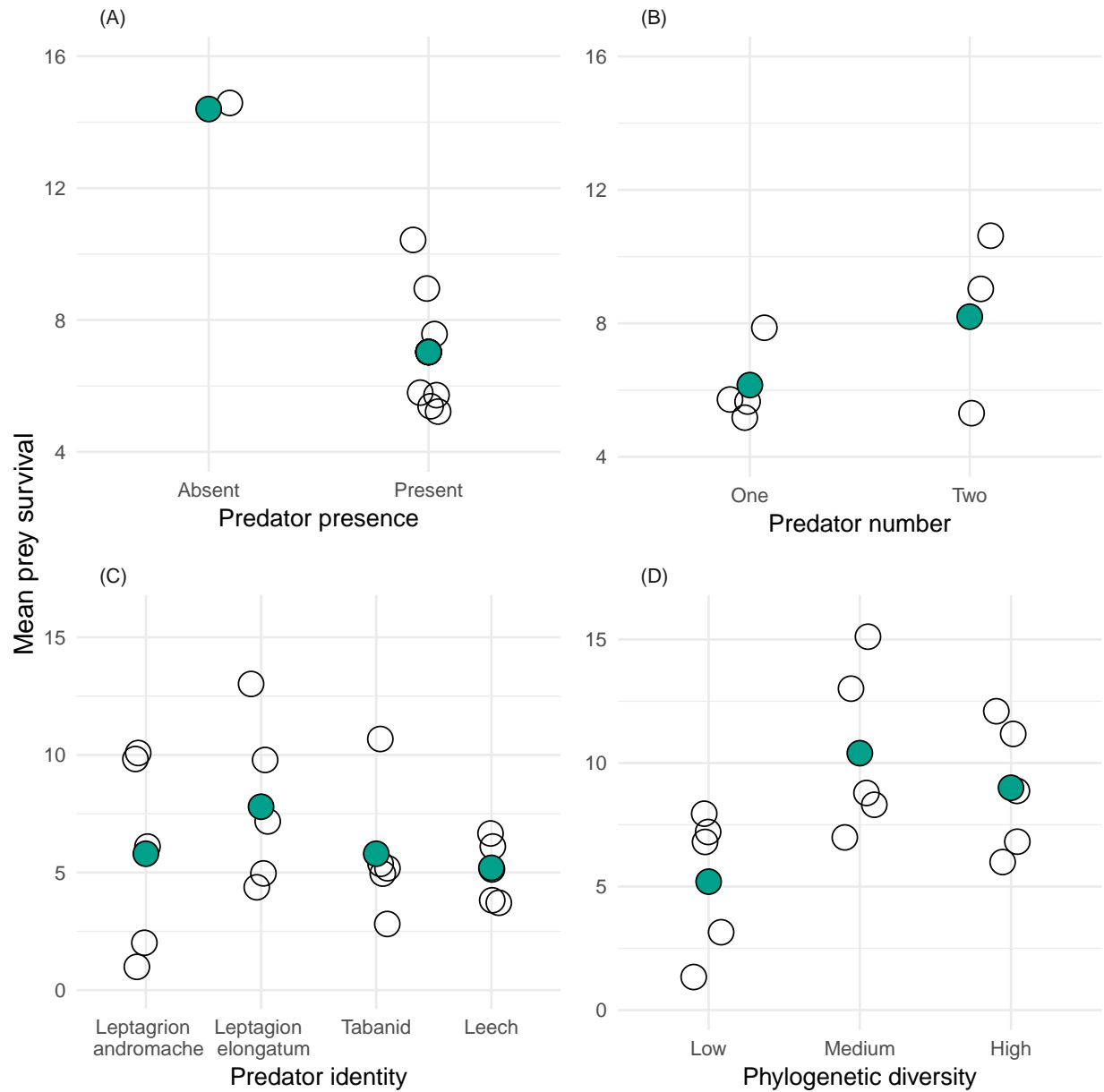
390 **Figures**



391

392 **Figure 1:** Phylogenetic distance between predators as a predictor of niche overlap among  
393 predators and impacts on prey composition. Our measures of niche overlap were: (a) distri-  
394 bution among bromeliads and (b) diet preferences. We also show the effect of phylogenetic  
395 distance between predators on (c) community dissimilarity of surviving prey (Bray-Curtis

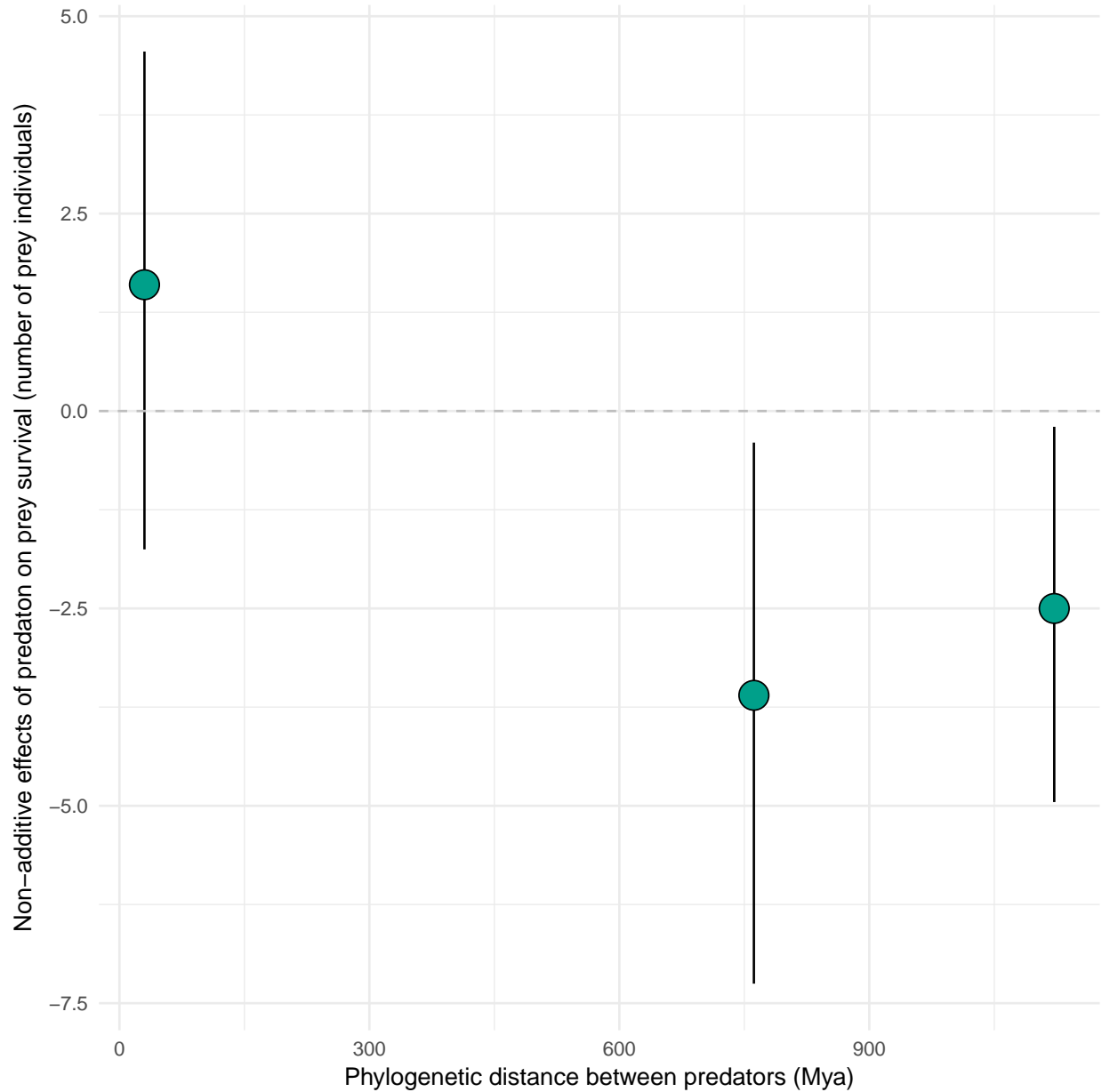
396 dissimilarity). We measured distributional similarity (a) by counting all predators in 25  
397 bromeliads, estimating their total metabolic capacity, and calculating niche overlap (Pi-  
398 anka's index) among all pairs of species. We measured diet preferences (b) for a subset of  
399 these predators by offering them various prey in no-choice trials, and again calculated niche  
400 overlap among them. Finally, we measured community composition of surviving prey (c) at  
401 the end of an experiment in which predators were placed in bromeliads with standardized  
402 prey communities. For (a) and (b) we used Pianka's index of niche overlap (1 = complete  
403 niche overlap) and tested various nonlinear and linear models (see Appendix) of the rela-  
404 tionship between this index and phylogenetic distance. Solid lines show significant model fit,  
405 and dashed lines show bootstrap 95% quantiles.



406

407 **Figure 2:** Orthogonal comparisons of the effect of predators on prey survival. We show the  
408 effects of predator presence (a), and then within predator present treatments the effects of  
409 predator species number (b). Within treatments with one predator species, we show effects  
410 of predator identity (c). Within treatments with two predator species, we show the effect of  
411 increasing phylogenetic diversity (d, arranged in order of increasing phylogenetic distance:

412 Low = *L. andromache* + *L. elongatum*, Medium = *L. elongatum* + tabanid, High = *L.*  
413 *elongatum* + leech). Shaded dots represent grand means for each group; unshaded dots are  
414 either treatment means (2a and 2b, n = 5) or individual bromeliads (2c and 2d). Points are  
415 jittered horizontally slightly to reveal all datapoints.



416

417 **Figure 3:** Non-additive effects of predator combinations on prey decrease with increasing  
418 phylogenetic distance between predators. A difference of 0 indicates that two-predator treat-  
419 ments resulted in no more prey mortality than would be expected from simply averaging  
420 single-predator treatments. A negative difference indicates that two-predator treatments  
421 resulted in less mortality than expected. Error bars represent bootstrap 95% confidence



422 intervals.

423 **Table 1:** Predator diversity effects on community and ecosystem variables. We measured five community-level variables: total  
 424 prey survival (both emerged adults and surviving larvae; see Fig. 2 and 3), the breakdown of coarse detritus (decomposition), the  
 425 production of fine particulate organic matter (FPOM), the cycling of nitrogen from detritus to bromeliad tissue, and the growth  
 426 of the bromeliad itself. We contrast treatments in our experimental design in four orthogonal ways: comparing treatments with  
 427 predators to those without ("Predator Presence"), contrasting predator species ("Identity"), comparing predator communities  
 428 of 1 or 2 species ("Richness"), and considering the effects of phylogenetic distance between predators ("Pairwise PD"). Values  
 429 are slope  $\pm$  standard error and  $p < 0.05$

26

Response	Predator Presence	Identity	Richness	Pairwise PD
Total prey survival	$-7.37 \pm 2.45$ ; $F_{1,10} = 9.07^*$	$2.00 \pm 2.07$ ; $F_{3,16} = 0.60$	$2.05 \pm 1.46$ ; $F_{1,5} = 1.96$	$0.01 \pm 0.00$ ; $F_{1,13} = 7.64^*$
Decomposition (g)	$0.01 \pm 0.02$ ; $F_{1,10} = 0.47$	$-0.01 \pm 0.03$ ; $F_{3,15} = 1.29$	$-0.01 \pm 0.02$ ; $F_{1,5} = 0.21$	$0.00 \pm 0.00$ ; $F_{1,13} = 0.40$
FPOM (g)	$-0.06 \pm 0.09$ ; $F_{1,10} = 0.46$	$-0.06 \pm 0.11$ ; $F_{3,15} = 0.28$	$0.18 \pm 0.07$ ; $F_{1,5} = 6.19$	$-0.00 \pm 0.00$ ; $F_{1,13} = 1.45$
Bromeliad growth	$-0.79 \pm 1.10$ ; $F_{1,10} = 0.51$	$-1.08 \pm 1.62$ ; $F_{3,16} = 0.96$	$0.59 \pm 0.84$ ; $F_{1,5} = 0.49$	$0.00 \pm 0.00$ ; $F_{1,12} = 1.29$
nitrogen cycling	$-5.69 \pm 4.03$ ; $F_{1,10} = 2.00$	$-0.22 \pm 8.66$ ; $F_{3,16} = 1.84$	$3.97 \pm 5.63$ ; $F_{1,5} = 0.50$	$-0.00 \pm 0.01$ ; $F_{1,13} = 0.15$

## 430 **Discussion**

431 We found that the phylogenetic distance between predators had variable importance in the  
432 bromeliad system. The phylogenetic distance between predators was unrelated to their co-  
433 occurrence (Hypothesis 1). The phylogenetic distance between predator species was also  
434 unrelated to diet overlap, although there was a tendency of diet overlap to decrease by  
435 about 20% over the observed range of phylogenetic distance (Hypothesis 2). Perhaps as a  
436 consequence of diet similarity, the phylogenetic distance between predators could not predict  
437 their individual effects on prey composition or survival (Hypothesis 3a). However, greater  
438 phylogenetic diversity caused an increase in prey survival (i.e. a decrease in predation);  
439 phylogenetically distant pairs of predators that co-occurred in bromeliads had less impact  
440 on prey than expected from their performance in isolation (Hypothesis 3b). We examine  
441 each of these main results in turn.

### 442 **Phylogenetic distance and similarity in distribution**

443 Phylogenetic distance between predators did not explain overlap in habitat distribution. This  
444 similarity in distribution could be caused by two processes: low habitat variability among  
445 bromeliads, or low variability in preference of predators for different habitats. Bromeliads  
446 at this site vary widely in abiotic conditions, size, detritus amount and prey community;  
447 therefore it seems unlikely that low patch variation explains the lack of pattern. It appears  
448 instead that predators do not possess any strong phylogenetically-conserved preferences for  
449 different habitat characteristics, showing instead very generalist habitat preferences. This  
450 is not surprising, given that these organisms live in small, fluctuation-prone habitats. As a

451 group, predatory invertebrates in bromeliads do not show more sensitivity to bromeliad size  
452 or drought than other invertebrates (Amundrud and Srivastava 2015). The co-occurrence  
453 of predator species within bromeliads suggests that antagonistic interactions among preda-  
454 tors do not limit species distributions. Additionally, it appears that predator species are  
455 able to co-occur in many different combinations, creating a range of phylogenetic diversities  
456 within bromeliads. This suggests that the range of phylogenetic diversity we tested in our  
457 experiment was realistic.

#### 458 **Phylogenetic distance and similarity in diet**

459 There was no significant relationship between phylogenetic distance and overlap in diet as  
460 measured by laboratory feeding trials. In part, this reflects the ability of many predator  
461 species to consume a range of prey. However, predator species still showed some differences  
462 in prey preference. For example, damselflies are visual predators that engulf prey whole  
463 using specialized mouthparts; they are gape-limited and cannot eat prey that are too large.  
464 Leeches, in contrast, lack eyes but are able to pierce prey and consume them without swal-  
465 lowing. Damselflies showed a much stronger preference for culicid larvae than did leeches,  
466 whereas leeches were slightly better able to kill and consume scirtids. Culicid larvae are free  
467 swimming in the water column, and are therefore easily captured by engulfing predators,  
468 whereas scirtid larvae crawl on surfaces and are difficult to remove. Despite these modest  
469 differences between predator species in diet, such differences appeared largely unstructured  
470 by phylogeny. Other studies have also suggested that predator functional traits are more  
471 important than phylogeny *per se* to a predator's diet: Moody (1993) found that unrelated

472 decapod species which were morphologically similar were also functionally similar. Similarly,  
473 Rezende et al. (2009) found that both body size and phylogeny determined the food web  
474 “compartment” (shared predator-prey interactions) of predators in a marine foodweb.

#### 475 **Phylogenetic distance and non-additive effects**

476 We found that the presence of predators reduced prey survival, but that this reduction  
477 was less for phylogenetically-diverse combinations of predators. This was contrary to our  
478 hypothesis that more distant predators would show an increase in prey capture via niche  
479 complementarity. *L. andromache* did not produce an antagonistic (i.e. less than additive)  
480 effect in combination with *L. elongatum*, whereas the two more phylogenetically diverse  
481 combinations (*L. elongatum* with the Tabanid or leech) did. *Leptagrion* species may not  
482 distinguish between conspecifics and congeners. In predicting a synergistic non-additive  
483 effect of predators, we were imagining an outcome much like those reported by Nilsson et  
484 al. (2006); they found that stoneflies caused prey to move into habitats where fish predators  
485 could consume them, increasing total predation (a synergistic effect, caused by a phyloge-  
486 netically distinct predator). Our results are more consistent with those of Finke and Denno  
487 (2005), who found that combinations with two insect predators had a higher per-capita  
488 effect on leafhopper prey than combinations with an insect and a spider. That is, more  
489 phylogenetically diverse combinations of predators showed less predation on lower trophic  
490 levels.

491 When *L. elongatum* occurred with more distantly related predators, prey survivorship was  
492 greater than expected. This non-additive effect may have been due to a reduction in preda-

493 tion by odonates in the presence of non-odonate predators. Odonates have been shown to be  
494 sensitive to chemical cues (Barry and Roberts 2014) or tactile cues (Atwood et al. 2014) of  
495 potential predators, which causes a decrease in feeding rate. For example, a different species  
496 of bromeliad damselfly – *Mecistogaster modesta* Selys – reduces predation when it is housed  
497 with Dytiscid adults (Atwood et al. 2014). If there is a phylogenetic signal to the chemical  
498 cues released by predators, individuals of one species might be unable to distinguish close  
499 relatives (congenerics in our case) from conspecifics. One limitation of our approach is that  
500 all phylogenetic diversity treatments contained one species in common, *Leptagrion elonga-*  
501 *tum*. It is possible that this species is more sensitive to the presence of other predators, and  
502 therefore shows a larger effect in combination than would other species in this community.  
503 However, this is the most common predator in this community and our results indicate that  
504 its top-down effects are likely to be frequently reduced by the presence of other predators.

505 In our experiment, we did not see any effect of predator presence, nor of increasing preda-  
506 tor phylogenetic diversity, on ecosystem function (defined here as nitrogen cycling, detritus  
507 decomposition and bromeliad growth). This was contrary to our predictions based on previ-  
508 ous studies from rainforest bromeliads, which found that adding predators to a community  
509 increased nitrogen cycling and reduced detrital decomposition (Ngai and Srivastava 2006;  
510 Srivastava and Bell 2009). While we did observe substantial consumption of detritivorous  
511 prey by predators, the resulting reductions in detritivore density did not cause differences  
512 in either the decomposition of detritus or the uptake of detrital nitrogen into bromeliad  
513 leaf tissue. These differences between our results and those from rainforests may be due to  
514 leaf traits of the *restinga* vegetation. In *restinga* vegetation, leaves are generally extremely

515 tough and waxy, whereas in rainforests, leaves tend to be softer – with the result that, in  
516 *restinga*, invertebrates are unable to consume leaves directly. Several lines of evidence sup-  
517 port this assertion. Romero and Srivastava (2010) studied the effects of the spider *Corinna*  
518 *demersa* (Corinnidae) on bromeliad ecosystems. This spider has no effect on the composi-  
519 tion of detritivore communities, nor on decomposition rates, but increases nitrogen content  
520 in bromeliads, probably by depositing feces or the carcasses of terrestrial prey. This indi-  
521 cates that *restinga* bromeliads may derive less of their nitrogen from terrestrial detritus, but  
522 may benefit more from terrestrial inputs. A separate experiment (GQ Romero, pers comm)  
523 supports the hypothesis that lower decomposition in *restinga* is due to plant traits. This  
524 second experiment contrasted decomposition caused by invertebrates and bacteria with that  
525 caused by bacteria alone (by comparing bagged detritus enclosed in coarse vs fine mesh).  
526 The experiment used two species of detritus: leaves from a rainforest tree, and leaves from a  
527 *restinga* tree. Invertebrates only caused an increase in decomposition for the rainforest tree,  
528 not the *restinga* tree.

529 In most natural communities, multiple predator species co-occur and often simultaneously  
530 affect prey species. This study is one of the first to examine how phylogenetic diversity of a  
531 guild of predators affects both food web structure and ecosystem functioning. By combining  
532 an observational study, laboratory trials, and a field experiment that controlled number and  
533 phylogenetic diversity of predators we have shown that phylogenetic relatedness of species  
534 can help predict food web responses.

535 Previous studies have usually addressed this question in the context of species that only com-  
536 pete for resources, typically plants that compete for nutrients and water (Cavender-Bares

537 et al. 2009). The predators in our system not only compete for prey, but also have the  
538 potential for intraguild predation. This adds a new way in which phylogenetic diversity can  
539 affect food webs and ecosystems. Phylogenetically distant predators may be more likely to  
540 prey on each other, either because injury is less likely when species differ in size and morpho-  
541 logical defenses or, as suggested by Pfennig (2000), because the risk of disease transmission  
542 is less. If the risk of intraguild predation increases with predator phylogenetic diversity, this  
543 may counteract any ecosystem effects of diminished competition. When this is the case,  
544 increasing phylogenetic diversity may reduce overall predation rates, because predators fear  
545 intraguild predation from distantly-related predators, and simultaneously increase predation  
546 rates, because predators overlap less in prey preferences or in hunting mode. The net effects  
547 of these processes will be difficult to predict without detailed experiments like those that we  
548 report here.

549 Our results suggest that phylogenetic relationships among organisms at higher trophic levels  
550 may have more complex ecosystem consequences than when only a single, lower trophic  
551 level is considered. In order to apply phylogenetic community ecology to food webs, we  
552 will need to consider a broader suite of potential interactions between species and extend  
553 our theoretical framework beyond simple niche complementarity (Srivastava et al. 2012).  
554 However, this is a worthwhile goal. An approach based on phylogenetic diversity offers an  
555 organizing framework around which to compare diverse datasets on the distribution, trophic  
556 interactions and combined effect of multiple predator species, and to predict the top-down  
557 effect of diverse predator assemblages.



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