Predator phylogenetic diversity decreases predation rate via antagonistic interactions

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#dropping a record that seems to have been 90% decomposed!  
pd <- pd %.%  
 transform(decomp=ifelse(decomp>0.7,NA,decomp))

## Introduction

Predator assemblages can have strong top-down effects, both on community structure and ecosystem processes (Estes et al. 2011). Detailed studies manipulating predators have identified a great diversity of direct and indirect mechanisms for these effects, related to interspecific variation in habitat selection and interactions with both prey and other predators. Within a community predators will have widely different preferences for different microhabitats, or behavioural responses to fine-scale environmental variation. When predators do co-occur in a local patch, they may feed on different prey species as determined by microhabitat preference, foraging behaviour, and other traits (Schmitz 2007). Predator-predator interactions will further modify the effect of a diverse consumer assemblage, as predators may feed directly on each other (Intra-guild predation) or may 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, we lack a means of estimating the importance of each in a community. Srivastava et al. (2012) hypothesized that the phylogenetic diversity of a community or assemblage may correlate with increased ecosystem function, via increases in trait diversity; however this has yet to be tested. Here we quantify phylogenetic diversity (PD) of a diverse invertebrate predator assemblage and ask if PD is associated with variation in habitat preferences, diet composition and intraguild interactions.

Phylogenetic diversity measures have provided useful insights into diverse plant communities (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 consumer 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 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-occur (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 he 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 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 of predators will determine which prey they consume and the total potential amount of predation that occurs. 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 (Finke 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 all of 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 an 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 (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-occurance 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 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. decreasing rates of insect emergence (Starzomski, Suen, and Srivastava 2010) and increasing nutrient cycling (Ngai and Srivastava 2006)).

1. *species co-occurance*: 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 phylogentically 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.
   * 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.

### metabolic capacity and phylogenetic distance

nodeages <- lapply(list.files(path="../data/TreeData/",pattern="\*.csv",full.names=TRUE),read.csv)  
names(nodeages) <- list.files(path="../data/TreeData/",pattern="\*.csv")  
nstudies <- sapply(nodeages,nrow)  
#names(nodeages)[which(nstudies>1)]  
n.nodes <- length(nodeages)

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

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).

### 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

## predator x prey trials  
  
feeding\_trials <- foodweb %.%  
 group\_by(Prey.species,predator.names) %.%  
 summarize(number.trials=n(),  
 eaten=sum(eaten.numeric)  
 ) %.%  
 filter(!is.na(predator.names)) %.%  
 filter(predator.names!="Leptagrion.small") %.%  
 ungroup()  
  
## numbers for text  
ntrials <- sum(feeding\_trials$number.trials)  
npred <- length(unique(feeding\_trials$predator.names))  
nprey <- length(unique(feeding\_trials$Prey.species))  
ncombos <- nrow(feeding\_trials)  
rep\_range <- range(feeding\_trials$number.trials)

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 5 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 5 times where possible, and allowed 1 day for predation to occur.

We evaluated overlap in predator diet preference using Pianka (1973 CITE) 's index of niche overlap :

For each pair of predators, and represent the preference of predator (r ) for prey species . The number of prey species () is defined as the total number of prey species assayed with both predator taxa, and preference is defined as the proportion of trials for each predator-prey assay that resulted in prey mortality.

### 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

### patterns of occurance

####### metabolic matrix ####  
## we need to calculate two distance matrices:  
## 1) metabolic capacity distance  
## 2) phylogenetic distance  
  
## metabolic matrix -- the "distance" between predator co-occurance, measured as metabolism  
  
dist\_to\_df <- function(matrix\_for\_df){  
 melt(matrix\_for\_df)[melt(upper.tri(matrix\_for\_df))$value,]  
}  
  
  
####### phylogeny matrix ####  
## Calculate distances  
phylogenetic\_distance <- predtree\_timetree\_ages %.%  
 cophenetic() %.%  
 dist\_to\_df() %.%  
 rename(c("Var1"="phylopred1",  
 "Var2"="phylopred2",  
 "value"="phylodistance")) %.%  
 mutate(pairs\_RH=paste(phylopred1,phylopred2,sep="\_"),  
 pairs\_LH=paste(phylopred2,phylopred1,sep="\_")) %.%  
 melt(id.vars=c("phylopred1","phylopred2","phylodistance"),  
 value.name="species\_pair",  
 variable.name="L\_or\_R")

metabolic\_distance <- metabolic %.%  
 data.frame(row.names="Taxa") %.%  
 as.matrix() %.%  
 vegdist(method="euclid") %.%  
 as.matrix() %.%  
 dist\_to\_df() %.%  
 rename(c("Var1"="metapred1",  
 "Var2"="metapred2",  
 "value"="metadistance")) %.%  
 mutate(species\_pair=paste0(metapred1,"\_",metapred2))

# Check for TRUE ZEROS in cast matrix.  
  
## Fill = 0 !!!? correct ??!!!  
  
## similarity in diet is about how much they eat  
  
## Should this be the proportion of eating?!?  
  
prop.eaten <- feeding\_trials %.%  
 mutate(prop.eaten=eaten/number.trials) %.%  
 dcast(predator.names~Prey.species,value.var="prop.eaten")  
  
predators <- expand.grid(pred1=unique(feeding\_trials$predator.names),  
 pred2=unique(feeding\_trials$predator.names)) %.%  
 filter(pred1!=pred2) %.%  
 transform(pred\_pair=paste0(pred1,"\_",pred2)) %.%  
 melt(id.vars="pred\_pair",value.name="predator.names",variable.name="p") %.%  
 left\_join(prop.eaten) %.%  
 select(-p,-predator.names)

## Joining by: "predator.names"

## both ecopath and ecosim documentation (and those sources derived from them)  
## imply a different formula for Pianka's index.  
pianka <- function(df){  
 mat <- as.matrix(df[,-1])  
 rowtotal <- rowSums(mat)  
 mat <- apply(mat,2,function(x) x/rowtotal)  
  
 squares <- mat^2  
 sum\_sq\_prod <- prod(rowSums(squares))  
   
 prod <- apply(mat,2,prod)  
 sum\_prod <- sum(prod)  
   
 overlap <- sum\_prod/sqrt(sum\_sq\_prod)  
 nspp <- ncol(mat)  
 data.frame(overlap,nspp)  
}  
  
outer\_paste <- function(x) outer(x,x,paste,sep="\_")  
  
prednames <- feeding\_trials$predator.names %.%  
 unique() %.%  
 outer\_paste()  
  
predpairs <- prednames %.%  
 melt(value.name="species\_pair") %.%  
 transform(species\_pair=as.character(species\_pair)) %.%  
 semi\_join(  
 {  
 prednames %.%  
 upper.tri() %.%  
 melt(value.name="corner") %.%  
 filter(corner)  
 },  
 by=c("Var1","Var2")  
 ) %.%  
 transform(pred1=unique(feeding\_trials$predator.names)[Var1],  
 pred2=unique(feeding\_trials$predator.names)[Var2]) %.%  
 select(pred1,pred2,species\_pair) %.%  
 arrange(pred1,pred2)  
  
diet\_overlap <- split(predators,predators$pred\_pair) %.%  
 lapply(function(x) x[colSums(!is.na(x))>1]) %.%  
 lapply(pianka) %.%  
 ldply(stringsAsFactors=FALSE) %.%  
 rename(c(".id"="species\_pair")) %.%  
 semi\_join(predpairs)

## Joining by: "species\_pair"

## summarize randomization test results  
  
summarize\_random\_test <- rand.means %.%  
 # remove annoying X column  
 select(-X) %.%  
 # melt, so that all responses can be summarized at the same time  
 melt(id.vars="sp.pair") %.%  
 group\_by(sp.pair,variable) %.%  
 summarise(mean=mean(value),  
 lower=quantile(value,probs=c(0.025)),  
 upper=quantile(value,probs=c(0.975))  
 ) %.%  
 # sequence of increasing PD  
 ungroup() %.%  
 mutate(sp.pair.names=factor(sp.pair,levels=c('elong + andro',  
 'elong + tab',  
 'elong + leech')  
 ),  
 sp.pair=as.character(sp.pair),  
 sp.pair=ifelse(sp.pair=="elong + andro","Leptagrion.elongatum\_Leptagrion.andromache",  
 sp.pair),  
 sp.pair=ifelse(sp.pair=="elong + tab","Leptagrion.elongatum\_Tabanidae.spA",  
 sp.pair),  
 sp.pair=ifelse(sp.pair=="elong + leech","Leptagrion.elongatum\_Hirudinidae",  
 sp.pair)  
   
 ) %.%  
 rename(c("sp.pair"="species\_pair"))

## we need to merge together several matrices:  
## metabolic occurance + predator phylogenetic distance  
## diet similarity + predator phylogenetic distance  
## experiment randomization results + predator phylogenetic distance  
  
## note that the nomeclature of the columns keeps `sp.pair` as the only shared name among columns.  
metabolic\_occur\_phylo <- left\_join(metabolic\_distance,phylogenetic\_distance)

## Joining by: "species\_pair"

diet\_overlap\_phylo <- left\_join(diet\_overlap,phylogenetic\_distance)

## Joining by: "species\_pair"

summarize\_randoms\_phylo <- left\_join(summarize\_random\_test,phylogenetic\_distance)

## Joining by: "species\_pair"

## numbers for text:  
meta\_range <- metabolic %.%  
 melt(id.vars="Taxa") %.%  
 select(-variable) %.%  
 filter(value>0) %.%  
 filter(value%in%range(value)) %.%  
 transform(value=signif(value,2)) %.%  
 unique()  
  
smallsp <- meta\_range[1,]  
largesp <- meta\_range[2,]  
  
nspp <- metabolic %.%  
 melt(id.vars="Taxa",variable.name="brom") %.%  
 filter(value>0) %.%  
 group\_by(brom) %.%  
 summarize(nspp=n()) %.%  
 summarize(meanpred=mean(nspp),  
 sdpred=signif(sd(nspp),2))

meta\_phylo\_lm\_summary <- with(metabolic\_occur\_phylo,lm(metadistance~phylodistance)) %.%  
 summary()  
  
## caculate summaries   
pval\_metabol <- round(pf(meta\_phylo\_lm\_summary$fstatistic[1],  
 meta\_phylo\_lm\_summary$fstatistic[2],  
 meta\_phylo\_lm\_summary$fstatistic[3],lower.tail=FALSE)  
 ,digits=2)

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-occured in bromeliads (4.4 ± 2.9 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

## Diet numbers for text:  
## what percentage of total trials resulted in predation?  
percentpredation <- feeding\_trials %.%  
 transform(percent.eaten=eaten/number.trials) %.%  
 group\_by(predator.names) %.%  
 summarize(mean.pred=mean(percent.eaten),  
 totaltrials=sum(number.trials),  
 nprey=n())  
   
andro <- percentpredation %.%  
 filter(predator.names=="Leptagrion.andromache") %.%  
 select(mean.pred) %.%  
 transform(mean.pred=round(mean.pred\*100,1)) %.%  
 as.numeric()  
  
elong <- percentpredation %.%  
 filter(predator.names=="Leptagrion.elongatum") %.%  
 select(mean.pred) %.%  
 transform(mean.pred=round(mean.pred\*100,1)) %.%  
 as.numeric()

## test a squared term with   
#   
# diet\_overlap\_phylo %.%  
# #filter(nspp>1) %.%  
# with(lm(overlap~phylodistance,weights=nspp)) %.%  
# pander(caption="Linear model of diet overlap as a function of phylogenetic distance between predators.")  
  
#summary(dietoverlap\_lm)  
  
diet\_phylo\_lm\_summary <- diet\_overlap\_phylo %.%  
 #filter(nspp>1) %.%  
 with(lm(overlap~phylodistance,weights=nspp)) %.%  
 summary()  
  
  
dietmat <- diet\_overlap\_phylo %.%  
 select(-species\_pair) %.%  
 unique() %.%  
 dcast(phylopred1~phylopred2,value.var="overlap") %.%  
 data.frame(row.names="phylopred1") %.%  
 as.matrix()

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 (F1, 19=6.72, p=0.018, regression weighted by the number of prey species assayed.)

### Ecosystem-level effects and phylogenetic distance

predeffect <- function(resp="total.surv"){  
 diffeffect <- (mean(pd[[resp]][pd$treatment!="control"],na.rm=TRUE)-mean(pd[[resp]][pd$treatment=="control"],na.rm=TRUE))/mean(pd[[resp]][pd$treatment=="control"],na.rm=TRUE)  
 round(diffeffect,digits=2)\*100  
 }  
#   
# ddply(pd,.(treatment),summarize,meansurv=mean(total.surv))  
#   
# mean(pd$emerged)  
# mean(rowSums(pd[c("Culicidae","Chironomidae","Tipulidae","Scirtidae")])

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.

polyeffect <- function(resp="total.surv"){  
 diffeffect <- (mean(pd[[resp]][pd$treatment%in%c("elong + andro","elong + leech","elong + tab")],na.rm=TRUE)-mean(pd[[resp]][pd$treatment%in%c("andro","tabanid","leech","elong")],na.rm=TRUE))/mean(pd[[resp]][pd$treatment=="control"],na.rm=TRUE)  
 round(diffeffect,digits=2)\*100  
 }

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.

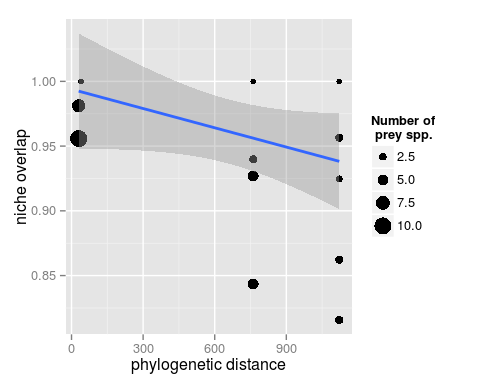
We found the greatest effect for prey survival: while effects of *L. andromache* and *L. elongatum* in combination were quite similar to the effect of either alone, when *L. elongatum* was placed in the same plant as either a Tabanid larva or leeches, on average 5 more prey (18% of total prey community) 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

ggplot(metabolic\_occur\_phylo,  
 aes(x=phylodistance,y=metadistance))+geom\_point()+xlab("phylogenetic distance")+ylab("euclidian distance between total metabolic capacity")



diet\_overlap\_phylo %.%  
 #filter(nspp>1) %.%  
 ggplot(aes(x=phylodistance,y=overlap,size=nspp)) %.%  
 +geom\_point() %.%  
 +stat\_smooth(method="lm",size=1) %.%  
 +scale\_size\_continuous(range=c(2,6),name="Number of \n prey spp.") %.%  
 +xlab("phylogenetic distance") + ylab("niche overlap")



ggplot(subset(summarize\_randoms\_phylo,summarize\_randoms\_phylo$variable=="survival"),  
 aes(x=phylodistance,y=mean))+geom\_errorbar(aes(ymin=lower, ymax=upper),width=0)+geom\_point(size=3)+ylab("Mean treatment difference, Control-Treatment")+xlab("Time (Mya)")



#   
# ggplot(summarize\_randoms\_phylo,  
# aes(x=Time,y=mean))+geom\_errorbar(aes(ymin=lower, ymax=upper),width=0)+geom\_point(size=3)+ylab("Mean treatment difference, Control-Treatment")+xlab("Time (Mya)")+facet\_wrap(~variable)

exp\_summary <- pd %.%  
 select(treatment,total.surv,fine,decomp,growth,N) %.%  
 melt(id.vars="treatment") %.%  
 group\_by(treatment,variable) %.%  
 summarise(meanval=mean(value),  
 n=n(),  
 sd=sd(value)) %.%  
 mutate(SE=sd/sqrt(n),  
 meanval\_sig=signif(meanval,2),  
 SE\_sig=signif(SE,2),  
 meanSE=paste(meanval\_sig,"±",SE\_sig)) %.%  
 dcast(treatment~variable,value.var="meanSE")  
  
test <- exp\_summary[c(2,1,3,7,8,4,5,6),] %.%  
 data.frame(row.names="treatment") %.%  
 rename(c("total.surv"="surviving",  
 "fine"="fine detritus",  
 "decomp"="decomposition",  
 "growth"="bromeliad growth"))  
  
  
coltext <- expression("surviving insects","fine detritus (g)","leaf decomposition (g)",  
 "bromeliad growth (g)","Nitrogen cycling")  
  
  
grid.table(test,cols=coltext,gpar.colfill=gpar(fill="white",col="white"),  
 row.just="left",gp=gpar(cex=0.6),gpar.rowtext=gpar(),show.vlines=TRUE  
 )



## Discussion

### co-occurrence

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 occurring 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 (). Srivastava found that such habitat complexity within a bromeliad -- specifically the presence of coarse detritus -- reduces the amount of predation by damselflies. It is not clear how these factors might influence the other predators in this system. Effects might be similar for leeches, which are also active predators. Tabanids are sit-and-wait predators, living deep in leaf axils, so it is likely that they are less affected by local patch structural conditions than other predators.

two important steps -- oviposition decisions and survival -- determine organism coexistence in bromeliad patches.

Predator lifecycles can be quite long in this system, much longer than the lives of invertebrate prey (Robin). As a result, actively dispersing inverts are probably faced with choices among various predation-risks in patches. While this is beyond the sope of our work, we report evidence for both strong IGp nonliearities in predation amount, and a broad overlap in predator co-occurance. This indicates that, at the level of the metacommunity, discrete patches have varying amounts of predator biomass, which may not necessarily correlate with the amount of predation pressure they may face.

Habitat selection is difficult to ascertain from observational data. Especially given that animals in this system have difference lifecycles. The insects are rapidly changing (smaller insects) while large predators may say or a while,and physical detritus longer still.

hm. there's an idea: if there is IGP or TMII among predators, that means composition or biomass of predators can be decoupled from predation rate. That could lead to strange decisions by insects, with nonintuitive results.

### 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.

calulate predatr's feeding rate nd diet breath simultaneously, and relate this to their phylogenetic distance from each other. could be that there is a phylgenetic signal in the prey eaten? not really our focus here. in fact we are more interested in whether similar predators have similar effects on communities.

* The differences in predation rates and diet breadth among our predators represents important trait differences between the groups involved, including differences in metabolic rate (physiological literature) and feeding mode. (for example, Tabanids and leeches are peircing predators, while Leptagrion is gape-limited.)

Diet similarity, like occurance, also has two components: predator

### 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.

Trait-mediated indirect effects may be common in nature (E. Werner and Peacor 2003). In our system we observed less predation in predator combinations, perhaps because the damselflies lowered their predation rates when they were exposed to other predators. Trait mediated interactions might be frequent in this system: for example, in close quarters of bromeliads it may be more likely that predators are aware of each other's densities. Physical touch and chemical cues can both be frequent cues for the presence of predators, and can trigger trait-mediated-effects. In bromeliads, a diverse community occurs at a very small spatial scale and diverse predators are quite likely to overlap. Such predator-induced decreases in feeding might actually be common, although we would not estimate them directly by densities of predators (E. Werner and Peacor 2003).

* 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

Predators have different feeding rates, feed in different parts of the bromeliad, and have different effects on each other. The presence of a predator with a low feeding rate may have a strong positive effect on prey survival, if it decreases the predation rate of *Leptagrion* sp.. This uncouples predation rate and predator biomass, and creates a constantly changing amount of top-down regulation in this system. These predators might also differ in dispersal rates, and in vulnerability to other predators. for example, Leptagrion spp are frequent prey for semi-aquatic spiders, but tabanids are likely safe from most large predators because of their position deep in leaf axils.

* 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?).

Insects sometimes can be the major group which determines the speed of decomposition. However, when substrate is very recalcitrant the insects are only able to break down small amounts of detritus. In restingas, the leaves are very thick and waxy, a possible adaptation to the poor growing conditions. As a result, invertebrates in this system do not eat the leaves directly; rather microinverterbrates (zooplankton) and bacteria do most of the decomposition. This hypothesis could be tested, for example, by performing bacterial community "transplants" from a host bromelid to a sterile bromeliad, which could then be monitored for a decomposition rate similar to the original bromeliad. Ngai et al hypothesized that their increase in nutrient cycling that they observed was due to increased mortality of insects, and that bromeliads were absorbing N from odonate predator waste. In our system, a more diverse predator community leaves different kinds of dead prey, and also different dead insects. Tabanids are primarily sucking predators, which leave the integument of their prey behind. The waste products of these different predators might also be very different, depending on the physiology and nutrient requirements and efficienty of each predator.

Leaf decomposition does not show a strong relationship with bromeliad size in Cardoso, even though there is a strong relationship in Costa Rica (Robin)

It may be that different predators influence the composition of the detritus (animal, fecal and leaf), and that this bottom-up effect determines the success of different taxa, as well as rates of nutrient cycling.

## Supplementary

|  |  |
| --- | --- |
| 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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