Predator phylogenetic diversity decreases predation rate via antagonistic interactions

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## Introduction

* Predator interactions are common in many communities and occur at many scales -- however, while we know much about the types of interactions between predators, and which traits are important, we know little about the role of phylogenetic relatedness (Naisbit ) in determining the combined effect of predators.
  + Decreasing predator richness has been shown to increase herbivory (Byrnes et al. 2006) in a three-level kelp food web.
* Direct top-down effects of predator combinations may be predicted by the similarity of habitat preference among predators, and on the similarity among their diets.
* Predators may show variation in habitat preference, connected to traits (body size) or phylogenetic similarity; where predators co-occur there is the potential for further interactions.
* Once predators are found in the same habitat patch, their direct influence on the community will be determined in part by their diet requirements; predators with strongly overlapping diets may compete for prey, while predators with divergent diets may show complementarity.
* These direct effects of predators, based on their diet preferences when in isolation, change prey composition by lowering densities of preferred prey.
* The effect of predators on prey may also be non-additive, the result indirect interactions either with prey species or other predators. For example, 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) .
* Predator indirect interactions may occur when the presence of other predator species alters the distribution, diet, or feeding rate of a focal predator population. In the extreme case, intra-guild predation reduces the focal predator's abundance.

### phylogenetic diversity

* Phylogenetic methods have been useful in understanding the effects of diversity in other functional groups (for example, in plants (Cadotte, Cardinale, and Oakley 2008; Cadotte et al. 2009)); a similar approach might help to synthesize the diverse literature on predator diversity effects.
  + Phylogenetic information can provide predictive insight beyond a system, and also can allow us to make comparisons between partly-overlapping or nested sets of species interactions, by supplying a common measure of dissimilarity between a wide range of species
  + Phylogeny, along with body mass, predicts trophic structure across many animal groups (Bersier and Kehrli 2008).
  + Related wasps share similar stinging patterns (Budriene and Budrys 2004)
  + Phylogeny is *not* related to the strength of competition in vascular plants [@CahillJr.2008]
* Phylogenetic distance among predators in a community may correlate with predator coexistence in local patches: close relatives may compete too closely, or face limitation via similar environmental variables.
* Similarly, phylogenetic distance may predict diet similarity, with closer relatives sharing diet requirements.
  + Warbler "ecologically relevant" morphological traits are only very weakly related to phylogeny (Böhning-Gaese, Schuda, and Helbig 2003)
* Perhaps most critically, phylogenetic distance might correlate with non-additive effects, which are difficult to predict from traits measured in isolation.

### Mesocosm experiments of predator diversity effects

* The top-down effects of predators, alone and in combinations, can be measured at the scale of an entire ecosystem by using mesocosm experiments.
* We test three related hypotheses concerning co-occurance patterns, diet similarity and top-down ecosystem effects of diverse predators, using a natural mesocosm: the community of invertebrates living within bromeliads.

1. *species co-occurance*: closely-related predators may occur together more frequently than less-related predators, due to their similar habitat requirements. Alternatively, very closely related species may never co-occur because they occupy too-similar ecological niches.
2. *diet similarity*: similarity in diet (as measured by feeding trials) decreases with phylogenetic distance if diet is phylogentically conserved. Alternatively, diet differentiation allows close relatives to coexist.
3. *ecosystem-level effects*: Our experiments at the level of the whole habitat (bromeliad) allows us to examine direct and indirect effects of predator combinations.
   * monoculture treatments allow us to assess the effect of each predator on a complete prey community and ecosystem function. Phylogenetic similarity among predators may positively correlate with similarity in these effects
   * In our predator combination treatments we force pairs of predators to co-occur. If phylogenetic distance is negatively correlated with similarity in diet, then increasingly divergent pairs should show increased total predation, as they feed on different parts of the prey community.
   * predator combination treatments also allow the estimation of non-additive effects, by comparison with monocultures. The magnitude of these non-additive effects may increase with phylogenetic distance.

## Methods

## Site and Species

We conducted all observations and experiments in Parque Estadual da Ilha do Cardoso ( S, 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. More than 47 species of macroinvertebrates are found in these aquatic communities. This diversity encompasses an entire foodweb, from detrital shredders (Tipulidae, Trichoptera), detrital scrapers (Scirtidae), collectors (Chironomidae, Syrphidae, Psychodidae), and filter feeders (Culicidae) to a diverse predator assemblage consisting of at least 3 species of *Leptagrion* (Zygoptera:Coenagrionidae), 2 species of predatory fly (Tabanidae), and 2 species of leech (Hirudinidae). Many other smaller or occasional predators also occur, such as predatory midges (Chironomidae:Tanypodinae) and Dytiscid beetles.

### Observations of predator co-occurance

We used an observational dataset collected in 2008 to examine patterns of co- occurance among predator taxa. This dataset was collected by completely dissecting bromeliads and washing all leaves 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.

Because predators in this system vary widely in size, we used "metabolic capacity", which correlates with predator feeding rate (Brown et al. 2004; Wilby, Villareal, and Lan 2005). We calculated body mass using allometric equations which related dry biomass to body length. Metabolic capacity is calculated as the sum of individual body mass raised to the power of 0.69; this reflects the nonlinearity of feeding rate on body size across many invertebrate taxa. We calculated total metabolic capacity of each predator species in each bromeliad by summing estimates for all individuals of the same species within a plant. We quantified "coexistence" as a distance measure: the euclidian distance among the total metabolic capacity among occupied bromeliads.

### Diet similarity

We quantified diet similarity between predators in a series of feeding trials. We covered all potential predator-prey pairs present in the experiment (described below), and attempted to perform all other trials whenever possible. We were limited by the density of animals we could find in the field, with some predators being rarer than others.

We conducted our feeding trials between March and April 2011. We placed predators together with prey in a 50ml vial, with a leaf or stick for substrate. The only exception to this setup 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 5 times where possible, and allowed 1 day for predation to occur.

### Community effect experiment

Our experiment was created with two goals in mind: first, to measure the major effects of these predators on their prey and second, to estimate the non- additive effects of pairwise predator combinations. The strength of these non additive effects can then be related back to the phylogenetic distance between each member of a pair of predators.

We selected the 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. Response variables included the rate of decomposition of leaves, bromeliad growth and insect emergence. 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 Feburary 2011, bromeliads between 90 and 200ml were collected, thoroughly washed 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 N-15 by fertilizing five (Jabuticaba, *Plinia cauliflora*) plants with 40ml pot-1 day-1 of 5g/L ammonium sulphate containing 10% atom excess of N15. *duration*. started on 27 January 2011 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 (1.5006g ± 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. After addition of the prey community, 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, cycling of nitrogen into plant tissue, and survival of prey (emerged adults + surviving larvae). We analyzed each of these responses with ANOVA. We calculated the non-additive response as follows: the difference between the polyculture mean (n=5) and the mean of both monoculture means for each predator (n=5 for each monoculture). We generated bootstrap confidence intervals for these nonadditive effects; confidence intervals which do not overlap zero indicate a significant nonadditive effect of a predator combination.

## Results

### metabolic capacity and phylogenetic distance

Within the 2008 observational dataset, we identified 14 species as predators. These predators vary in taxonomic relatedness: from congeners -- *Bezzia* sp. (Diptera:Ceratopogonidae) with two species and *Leptagrion* sp. (Odonata:Coenagrionidae) with three -- to confamilials (three species of Tabanidae and two of Empididae, all Diptera). Three families of Diptera are represented by a single species each: Dolichopodidae, Corethrellidae and Chironomidae. The deepest taxonomic divide is between all insects present and a species of leech (Annelida:Hirudinidae). 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).

We obtained node age estimates for all 7 internal nodes of the tree. These were usually provided by only a single study, with more studies available for deeper nodes: 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). We used the median estimate of age for these nodes.

In 2008, insects were counted and measured in an observational study of 25 bromeliads.

Across all bromeliads, predator species differed widely in metabolic capacity, from 0.0062 for a species of Empididae, to 0.4804 for the abundant predator *Leptagrion andromache*. Predators often co-occured in bromeliads ( species per plant). However, the euclidian distance between the total metabolic capacity of two predators did not show any relationship with phylogenetic distance between them (F1,89=1.5558, p=0.22).

### diet similarity and phylogenetic distance

We conducted 237 feeding trials of 8 predator taxa fed 14 prey taxa. However, due to the rarity of some taxa many predator-prey pairs were not possible; we tested 46 pairwise combinations. Most trials were replicated at least 5 times, but the number of replicates for various combinations ranged from 1 to 11.

Two damselflies, *Leptagrion andromache* and *Leptagrion elongatum*, showed the higest rates of prey consumption (prey consumed in 94% and 67% of trials, respectively).

All predators showed a very generalist diet breadth, consuming nearly all species offered to them. However, more phylogenetically distant predators preferred slightly different diets, as measured by euclidian distance between feeding trial outcomes (F1, 19=5.16, p=0.035, regression weighted by the number of trials conducted.)

### 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 relative to 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 (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 mere 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 5 more prey (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 0.

### Figures

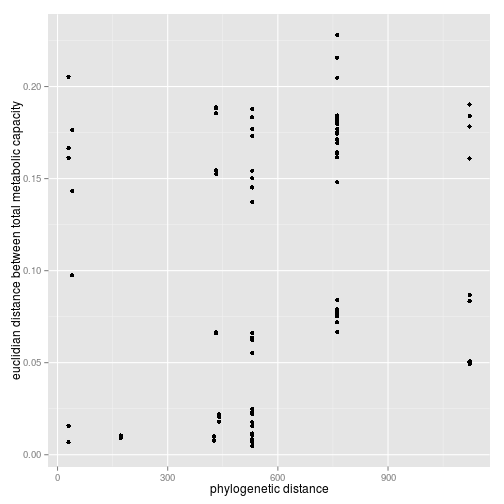


Figure 1: Phylogenetic distance and predator co-occurance. Each point represents a pair of predator species. We caluclated total metabolic capacity for each predator species in each bromeliad, and then calculated co-occurance between two predators as the euclidian distance between total metabolic capacity of two species.

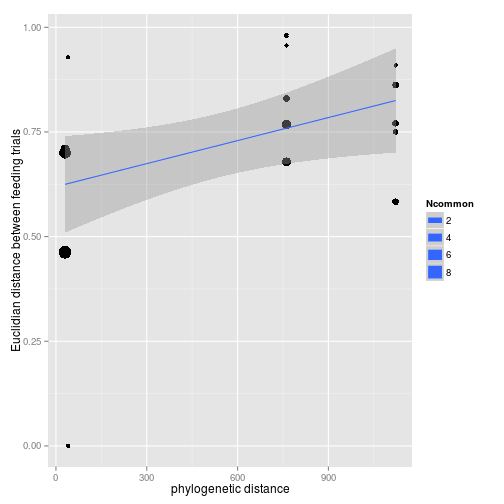


Figure 2: Phylogenetic distance and diet similarity. We performed 237 feeding trials with the 8 major predator taxa found in this system. We found that more distantly-related predators consume more dissimiliar prey. We measured diet similarity as euclidian distance among feeding trial outcomes; this measure includes information about the number of predation events in each predator-prey pairing. Regression was weighted by the sample size of the predator-prey pair.

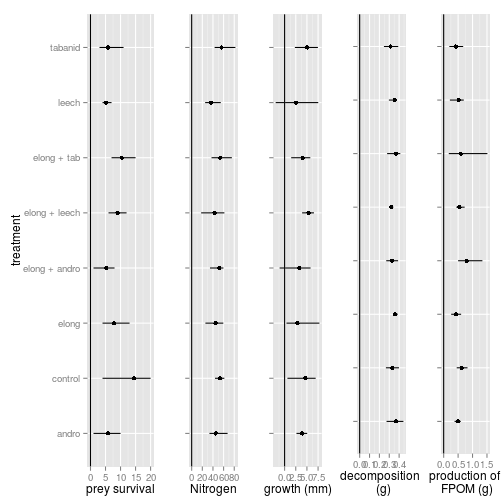


Figure 3: Treatment responses for the manipulative experiment. Points are means, and horizontal lines represent minimum and maximum values for each response. n=5 for all means.

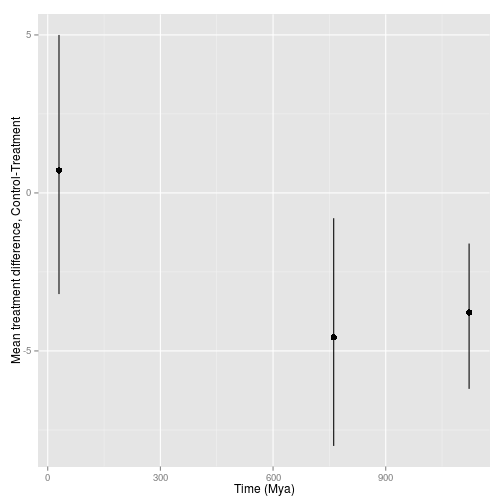


Figure 4: Combinations of predators beyond congenerics show a negative non-additive effect on predation rate. Points represent the mean difference between the means of two monocultures compared to the mean of a polycultures. These values are presented as differences from (predator free) controls; therefore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

## Discussion

### co-occurrance

* Predators appear to be generalist with regard to their habitat preference; indicating that prey face a heterogeneous landscape of predator risks, and demonstrating that our experimental design captures natural variation in predator composition.
* Predators occuring together at smaller spatial scales (i.e. within the same plant) may have limited direct interactions due to habitat structure, for example via the physical obstructions caused by detritus

### diet similarity

* We demonstrate a slight but important decrease in feeding preferences with phylogenetic distance, indicating that food web structure itself might vary with phylogenetic diversity, becoming more compartmentalized when predators are more dissimilar.
* The differences in predation rates and diet breadth among our predators represents important trait differences between the groups involved, including differences in metabolic rate and feeding mode. (*for example, Tabanids and leeches are peircing predators, while Leptagrion is gape-limited.*)
* Feeding differences between predators, combined with their patchy but unpredictable distribution among bromeliads, creates a large variation in food web structure and total amount of predation per patch within this bromeliad metacommunity

### community experiment

* Phylogenetically diverse predator assemblages showed more prey survivorship (i.e. less predation) than expected; this may be to strong trait-mediated indirect effects on the feeding rate of *Leptagrion elongatum* when in the presence of other non-damselfly predators.
* In response to predator manipulations we observed less transfer of Nitrogen into bromeliad tissue than did Ngai and Srivastava (2006); this may be due to a greater role for bacterial decomposition in this system (cite?).

## Supplementary

|  |  |  |  |
| --- | --- | --- | --- |
| Right | Left | Default | Center |
| 12 | 12 | 12 | 12 |
| 123 | 123 | 123 | 123 |
| 1 | 1 | 1 | 1 |

Demonstration of simple table syntax.

## my table

|  |  |
| --- | --- |
| Species | density |
| *Chironomus detriticula* | 10 |
| *Polypedium sp. 1* | 4 |
| *Polypedium sp. 2* | 2 |
| *Psychodid sp. 1* | 1 |
| *Scyrtes sp. A* | 5 |
| *Culex spp.* | 4 |
| *Trentepholia sp* | 1 |

Densities of insects used in the experiment.

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