

Predator phylogenetic diversity decreases predation rate via antagonistic interactions

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Introduction

Predators can have strong top-down effects, both on community structure and ecosystem processes (Estes et al. 2011); however their effects in combination are not well understood. The net effect of a predator assemblage is often dependent on species identity, and can be more or less than the additive effects of individual predators (Sih, Englund, and Wooster 1998; Ives, Cardinale, and Snyder 2005). Non-additive effects of predator diversity occur when predators interact directly with each other, or indirectly via prey species, in a way that increases or decreases total predation. Antagonistic among-predator interactions can reduce the top-down effects of a diverse consumer assemblage, for example when predators feed directly on each other (intra-guild predation), consume the same prey (resource competition) or modify the behaviour of predators or prey via non- consumptive (i.e. trait- mediated) interactions (Sih, Englund, and Wooster 1998; Griswold and Lounibos 2006; Nyström et al. 2001). Synergy between predators is also possible, for example if one predator causes behavioral shifts in prey that increase their chance of being eaten by another predator species. These interactions depend on predators actually co-occurring, and predators in the same

community may not always co-occur, for example because of microhabitat preference differences (Schmitz 2007). While there are many mechanisms potentially underlying predator compositional effects, we lack a means of predicting *a priori* which combinations are likely to have antagonistic versus synergistic effects on ecosystem functions.

One possible predictor of the effect of predator combinations is predator phylogenetic diversity. The measurement of phylogenetic diversity has become a popular means for ecologists to make inferences about ecological and evolutionary mechanisms behind observed patterns in natural communities (Cavender-Bares et al. 2009). For example, the phylogenetic diversity of plant communities is a better predictor of productivity than is either species richness or diversity (e.g. M. W. Cadotte et al. 2009; M. W. Cadotte, Cardinale, and Oakley 2008; Godoy, Kraft, and Levine 2014). A central assumption of this approach is that increased phylogenetic distance implies increased ecological dissimilarity – either in the form of differences in species niches, interactions, or functional traits. When this is true, high phylogenetic diversity could create the ecological conditions needed for strong ecosystem functioning (Srivastava et al. 2012). Despite the prevalence of phylogenetic community ecology and the importance of predators to natural systems, the phylogenetic diversity of local predator assemblages has rarely been measured (L. Bersier and Kehrli 2008; Naisbit et al. 2011). Many studies of phylogenetic signal in predator traits focus on whole clades, rather than local assemblages (e.g. *Anolis* lizards (Knouft et al. 2006), warblers (Gaese 2003), tree boas (Henderson, Pauers, and Colston 2013) and wasps (Budriene and Budrys 2004)) making it difficult to connect these results to top-down effects at the scale of a local community. While these clade-specific studies often find weak evidence for phylogenetic signal in ecologically-rele-

41 vant traits, studies at the level of the whole biosphere (Gómez, Verdú, and Perfectti 2010; L.
42 Bersier and Kehrli 2008) demonstrate that related organisms often have similar interspecific
43 interactions – i.e. related predators often consume similar prey. At the level of a commu-
44 nity, the effect of a predator assemblage will depend on both the microhabitat distribution
45 and trophic interactions of all predator species. Phylogeny may constrain local species com-
46 position when distant relatives have distinct fundamental niches, while close relatives are
47 too similar to co-exist (Webb et al. 2002; Emerson and Gillespie 2008). Other predators
48 constrain distribution not only through direct interactions, but also colonization: predators
49 may use cues of prey, competitors, or intra-guild predators when selecting a habitat patch
50 (Chase and Shulman 2009; McCauley et al. 2008; Srivastava et al. 2008). After colonization,
51 patterns of co-occurrence may be further modified by intraguild predation (L. P. Lounibos
52 et al. 2008; Juliano 2009) or competition (Fincke, Yanoviak, and Hanschu 1997).

53 When predators do co-occur, their direct effects on each other and on their prey is in part
54 determined by their overlap in diet. Diet overlap (shared prey species between predators) will
55 depend on the feeding traits and nutritional requirements of predators – both of which may
56 be phylogenetically conserved (CITEAngelica). If this is the case, then predator assemblages
57 with higher phylogenetic diversity will show greater prey consumption and a stronger top-
58 down effect on ecosystem function (Finke and Snyder 2008). For example, some predators are
59 gape-limited, and can swallow any prey smaller than their mouth; these predators typically
60 broaden their diet as they grow (e.g., larvae of Odonata) (E. Werner and Gilliam 1984). Such
61 ontogenetic changes in diet can radically influence food web structure (Moya-Laraño 2011).
62 Other predators (e.g. Leeches, or Diptera:Tabanidae) are “piercing-sucking” predators (Bay

1974) and may be more general consumers at all life stages, since they can feed on larger prey individuals even at very early predator life stages. In some cases, predator diets may extend to include other predators, leading to direct negative interactions such as intraguild predation consequently have a phylogenetic signal (Pfennig 2000).
1 cm final instar).

Diet Similarity: feeding trials

We tested for similarity in predator diets (Question 2) using a series of laboratory feeding trials. We conducted 314 feeding trials of 10 predator taxa fed 14 prey taxa between March and April 2011. We covered all potential predator-prey pairs present in the experiment (described below), and attempted to perform all other trials whenever possible. However, due to the rarity of some taxa many predator-prey pairs were not possible; we tested 56 pairwise combinations. Most trials were replicated at least five times, but the number of replicates ranged from 1 to 11. We placed predators together with prey in a 50ml vial, with a leaf or stick for substrate. The only exception was the tabanid larvae, which we placed between two vertical surfaces to imitate the narrow space found in bromeliad leaf axils (their preferred microhabitat). Generally our trials contained a single predator and a single prey individual, except in the case of very small prey (*Elpidium* sp.) or predators (*Monopelopia* sp.) in which case we increased the density. We replicated each combination up to five times where possible, and allowed 24 hours for predation to occur.

Community effect experiment

Our third question had two parts: (a) how do predator species differ in their effects on the whole community and (b) do predators show nonadditive effects on the community in combination, and are these related to phylogenetic distance? We tested these questions with an experiment involving the four most common predators, paired to create a range of phylogenetic relatedness: two congeneric damselflies (*Leptagrion andromache* and *Leptagrion elongatum*), two insects (*L. elongatum* and a Tabanid predatory fly), and two invertebrates (*L. elongatum* and a predatory leech). Our experiment also included species in monoculture, and a predator-free control (total of 8 treatments, n=5). Treatments were substitutive, maintaining the same amount of total predator metabolic capacity (see below) to isolate the effects of predator behaviour and traits. Substitutive experiments often hold total abundance constant, but when species differ substantially in body size - as in this experiment - allometric effects of body size on feeding rate can confound detection of effects based on trophic traits or species interactions, and standardizing to community metabolic capacity is preferred (Srivastava and Bell 2009). This experiment allows the estimation of the effect of each predator species (monoculture treatments), as well as the detection of non-additive effects in predator combinations.

In February 2011, bromeliads between 90 and 200ml in capacity were collected, thoroughly washed to remove organisms and detritus and soaked for 12 hours in a tub of water. They were then hung for 48 hours to dry. One bromeliad dissected after this procedure contained no insects. Each bromeliad was supplied with dried leaves, simulating natural detritus inputs from the canopy. In order to track the effects on detrital decomposition on bromeliad

104 nutrition, we enriched these leaves with ^{15}N by fertilizing five (Jabuticaba, *Plinia cauliflora*)
105 plants with $40\text{ml pot}^{-1} \text{ day}^{-1}$ of 5g L^{-1} ammonium sulphate containing 10% atom excess of
106 ^{15}N over 21 days. Whole leaves were then picked from plants and air-dried until constant
107 weight, and then soaked for three days and the water discarded. About 1.5 g of leaves were
108 placed in each bromeliad ($1.5006\text{g} \pm 0.0248$).

109 Each bromeliad was stocked with a representative insect community. The densities of each
110 prey taxon were calculated from the 2008 observational dataset, using data from bromeliads
111 of similar size to those in our experiment. All densities used were within the range of these
112 calculated abundances, and all experimental bromeliads received the same insect community.
113 Halfway through the experiment, insects were added to bromeliads a second time to simulate
114 the continuous oviposition that characterizes the system. Throughout the experiment, all
115 bromeliads were enclosed with a mesh cage topped with a malaise trap and checked daily
116 for emergence of adults.

117 In this experiment we measured five response variables: production of fine particulate organic
118 matter (FPOM), decomposition of coarse detritus, bromeliad growth, uptake of detrital
119 nitrogen into bromeliad tissue, and survival of invertebrate prey (emerged adults + surviving
120 larvae). We analyzed each of these responses with ANOVA. For each pair of predator species
121 and each response type, we calculated the non-additive effect as the difference between
122 the response in bromeliads with both predator species ($n=5$) and the mean response in
123 bromeliads with either one of these two predator species ($n=5$ for each predator species). We
124 generated bootstrap confidence intervals for these nonadditive effects; confidence intervals
125 which do not overlap zero indicate a significant non-additive effect of a predator combination.

Phylogenetic distance, metabolic capacity and niche overlap

Our observational data contains data from 25 bromeliads, containing 14 predator taxa. These include two groups of congeneric taxa – *Bezzia* sp. (Diptera:Ceratopogonidae) with two species and *Leptagrion* sp. (Odonata:Coenagrionidae) with three species. There were also two groups of confamilial taxa – three species of Tabanidae and two species of Empididae, all Diptera. Deeper divisions were also present: three families of Diptera are represented by a single predator species each (Dolichopodidae, Corethrellidae and Chironomidae) and the deepest taxonomic divide is between all insects present and the predatory leeches (Annelida:Hirudinidae).

We obtained node age estimates for all seven internal nodes of the tree, using www.timetree.org, an online database of published molecular time estimates (Hedges, Dudley, and Kumar 2006). Most dates came from only a single study; where multiple dates were found we used the median estimate: Insecta–Hirudina (543 to 700 Mya, n=5 studies), Odonata–Tabanidae (151 to 543 Mya, n= studies) and Tabanidae–Diptera (106.2 to 474 Mya, n=7 studies). Node age data was available for all but the youngest nodes, where either a lack of taxonomic information (e.g. Tabanidae) or a lack of phylogenetic study (e.g. *Leptagrion*) prevented more information from being included. These branches were left as polytomies, and were all assigned identical, arbitrary and short branch lengths (15 Mya).

Species co-occurrence is often measured in terms of non-random patterns of species presence/absence or abundance, but such measures will only be poorly related to the functional effects of species when species differ substantially in body size. Integrating the allometric relationship between body size and feeding rate (Brown et al. 2004; Wilby, Villareal, and

Lan 2005) over all individuals of a species allows estimates of “metabolic capacity”, or the potential energy requirements of a species (Srivastava and Bell 2009). Metabolic capacity is equal to individual body mass raised to the power of 0.69 (an insect-specific exponent determined by Peters 19xx and confirmed by Chown et al, (2007)); this reflects the nonlinearity of feeding rate on body size across many invertebrate taxa. We used metabolic capacity to inform both our observational results and our experimental design (details below), with the exception of our feeding trial data. This is because the feeding trials were intended to measure which prey our predators ate, rather than their feeding rate (only the latter should scale with metabolic capacity).

Questions 1 and 2 above focus on similarity (“niche overlap”) between predator species. Question 1 hypothesizes that if habitat preference is phylogenetically conserved and competition between predators unimportant, then distributional similarity will decline with increased phylogenetic distance between a pair of predators. Question 2 hypothesizes that if diet is conserved, then diet similarity declines with increased phylogenetic distance between a pair of predators. We evaluated both distributional and diet similarity between predators using Pianka’s index of niche overlap (Pianka 1974):

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

For each pair of predators, p_{ik} and p_{il} represent the preference of predator k (or l) for resource or habitat i . When quantifying distributional similarity, $n=25$ bromeliads surveyed in the observational data; when quantifying diet similarity, the number of resources (n) is defined as the total number of prey species assayed with both predator taxa. In the survey data, preference (p_{ik}) is defined as the proportion of a predator’s total metabolic capacity

found in a particular bromeliad; in diet trials it is the proportion of diet trials (see below) for each predator-prey combination that resulted in prey mortality.

We quantified the effect of phylogenetic distance on each of distributional and diet similarity. First, we calculated phylogenetic distance between each pair of species, then fit several functions to the relationship between phylogenetic diversity and either distributional or diet similarity (linear, constant, and several appropriate nonlinear functions). We compared these models using AIC, selected the best model, and generated confidence intervals as appropriate (parametric or bootstrap for linear and nonlinear, respectively).

Results

Distributional similarity

Across all bromeliads, predator species differed widely in metabolic capacity, from 4.5×10^{-4} for a species of *Monopelopia* to 0.15 for large predatory flies in the family Tabanidae. Predators often co-occurred in bromeliads (4.4 ± 2.9 predator species per plant). However, the niche overlap between the total metabolic capacity of pairs of predators did not show any relationship with phylogenetic distance between them ($F_{1,89}=2.3918$, $p=0.13$).

Diet similarity

Among the most common predator taxa (i.e. those used in our experiment, described below) the damselflies (*Leptagrion andromache* and *Leptagrion elongatum*) showed the highest rates of prey consumption (prey consumed in 94.3% and 67.7% of trials, respectively). All preda-

tors showed a broadly similar diets, consuming nearly all species offered to them. However, more phylogenetically distant predators differed in their preference of prey species, as measured by the niche overlap index ($F_{1, 26}=5.98$, $p=0.022$, regression weighted by the number of prey species assayed.)

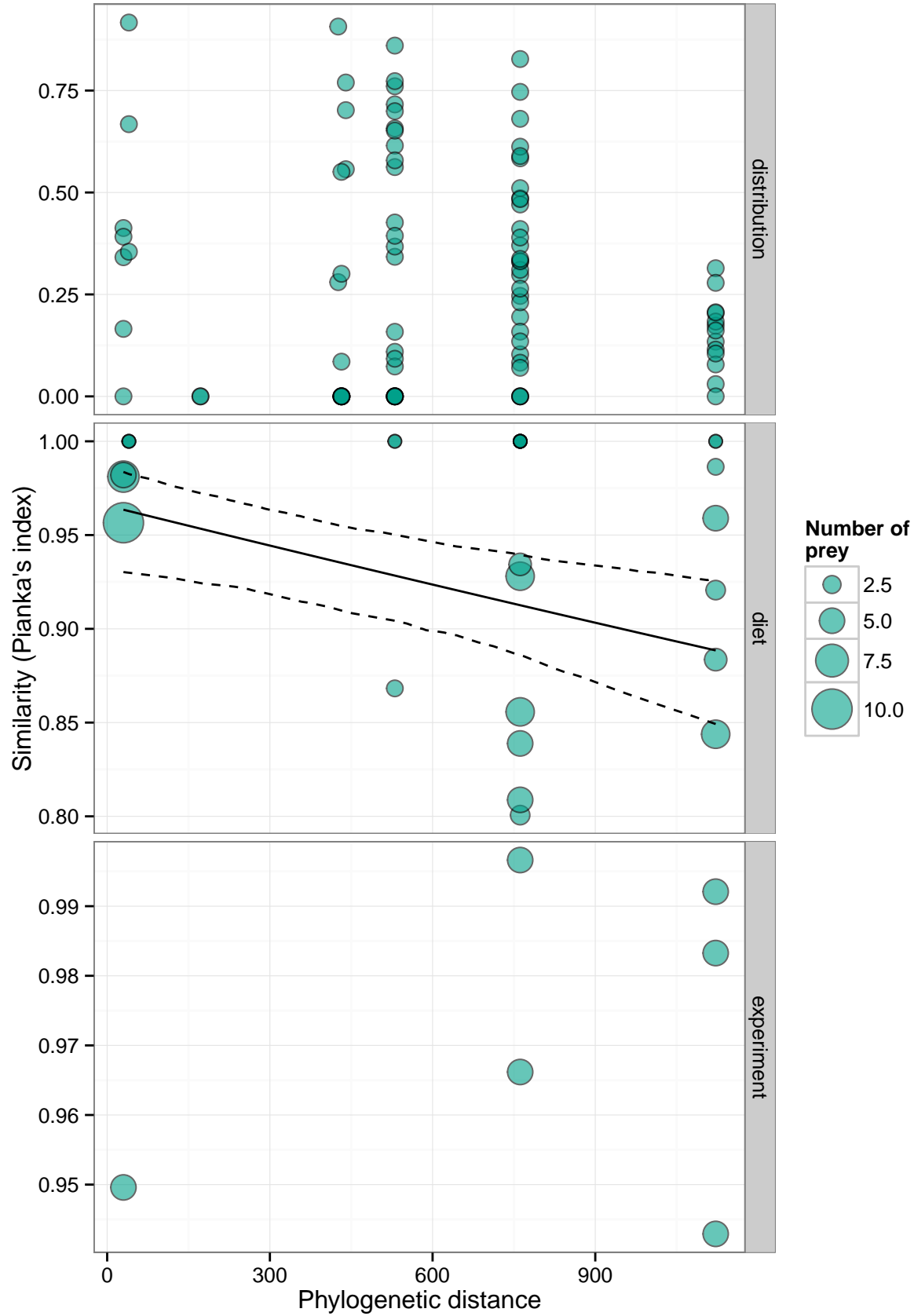
Ecosystem-level effects and phylogenetic distance

Predators had a large effect on prey survivorship: on average all predator treatments showed 51% lower prey emerging or surviving as larvae relative to the predator-free control. Nitrogen transport to bromeliad leaves was slightly decreased in bromeliads with predators relative to predator-free controls (-11%), and was only higher than the control in treatments including Tabanid predators. We found a similar pattern for plant growth: on average, predators had a -18% effect on growth of bromeliad leaves (leaf elongation in mm), though Tabanids seemed to create a slight increase. The decomposition of coarse detritus and production of fine organic matter showed no obvious pattern related to the presence of predators.

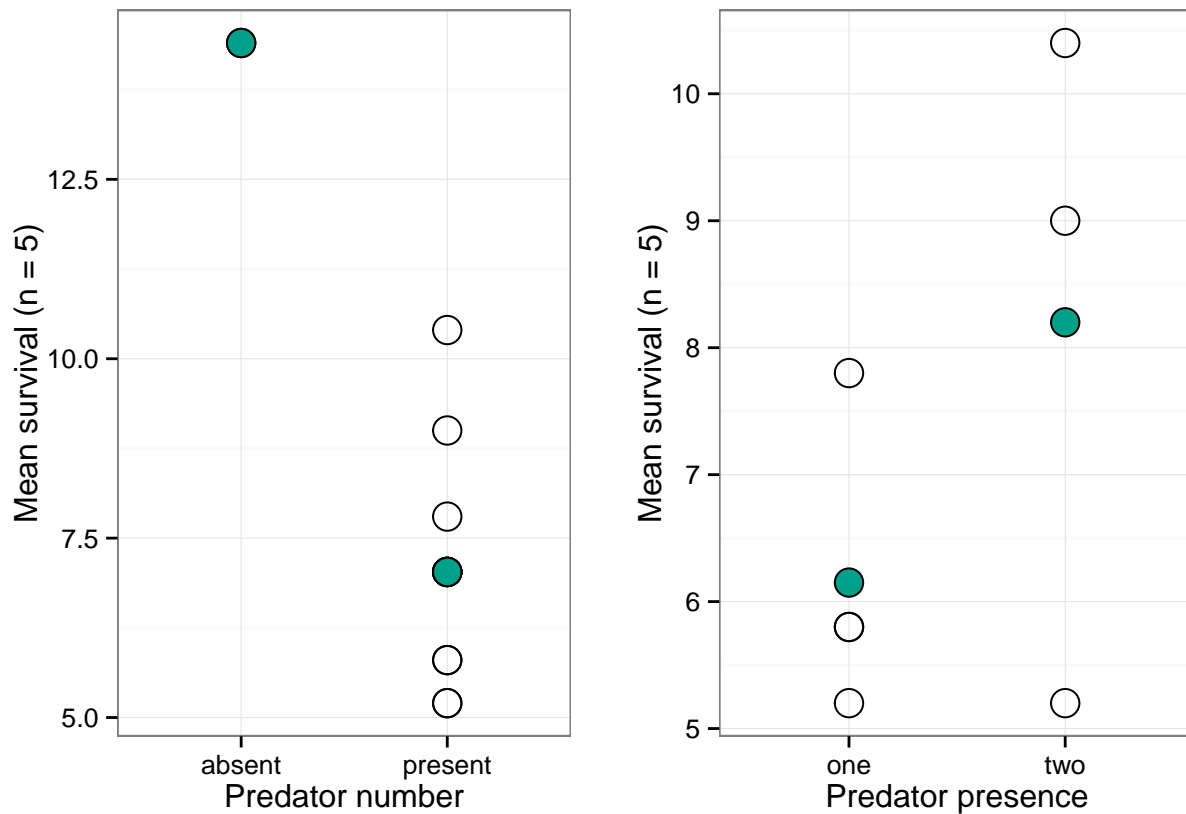
Predator combinations tended to have a non-additive effect on our response variables. Approximately 14% more prey survived in polyculture, on average, compared to all monocultures. Nitrogen uptake increased by (8%) and bromeliad growth by (11%). Production of fine particulate organic matter increased by 29% more when predators were present in combination.

We tested the hypothesis that increased phylogenetic distance between members of a predator pair results in a greater magnitude of nonadditive effect using randomization tests. We contrasted the differences of the mean individual predator treatments from the control with

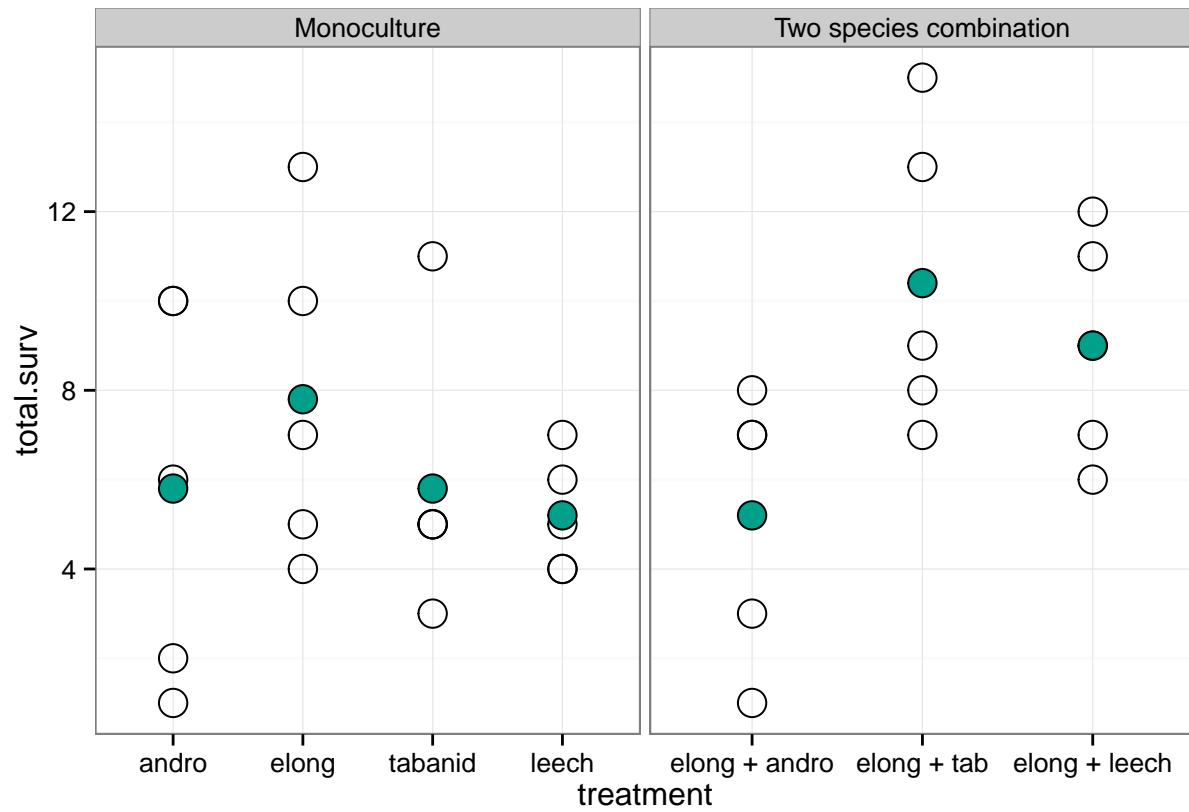
210 the mean difference of their pairwise combination from the control. We found the greatest
211 effect for prey survival: while effects of *L. andromache* and *L. elongatum* in combination were
212 quite similar to the effect of either alone, when *L. elongatum* was placed in the same plant
213 as either a Tabanid larva or leeches, on average five more prey individuals (18% of total prey
214 community) survived till the end of the experiment (Fig 3). This effect was smaller among
215 the other variables, most of which showed confidence intervals from the randomization test
216 which overlap zero.



219 **Figure 1:** Phylogenetic distance between predator pairs and their ecology. Each point
 220 represents a pair of predator species. Distributional similarity was quantified from the total
 221 metabolic capacity for each predator species in each bromeliad. Diet similarity is calculated
 222 from a series of feeding trials, and experimental similarity as the surviving prey community
 223 emerging from bromeliads. Similarity between each pair of predators was calculated using
 224 Pianka's index. Solid line shows the best fit non-linear model (see Appendix) and dashed
 225 lines show bootstrap 95% quantiles.



227 **Figure 2:** Adding predators reduces insect emergence, probably because they eat the prey.
 228 However, increasing predator number raises survival again. This is because the predators
 229 are interfering with each other.



230

231 **Figure 3:** Predator community compositon, in monoculture and polyculture, and its effects
 232 on prey survival. Prey emergence is lowest when damselflies are paired together, but increases
 233 when damselflies are combined with other species.

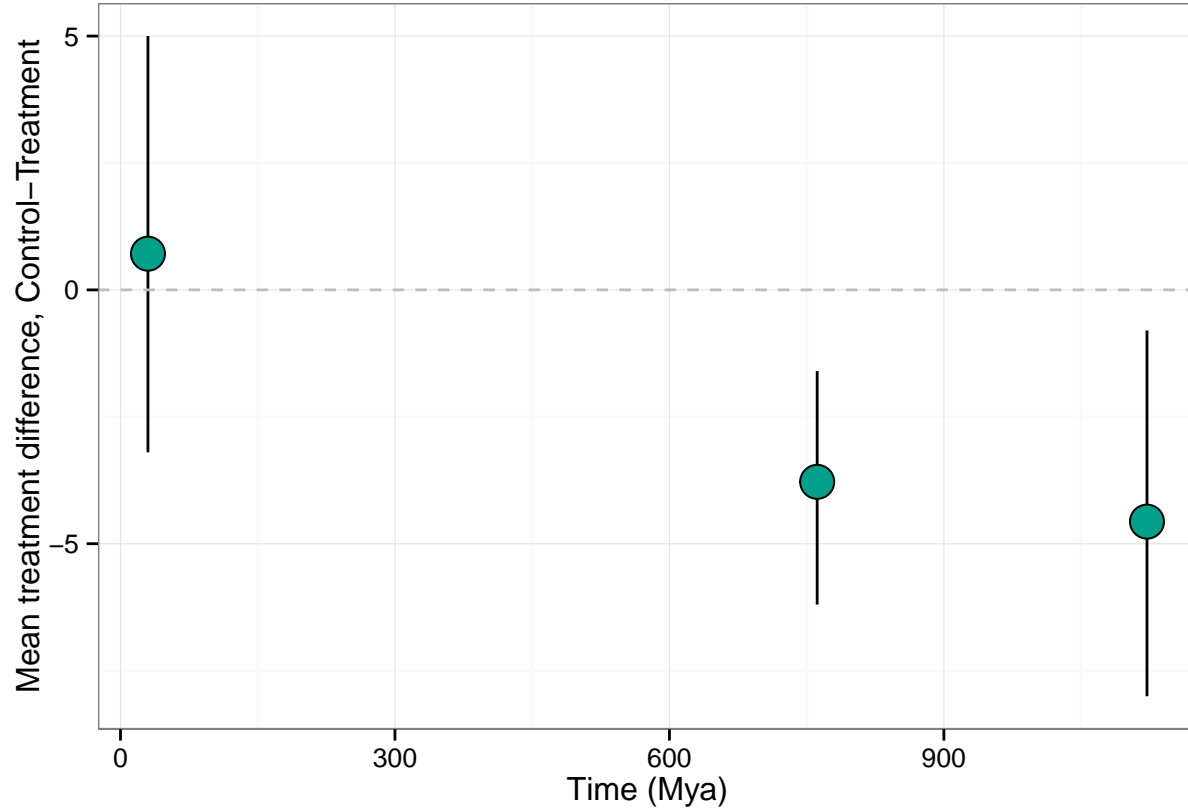


Figure 4: Combinations of predators beyond congenics show a negative non-additive effect on predation rate. Points represent the mean difference between the means of two monocultures compared to the mean of a polycultures. The dashed line represents differences = 0, i.e. no nonadditive effect. These values are presented as differences from (predator free) controls; therefore zero indicates no significant non-additive effect. Relative to control (no predator) plants, bromeliads containing two predators which were not congeneric showed less predation

Table 1 Experimental results. We measured for community-level variables: total prey survival (both emerged adults and surviving larvae), the breakdown of coarse detritus, the production of fine particulate organic matter (FPOM), and the growth of the bromeliad itself. We considered our experimental design at several levels: comparing treatments with

predators to those without, contrasting predator species, comparing predator communities of 1 or 2 species, and considering the effects of phylogenetic distance between predators.

Response	Predator Presence	Identity	Richness	Pairwise PD
Total prey survival	$F_{1,10} = \mathbf{9.07}$	$F_{3,16} = 0.6$	$F_{1,5} = 1.96$	$F_{1,13} = \mathbf{7.64}$
Decomposition (g)	$F_{1,10} = 0.47$	$F_{3,15} = 1.29$	$F_{1,5} = 0.21$	$F_{1,13} = 0.4$
FPOM (g)	$F_{1,10} = 0.92$	$F_{3,16} = 0.42$	$F_{1,5} = 6.47$	$F_{1,13} = 1.35$
Bromeliad growth	$F_{1,10} = 0.51$	$F_{3,16} = 0.96$	$F_{1,5} = 0.49$	$F_{1,12} = 1.29$

Discussion

In our system, distantly related predators are no more likely to be similar in distribution than are close relatives (Question 1). We also tested whether diet similarity decreased with predator phylogenetic distance (Question 2), and found a stronger pattern: diet similarity declined with phylogenetic distance between two predators, in a nearly linear relationship. However, this difference in diet did not translate into a difference in the composition of animals surviving in bromeliads stocked with different predators (3a). We did find an effect of phylogenetic distance when predators were placed in pairs - specifically, when damselflies were paired with non-damselfly predators. This resulted in more prey animals surviving to the end of the experiment; this could be caused by a reduction in feeding rate when predator taxa are very dissimilar.

Do related organisms occur in different bromeliads?

Predator pairs showed only a weak relationship between phylogenetic distance and differences in distribution. Such differences could have been caused by different species either having different preferences for environmental variables, or antagonistic interactions with each other. The absence of any signal suggests that either patches do not differ in variables which matter to the predators, or that predator taxa do not have strong impacts on each other's distribution. The lack of a relationship is probably not due to a lack of variation in bromeliad communities: We know already (CITE) that bromeliads in this and other systems vary considerably in many habitat variables, such as detritus content, amount of sunlight, and habitat size. It is more likely that these predator species are habitat generalists. Organisms which live in small, fluctuation-prone habitats – especially if they are long-lived – may evolve a wide physiological tolerance to those environmental fluctuations. Therefore we would not expect a high degree of habitat specificity among these organisms.

Although we found some evidence for negative intraspecific effects in our experiment, these do not appear to limit predator distribution. This could be caused by a low encounter rate of predators in natural plants, especially in larger bromeliads than those used in our experiment. Additionally, negative effects could still be occurring in nature, but not resulting in mortality. Indeed, if animals are actually able to adjust their development times and feeding rates when conditions are unfavourable (and if the presence of a competing predator creates such unfavourable conditions), then we would expect to observe more frequent, not less frequent, co-occurrences of predators. Non-consumptive negative interactions need not result in dissimilar distributions.

281 In our experimental treatments with paired predators we observed little predator mortality;
282 this suggests that predator indirect interactions might reduce predator feeding rates but do
283 not necessarily result in predator mortality. Our observational data indicate that at the
284 level of the patch (i.e. a single bromeliad) a wide range of predator phylogenetic diversity is
285 possible, from very similar to very disparate. This justifies the phylogenetic diversities we
286 used in our experimental communities, as these are within the range found in nature.

287 **Do related organisms have similar diets?**

288 Predators consumed very similar prey, except those most phylogenetically distinct. There
289 were some slight taxon-specific diet preferences which accounted for this. Leeches and ta-
290 banids showed different patterns of consumption compared with *Leptagrion* predators: they
291 consumed less frequently, and notably consumed prey in less than half of trials with *Culex*
292 (leech) or *Scirtes* (Tabanid). This may be because these predators lack the strong jaws and
293 “mask” of odonata, and these two prey species are particularly active (in the case of culi-
294 cids) or difficult to handle (scirtids). Tabanids in particular differ in microhabitat use from
295 odonates; living deep within leaf axils, where culicids are rarely found. One of our *Leptagrion*
296 morphospecies showed a greater preference for harder-bodied prey species (i.e. Ostracoda,
297 *Scirtes* and *Phylloicus*, which is a caddisfly.) All of these animals are consumed more fre-
298 quently by this damselfly than by the other species of *Leptagrion*, while the other damselflies
299 more frequently consumed *Culex* and *Polypedilum* prey. Thus, our data show some evidence
300 of a phylogenetic basis for diet dissimilarity, based on the very different traits of these in-
301 vertebrate taxa. Traits can be more important than phylogeny *per se* to a predator’s diet:

(Moody 1993) found that unrelated decapod species which were morphologically similar were also functionally similar. Similarly, (Rezende et al. 2009) found that both body size and phylogeny determined the food web “compartment” (shared predator-prey interactions) of a predator in a marine foodweb. In addition, our experimental results are consistent with high similarity among predator diets: all predator species had comparable effects on all response variables, including prey species survival.

Phylogenetic diversity and non-additive effects

Predator pairs which were more phylogenetically distant had a larger negative nonadditive effect on prey capture. This is contrary to our hypothesis that more distant predators would show an increase in prey capture via complementarity. *L. andromache* did not produce a negative effect in combination with *L. elongatum*, while more phylogenetically distinct predators did. It may be that these odonates have behavioural traits that reduce the probability of their interaction, for example each nymph occupying a single leaf-well. If this is the case, each damselfly may not experience many cues indicating the presence of other predators, resulting in no non-additive interaction.

Odonates can be sensitive to chemical cues of potential predators, which causes a decrease in feeding rate (Barry and Roberts 2014). However other research in bromeliads has demonstrated that it is physical contact with other organisms that reduces damselfly predation rate (Trish). If this is the case for *Leptagrion*, then when combined with leeches they may be responding to frequent contact with those very active predators. Tabanids, however, are rarely observed outside of a deep leaf axil – in this case, it may be chemical cues which

are responsible. There may also be a phylogenetic signal to the chemical cues which the damselflies perceive: i.e. close relatives (other *Leptagrion* sp. in this case) might induce less of an effect than other predators.

Interestingly, the pattern of induced defenses do not line up with predation risk, as observed in our feeding trials. In feeding trials with leeches, actual predation was rarely observed – except in one instance, where the damselfly ate the leech. However, trait-mediated indirect effects may not always reflect realized probability of predation: an animal may change behaviour when exposed to a “predator” which poses little threat (REF).

One limitation of our approach is the focus on a single focal predator, the odonate *Leptagrion elongatum*, which was common in all of our predator treatments. It is possible that this species is more sensitive to the presence of other predators, and therefore shows a larger trait-mediated indirect effect, than would other species in this community. However, this is the most common species in this community and our results indicate that its top-down effects are likely to be frequently reduced by the presence of other predators.

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