

Predator phylogenetic diversity decreases predation rate via antagonistic interactions

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Introduction

Predator assemblages can have strong top-down effects, both on community structure and ecosystem processes (Estes et al. 2011). However, the strength of top-down effects is often dependent on the composition of predator assemblages. While some combinations of predator species result in greater consumption or ecosystem processes than expected from their individual effects, other combinations result in less than additive effects (ref). Detailed studies manipulating predator assemblages have identified a great diversity of direct and indirect mechanisms for these compositional effects. For example, predators differ in their preferences for microhabitats resulting in spatial or temporal partitioning between predator species in their effects on prey and synergistic effects on net predation rates (REF). When predators do co-occur in a local patch, they may feed on different prey species and so have additive top-down effects (Schmitz 2007). Conversely, antagonistic predator-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) or modify the behaviour of predators or prey via non-consumptive (ie trait-mediated) interactions (Sih, Englund, and Wooster 1998; Griswold and Lounibos 2006; Nyström et al. 2001). 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.

Several authors have hypothesized that the phylogenetic diversity of a community or assemblage may correlate with increased ecosystem function, via increases in trait diversity (Diane S Srivastava et al. 2012).

Phylogenetic diversity measures have provided useful insights into diverse plant communities (e.g. M. W. Cadotte et al. 2009; M. W. Cadotte, Cardinale, and Oakley 2008; Godoy, Kraft, and Levine 2014), and yet have rarely been applied to local assemblages of predators (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), warbler (Böhning-Gaese, Schuda, and Helbig 2003), treeboas (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-relevant traits, studies at the level of the whole biosphere (Gómez, Verdú, and Perfectti 2010; L. Bersier and Kehrli 2008) demonstrate that related organisms often have similar interspecific interactions – i.e. related predators often consume similar prey. At the level of a community, the effect of a predator assemblage will depend on both the spatial distribution and trophic interactions of all predator species. Phylogeny may constrain species distributions when distant relatives have distinct fundamental niches, while close relatives are too similar to co-exist (Webb et al. 2002; Emerson and Gillespie 2008) – for predators, this means that similar taxa may not be able to occupy the same compartment of a food web (Rezende et al. 2009). By correlating with these properties, measures of phylogenetic diversity may allow us to predict the effect of a predator assemblage on ecosystem functioning.

Within predator assemblages, there may be considerable variation in the abundance and distribution of related taxa. If habitat patches are variable, and if the fundamental niche of different organisms varies with relatedness, then we would expect a phylogenetic signal to patterns of occurrence. Specifically, if related predators share habitat requirements, then we expect to find them in the same patches – unless their similarity precludes their co-occurrence. This relationship between relatedness and distribution is the most common way in which phylogenetic information is used in community ecology (Cavender-Bares et al. 2009). In metacommunities – i.e. when patches are connected by dispersal – variation in the composition of a local assemblage is also determined by species dispersal into, and selection among, habitat patches (M. A. Leibold et al. 2004; Howeth and Leibold 2010; Calcagno et al. 2011). The effects of other predators can be important too: during dispersal, assembly can be nonrandom if predators use cues of the presence of prey, competitors, or intra-guild predators when colonizing (Chase and Shulman 2009; McCauley et al. 2008; Diane S. Srivastava

et al. 2008). After colonization, patterns of co-occurrence may be further modified by intraguild predation (L. P. Lounibos et al. 2008; Juliano 2009) or competition (Fincke, Yanoviak, and Hanschu 1997).

When predators co-occur, their feeding mode, diet breadth and nutritional requirements will determine which prey they consume and the potential total amount of predation. Because such morphological traits may well be conserved over evolutionary time, the breadth of differentiation (and hence resource use) may also show a phylogenetic signal; this differentiation in resource use leads to complementarity and greater overall ecosystem function (Fincke and Snyder 2008). Among predators, feeding mode is an important trait that is conserved within lineages and determines a large part of diet breadth. For example, some predators are gape-limited, and can swallow any prey smaller than their mouth; these predators typically broaden their diet as they grow (e.g., larvae of Odonata) (E. Werner and Gilliam 1984). Such ontogenetic changes in diet breadth can radically influence food web structure (Moya-Laraño 2011). 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, which may also have a phylogenetic signal (Pfennig 2000).

Predator interactions are common in many communities, and can lead to nonlinearities which prevent the inference of predator effect from the additive combination of individual predators (Sih, Englund, and Wooster 1998). For example, decreasing predator richness has been shown to increase herbivory in a three-level kelp food web (Byrnes et al. 2006). The complex traits that underlie such species interactions (particularly “higher-order” interactions *sensu* Sih *et al.* (1998)) may also correlate with phylogeny, leading to a higher correlation with community processes than richness alone (M. W. Cadotte et al. 2009). For example, phylogenetically diverse assemblages of mycorrhizae increased primary productivity more than equally speciose treatments from the same lineage (Maherali and Klironomos 2007). The effect of predators on prey may also be non-additive, the result of indirect interactions either with prey species or other predators: prey species may respond to the presence of one predator by a behavioural shift that increases the predation by another predator population (Carey and Wahl 2010). These trait-mediated indirect effects (TMII, (E. Werner and Peacor 2003)) can be difficult to predict; however phylogenetic relatedness has been suggested as a possible means of predicting the combined effect of predators (Naisbit et al. 2011)

We used a series of observations, lab feeding trials, and manipulative field experiments to measure how the phylogenetic diversity of the predator assemblage predicts community composition and ecosystem function. We test three related hypotheses concerning co-occurrence patterns, diet similarity and top-down ecosystem effects of diverse predators, using a natural mesocosm: the community of invertebrates living within bromeliads. Bromeliads (Bromeliaceae) are epiphytic plants native to the Neotropics. Many bromeliad species contain water, detritus and a complex insect food web within their leaves; the decomposition of this detritus supplies nutrients for the bromeliad (Benzing 2000). The small size of these habitats permits direct manipulations of entire food webs, manipulations which would be difficult in most natural systems. Within this aquatic food web, damselfly larvae (e.g. *Leptagrion* spp., Odonata: Coenagrionidae) are important predators; their presence dramatically alters community dynamics (e.g. decreases insect emergence (Starzomski, Suen, and Srivastava 2010) and increases nutrient cycling (Ngai and Srivastava 2006)).

1. *species co-occurrence*: closely-related predators may occur together more frequently than less-related predators if there is a strong phylogenetic signal to habitat requirements. Alternatively, very closely related species may never co-occur because high overlap in ecological niches results in competitive exclusion.
2. *diet similarity*: similarity in diet (as measured by feeding trials) decreases with phylogenetic distance if diet is phylogenetically conserved. Alternatively, closely related species may have evolved different diets to allow coexistence.
3. *ecosystem-level effects*: Our experiments at the level of the whole habitat patch (i.e. a single bromeliad) allows us to examine direct and indirect effects of predator combinations.
 - a) monoculture treatments allow us to assess the effect of each predator on a complete prey community and ecosystem function. Phylogenetic similarity among predators is predicted to correlate with sim-

ilarity in single-species effects if related predators share similar trophic interactions (e.g. predation rate, diet breadth)

- b) By comparing treatments with pairs of predators to treatments which received a monoculture of each predator, we are able to estimate additive and nonadditive effects. If distance between species correlates with increasing difference, we will see an increase in these non-additive effects with phylogenetic distance. At the extreme, differences between predators may lead to IGP among predators.

Methods

Site and Species

We conducted all observations and experiments in Parque Estadual da Ilha do Cardoso (25°03' S, 47°53' W), a 22.5 ha island off the south coast of São Paulo state, Brazil. We worked in a closed coastal forest (restinga) the understory of which is mostly covered by *Quesnelia arvensis* Mez. (Bromeliaceae), a large terrestrial bromeliad that accumulates up to 2.8 L of rainwater in tanks formed by individual leaves. Previous observational surveys of this work found more than 47 species of macroinvertebrates in these aquatic communities (Romero and Srivastava 2010). This diversity encompasses multiple trophic groups. Detritivores include various functional groups: shredders (Diptera:Tipulidae, Trichoptera), scrapers (Coleoptera:Scirtidae), and collectors (All Diptera:Chironomidae, Syrphidae, Psychodidae). Filter feeders (Diptera:Culicidae) are supported by the microbial components of the food web. A diverse predator assemblage consists of at least 3 species of damselfly larvae (*Leptagrion* spp., Zygoptera:Coenagrionidae), 2 species of predatory Horse Fly larvae (Diptera:Tabanidae), and 2 species of leech (Hirudinidae). Other, smaller-bodied predators present include predatory midge larvae (Diptera:Chironomidae:Tanypodinae) and less abundant species such as Dytiscid beetles.

Phylogenetic distance, metabolic capacity and niche overlap

In 2008, we counted and measured macroinvertebrates in an observational study of 25 bromeliads. Within this observational dataset, we identified 14 species as predators. These predators include species related at the genus level – e.g. *Bezzia* sp. (Diptera:Ceratopogonidae) with two species and *Leptagrion* sp. (Odonata:Coenagrionidae) with three – and family level (three species of Tabanidae and two of Empididae, all Diptera). Deeper divisions are 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 a species of predatory leech (Annelida:Hirudinidae).

We obtained node age estimates for all 7 internal nodes of the tree, using www.timetree.org, an online database of published molecular time estimates from the literature (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=4 studies) and Tabanidae–Diptera (151 to 543 Mya, n=7 studies). Node age data was available for all but the shallowest nodes of the tree, 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 occurrence 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 (Diane S. 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, (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 niche overlap between predator species. Question 1 hypothesizes that if diet is conserved, then diet similarity declines with increased phylogenetic distance between a pair of predators. Question 2 hypothesizes that if habitat preference is phylogenetically conserved and competition between predators unimportant, then co-occurrence declines with increased phylogenetic distance between a pair of predators. We evaluated both diet similarity and co-occurrence 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 . In terms of predator co-occurrence, $n=25$ bromeliads surveyed in the observational dataset described below. In terms of diet similarity, the number of resources (n) is defined as the total number of prey species assayed with both predator taxa, and preference is defined as the proportion of diet trials (see below) for each predator-prey assay that resulted in prey mortality.

Observations of predator distribution

We used the 2008 survey to examine patterns of co-occurrence among predator taxa. Each bromeliad was dissected and washed to remove invertebrates. The resulting water was filtered through two sieves (250 and 850 μm), which removed particulate organic matter without losing any invertebrates. All invertebrates were counted and identified to the lowest taxonomic level possible. The body length of all individuals was measured, when possible for small and medium-sized taxa ($< 1\text{cm}$ final instar) and always for large-bodied taxa ($> 1\text{ cm}$ final instar).

We calculated total metabolic capacity of each predator species in each bromeliad by summing estimates of biomass for all individuals of the same species within a plant. We used these values to calculate niche overlap as measured by habitat occupancy. Overlap was calculated for each pair of predators across all bromeliads, even if neither species occurred there.

Diet similarity

We conducted 232 feeding trials of 7 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 41 pairwise combinations. Most trials were replicated at least five times, but the number of replicates for various combinations 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 one day for predation to occur.

Again, we estimated overlap between different predators using Pianka’s index, using the proportion of trials which resulted in predation as our measure of predator preference. Because not every predator/prey pair was equally replicated, we weighted our analysis by the number of trials conducted.

Community effect experiment

Our experiment was created with two goals in mind: first, to measure the major effects of each of these predators on their prey and ecosystem function and second, to estimate the non-additive effects of pairwise

predator combinations. The strength of these non-additive effects could then be related to the phylogenetic distance between a pair of predator species.

We selected the four most common predators in this system, which also created a range of relatedness: two congeneric damselflies (*Leptagrion andromache* and *Leptagrion elongatum*), two insects (*L. elongatum* and a Tabanid predatory fly), and two invertebrates (*L. elongatum* and leeches). We used each of the pairs of predators just described, as well as each species in monoculture, and a predator-free control (8 treatments, $n=5$). Combinations were substitutive, maintaining the same amount of total predator metabolic capacity 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 (Diane S. 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. We enriched these leaves with ^{15}N by fertilizing five (Jabuticaba, *Plinia cauliflora*) plants with 40ml $\text{pot}^{-1} \text{ day}^{-1}$ of 5g L^{-1} ammonium sulphate containing 10% atom excess of ^{15}N over 21 days. Whole leaves were then picked from plants and air-dried until constant weight, and then soaked for three days and the water discarded. About 1.5 g of leaves were placed in each bromeliad ($1.5006\text{g} \pm 0.0248$).

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

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

Results

Patterns of occurrence

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 67.2% of trials, respectively). All predators showed a very generalist diet breadth, 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 ($F_{1, 19}=6.72$, $p=0.018$, regression weighted by the number of prey species assayed.)

Ecosystem-level effects and phylogenetic distance

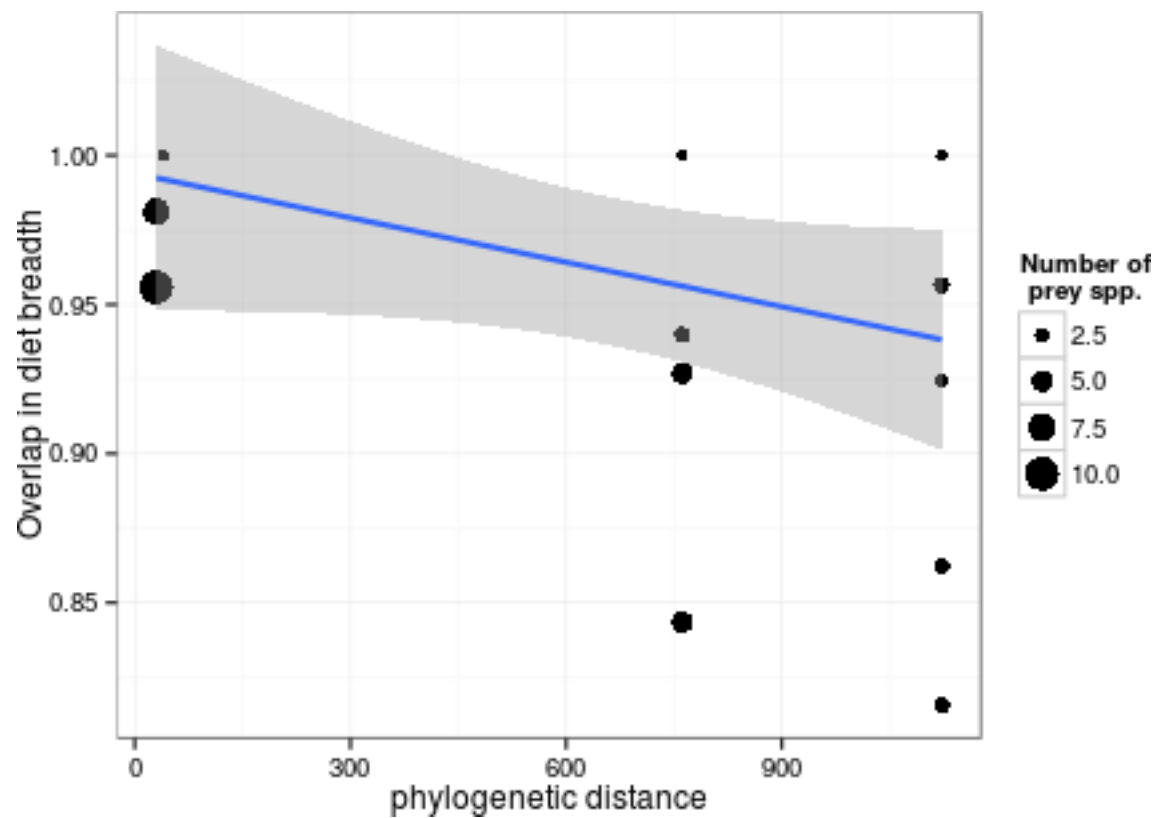
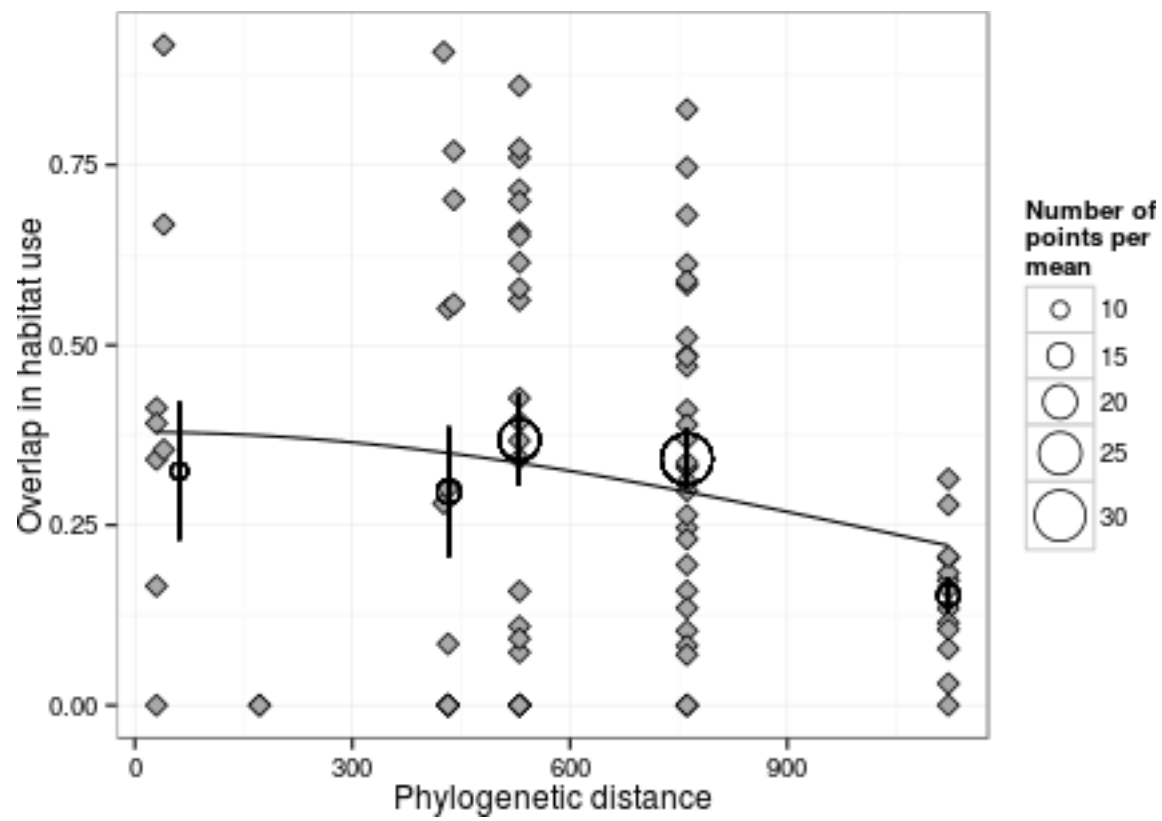
In our manipulative experiment, we placed a standardized prey community into bromeliads and measured five response variables. Predators had a large effect on prey survivorship: on average all predator treatments showed 51% lower prey emerging or surviving as larvae relative to the predator-free control. 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.

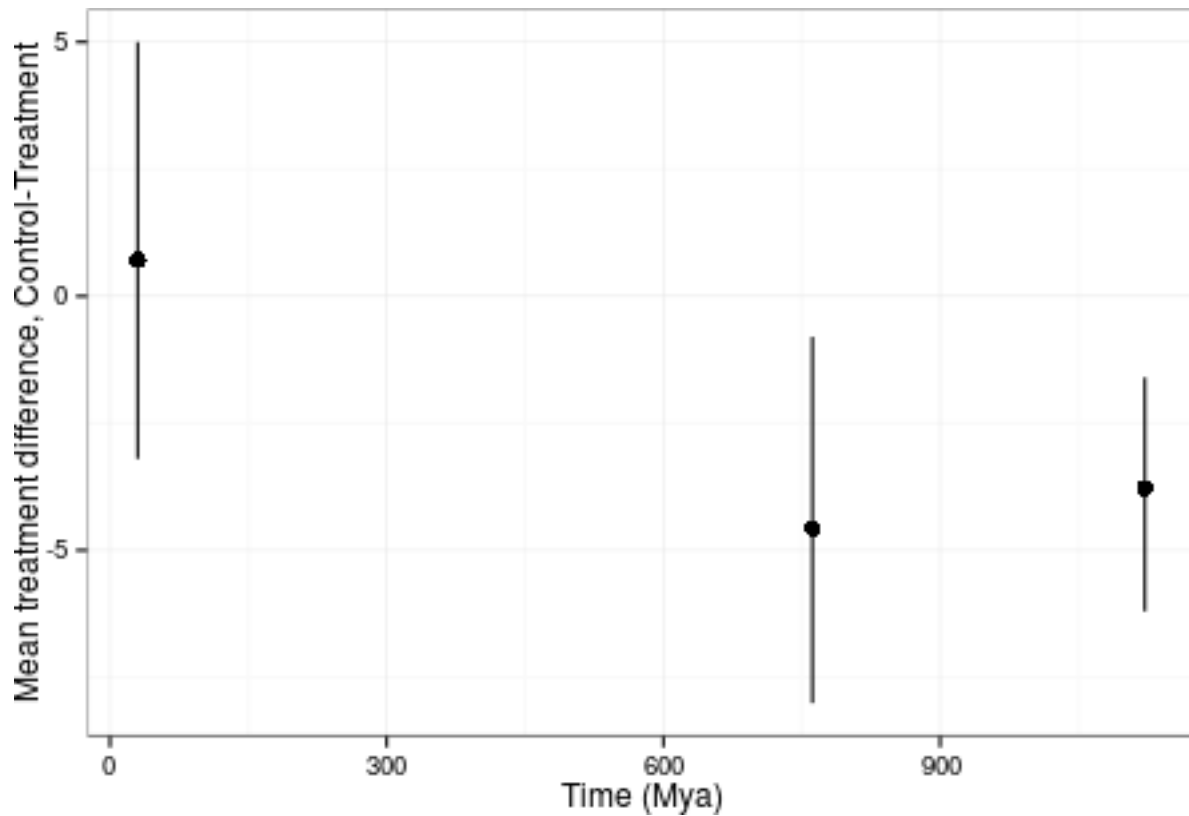
Predator combinations tended to have a non-additive effect on our response variables, even though we held total metabolic capacity constant amongst all treatments. Approximately 14% more prey survived in polyculture, on average, compared to all monocultures. Nitrogen uptake increased by (8%) and bromeliad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

Our experimental design allows us to estimate the non-additive effect of predator species pairs on whole communities of prey, and the functioning of the bromeliad ecosystem. We used randomization tests to test the hypothesis that increased phylogenetic distance between members of a predator pair results in a greater magnitude of nonadditive effect. We contrasted the differences of the mean individual predator treatments from the control with the mean difference of their pairwise combination from the control.

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

Figures





	surviving insects	fine detritus (g)	leaf decomposition (g)	bromeliad growth (g)	Nitrogen cycling
control	14 ± 2.7	0.62 ± 0.076	0.33 ± 0.023	4.7 ± 1.2	53 ± 2.9
andro	5.8 ± 1.9	0.5 ± 0.041	0.37 ± 0.028	4 ± 0.45	45 ± 6.2
elong	7.8 ± 1.7	0.42 ± 0.055	0.36 ± 0.0077	2.9 ± 1.3	45 ± 6
leech	5.2 ± 0.58	0.52 ± 0.09	NA ± NA	2.6 ± 1.6	36 ± 5.2
tabanid	5.8 ± 1.4	0.42 ± 0.11	0.31 ± 0.027	5.1 ± 0.95	56 ± 7
elong + andro	5.2 ± 1.4	0.8 ± 0.15	0.33 ± 0.024	3.3 ± 1.2	52 ± 4.8
elong + leech	9 ± 1.1	0.55 ± 0.049	0.32 ± 0.0083	NA ± NA	43 ± 7.5
elong + tab	10 ± 1.5	0.59 ± 0.24	0.37 ± 0.024	4 ± 0.98	54 ± 7.8

Discussion

results summary

We tested whether related predators are similar or dissimilar in their habitat distribution (Question 1). We found only weak support: There is no evidence for close relatives being either more or less likely to be found in association. Very distant relatives are less likely to co-occur, as shown by the decelerating curve in Fig 1.

We also tested whether diet similarity decreased with predator phylogenetic distance, and found a stronger pattern: diet similarity declined more rapidly than distributional similarity with PD.

Phylogenetic distance is negatively correlated with similarity in several responses.

We hypothesized that increasing PD in the top trophic level would increase the magnitude of the nonadditive effect (hypothesis 3b). We found that this is the case for total prey survivorship.

Do related organisms occur in different bromeliads?

Predator pairs showed only a weak relationship between phylogenetic distance and differences in distribution. This could be because bromeliads are actually more similar. While there are diet differences among the predators, and bromeliads do differ in species composition. Suppose there was lots of stochasticity in invertebrate colonization. Then long-lived predators would integrate over these, and prevent a strong signals of invertebrate community composition on predator distribution. It is true that our results show that the presence of distantly-related predators reduces feeding rate, in particular in *L. elongatum*. But on the other hand, as Rovin () found, these damselflies can persist in bromeliads even when there is rather a small amount of food. From this we can infer that perhaps they don't care about the eating. Since our experiment did not result in much predator *death*, but did provide evidence of reduced feeding, we can infer that perhaps we would not expect to see great differences in the distribution of predators, but perhaps in their growth rates. The only effect of phylogeny on similarity in habitat was among leeches. The leeches are both distantly related to the other predator taxa (all holometabolous insect species) and most different from them in distribution – together, the leeches determined the trend in figure 1. Why are leeches so different? Unlike other predators, they are passive dispersers. As a result, they probably disperse at random to site characteristics that other predators are able to select directly.

There are several reasons why the negative intraspecific effects that we found do not appear to limit distribution. First of all, the probability of interaction for real organisms could be quite low, especially in larger bromeliads than those used in our experiment. The negative effects could still be occurring, 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. My point is that negative interactions need not result in dissimilar distributions or “checkerboard units”.

Do related organisms have similar diets?

Supported. What is the mechanism here – is it feeding parts morphology (engulf vs pierce), foraging behaviour (sit and wait vs pursue) position within the bromeliad? Have a look at the prey items that differ between odonates and leeches to give you some cues here. But if there is no obvious answer, don't belabour it. What other studies in the literature support the hypothesis 2 pattern?

- look up feeding trial data. What animals are eaten by leeches? damselflies?
- reference about gape limitation in odonates
- reference about leech predation on invertebrates

predators and nonadditive

. Hypothesis three. Non-additivity. Relationship with evolutionary distance is opposite to predicted. We expect greatest antagonism between closely related species, as they are most similar in resource or habitat use, instead greatest antagonism is between unrelated species. Why? It can't be because of prey preferences, because related species actually prefer the same prey, which we would think would lead to antagonism amongst related species – not unrelated species. It can't be because related species didn't co-occur, because we forced them to in our experiment, and in nature relatedness is poorly related if at all to co-occurrence. Is it because leeches attack predatory insects? Do they? I assume you did feeding trials of the predators on each other...

We found a negative relationship between phylogenetic distance and the strength of the nonadditive effect of predators. In studies showing nonadditive effects, these are usually WE hypothesized that nonadditive effects would increase with predator dpd, because it seems like there would be more likely that there would be the

necessary differences in distribution or behaviour because of that. But in fact what happened is that the nonadditive effect actually decreased.

put this earlier: When are effects additive? When predators do not affect each other’s feeding, but rather consume different prey individuals. Beacuse our design was substitutive, if our

How do differences diet turn out in a substitutive design, when the predators are combined? if they eat e exact same thing, and then are combined in equal parts of metabolic capacity, then the combination should be equal to either of the monocultures (or, equivalently, to the mean of the two). If they eat different things we would expect monoculturese to be different – but, when predators are combined in equal portion, the result should again be similar to the mean effect of each alone. However, we found that combinations of increasingly diverse predators had a negative non-additive effect.

Do statistics for the monocultures. that is where I discuss how different predators actually have different effects on a community.

IF our predators had behaved in this way, we would have found that

Supplementary

Species	density
<i>Chironomus detriticula</i>	10
<i>Polypedium sp. 1</i>	4
<i>Polypedium sp. 2</i>	2
<i>Psychodid sp. 1</i>	1
<i>Scyrtes sp. A</i>	5
<i>Culex spp.</i>	4
<i>Trentepholia sp.</i>	1

Table 1: Densities of insects used in the experiment.

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