

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 CO₂ 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 μm), 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; 1.5g bromeliad⁻¹ ± 0.02, mean ± sd). In order to track the effects
250 of detrital decomposition on bromeliad N cycling, we enriched these leaves with ¹⁵N by
251 fertilizing five plants with 40ml pot⁻¹ day⁻¹ of 5g L⁻¹ ammonium sulphate containing 10%
252 atom excess of ¹⁵N. 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 (0.23g bromeliad⁻¹ ± 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 μm 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 N₂ 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 ± 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).

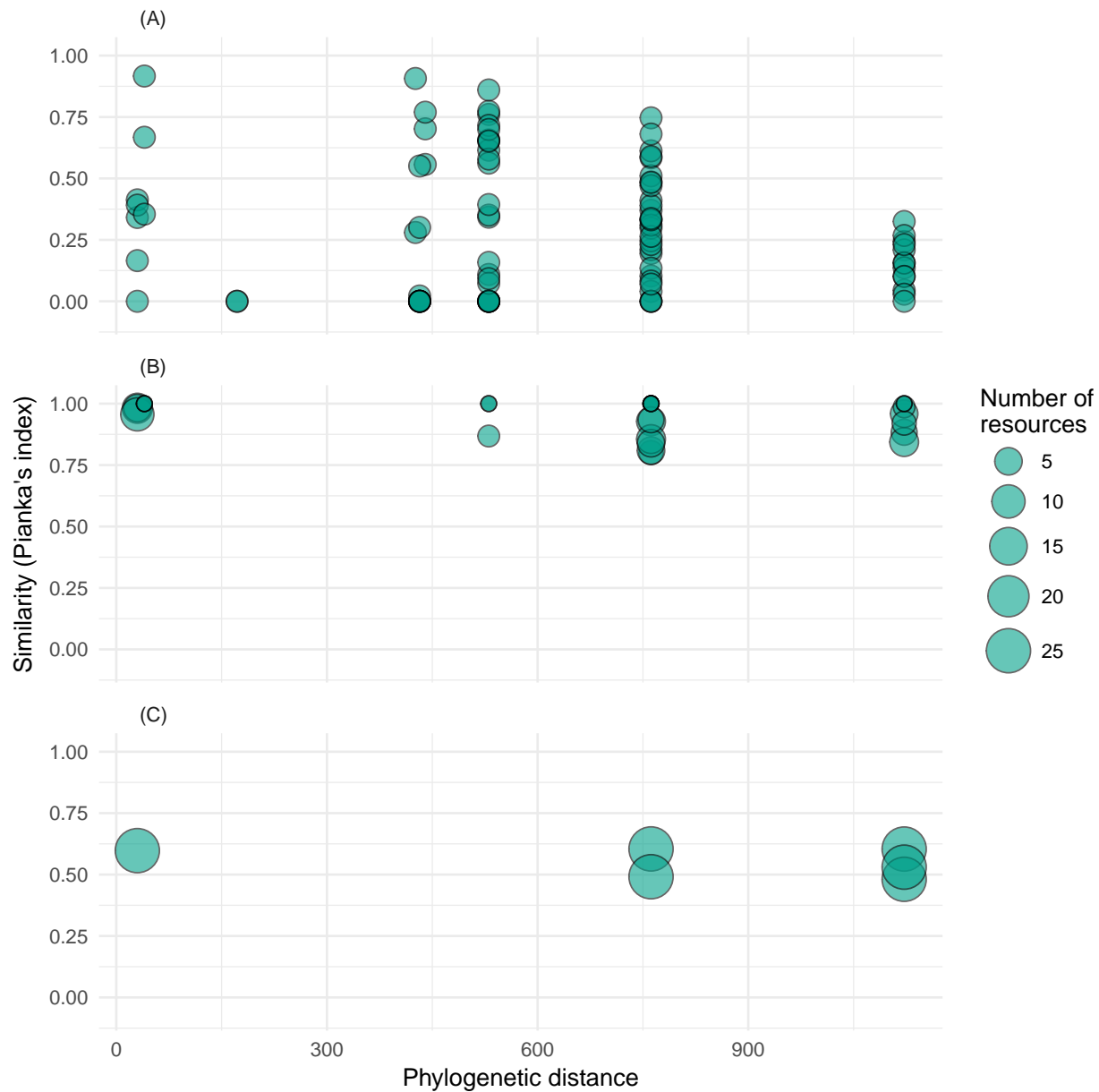
365 **Hypothesis 3: similarity in top-down effects**

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.

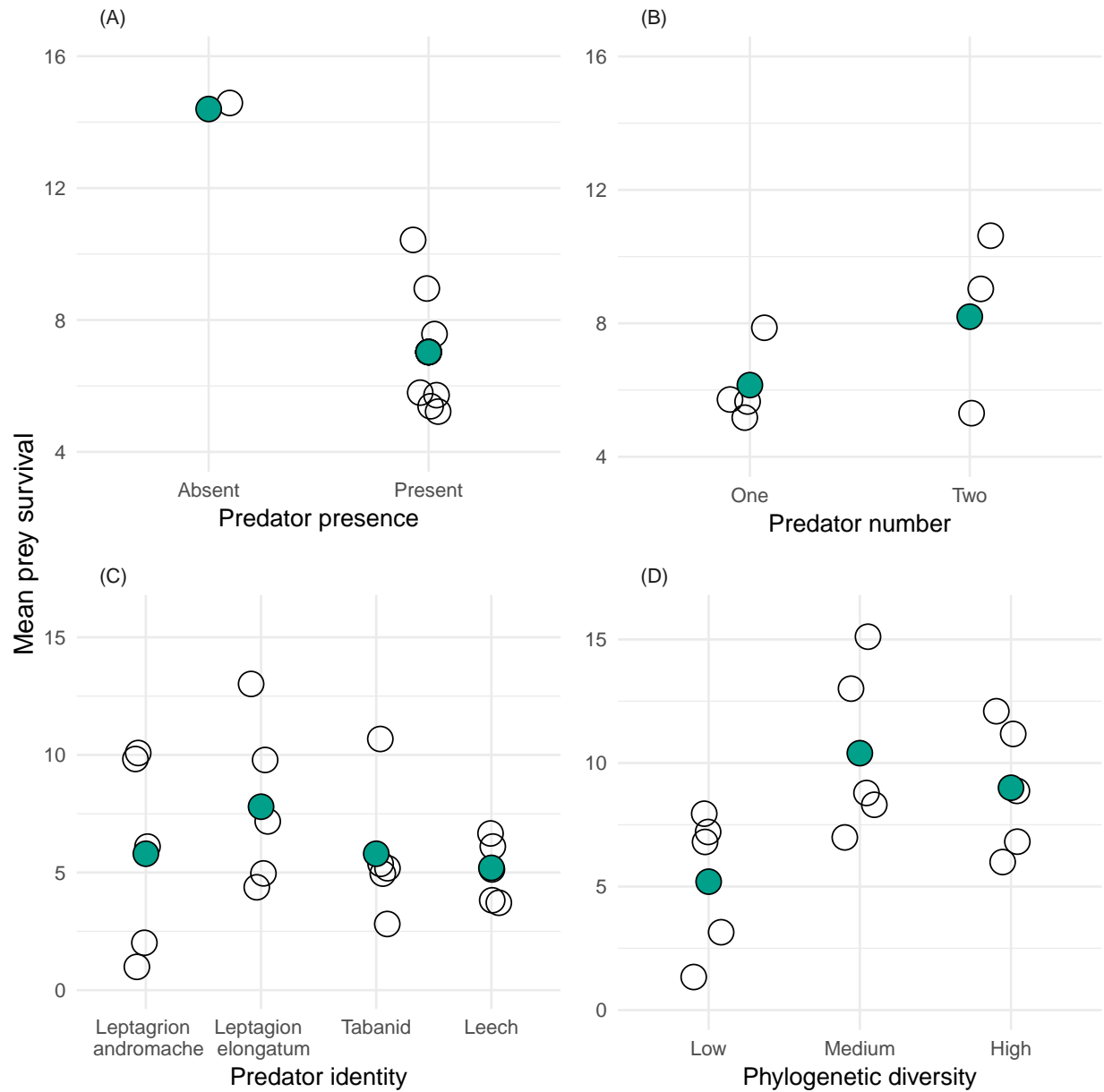
390 **Figures**



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

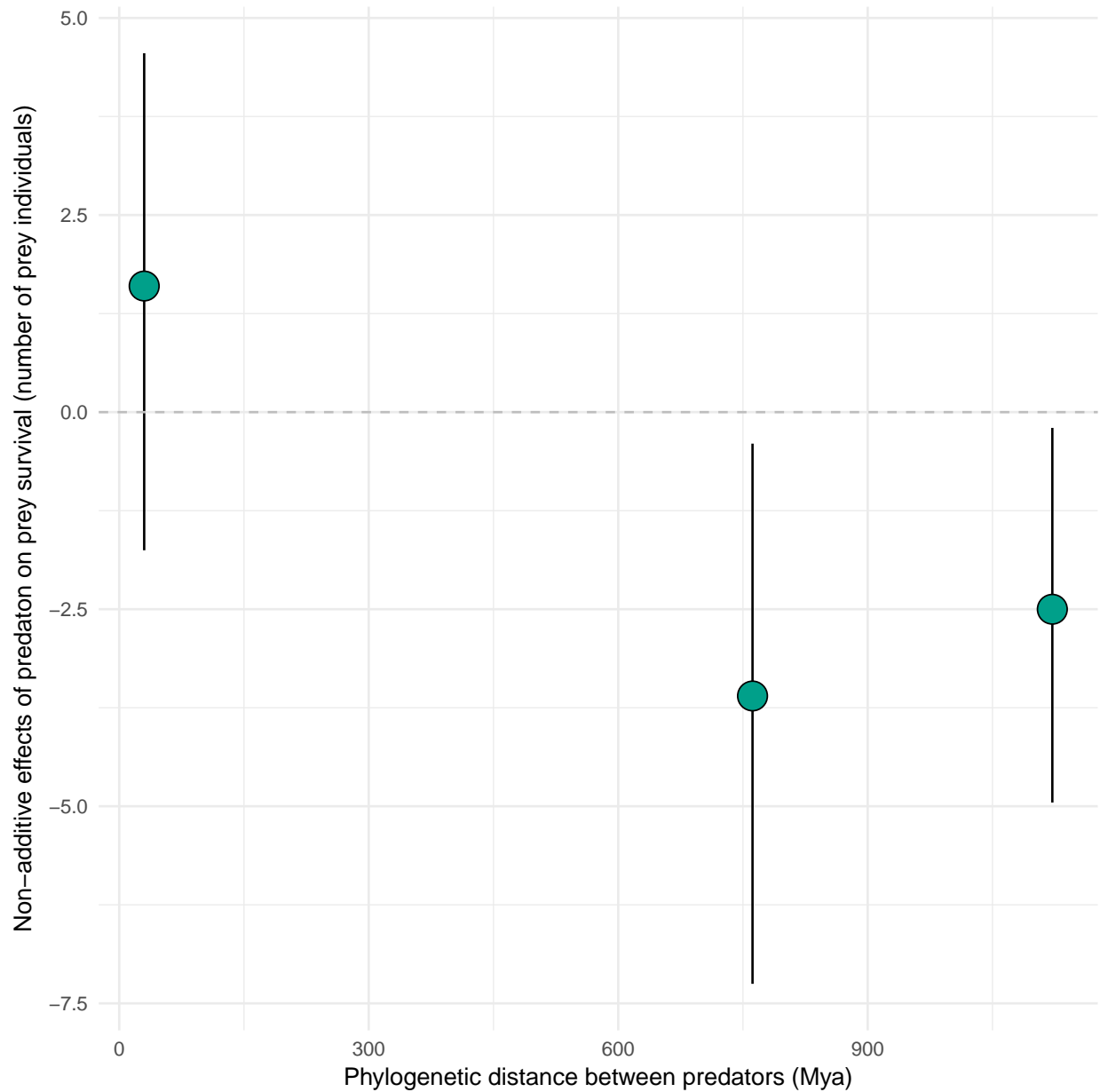
396 dissimilarity). We measured distributional similarity (a) by counting all predators in 25
397 bromeliads, estimating their total metabolic capacity, and calculating niche overlap (Pi-
398 anka's index) among all pairs of species. We measured diet preferences (b) for a subset of
399 these predators 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 ± 2.45 ; $F_{1,10} = 9.07^*$	2.00 ± 2.07 ; $F_{3,16} = 0.60$	2.05 ± 1.46 ; $F_{1,5} = 1.96$	0.01 ± 0.00 ; $F_{1,13} = 7.64^*$
Decomposition (g)	0.01 ± 0.02 ; $F_{1,10} = 0.47$	-0.01 ± 0.03 ; $F_{3,15} = 1.29$	-0.01 ± 0.02 ; $F_{1,5} = 0.21$	0.00 ± 0.00 ; $F_{1,13} = 0.40$
FPOM (g)	-0.06 ± 0.09 ; $F_{1,10} = 0.46$	-0.06 ± 0.11 ; $F_{3,15} = 0.28$	0.18 ± 0.07 ; $F_{1,5} = 6.19$	-0.00 ± 0.00 ; $F_{1,13} = 1.45$
Bromeliad growth	-0.79 ± 1.10 ; $F_{1,10} = 0.51$	-1.08 ± 1.62 ; $F_{3,16} = 0.96$	0.59 ± 0.84 ; $F_{1,5} = 0.49$	0.00 ± 0.00 ; $F_{1,12} = 1.29$
nitrogen cycling	-5.69 ± 4.03 ; $F_{1,10} = 2.00$	-0.22 ± 8.66 ; $F_{3,16} = 1.84$	3.97 ± 5.63 ; $F_{1,5} = 0.50$	-0.00 ± 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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