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Fear Mediates Trophic Cascades: Nonconsumptive Effects of Predators Drive Aquatic Ecosystem Function

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abstract: Predators control prey populations and influence communities and the functioning of ecosystems through a combination of consumptive and nonconsumptive effects. These effects can be locally confined to one ecosystem but can also be extended to neighboring ecosystems. In this study, we investigated the nonconsumptive effects of terrestrial avian predators on the communities of aquatic invertebrates inhabiting bromeliads and on the functioning of these natural ecosystems. Bromeliads with stuffed birds placed nearby showed a decrease in aquatic damselfly larvae abundance and biomass, and we can infer that these changes were caused by antipredator responses. These larvae, which are top predators in bromeliad ecosystems, changed the composition of the entire aquatic invertebrate community. While total species richness, mesopredator richness, and shredder abundance increased in the presence of birds, scraper biomass decreased, possibly as a consequence of the increase in mesopredator richness. High scraper biomass in the absence of birds may have accelerated detrital decomposition, making more nutrients available for bromeliads, which grew more. These results show that nonconsumptive effects triggered by terrestrial predators can cascade down to lower trophic levels and dramatically affect the functioning of aquatic ecosystems, which can in turn alter nutrient provision to terrestrial ecosystems.

Keywords: antipredatory behavior, damselfly, trait-mediated indirect interactions (TMIIs), predator cues, terrestrial predator, top-down effects.

Introduction

When predators reduce the density of prey populations, they can alter the richness and abundance of the species that coexist in ecological communities (Ripple and Beschta 2004; Schmitz 2010; Ripple et al. 2014). Apex predators can potentially limit prey populations, and their effects can cascade down to lower trophic levels via density-mediated indirect interactions (DMIIs; Schmitz 2010). They can also limit mesopredator populations via competition and/or intraguild predation (Prugh et al. 2009). Prey alter their behavior, natural history, morphology, and development in the face of predation risk, resulting in possible effects on their dynamics and possibly altering their densities (Lima and Dill 1990; Lima 1998; Brown et al. 1999; Peckarsky et al. 2001; Werner and Peacor 2003; Brown and Kotler 2004; Binckley and Resetarits 2008; Touchon et al. 2013). Consequently, predators can also structure communities along multiple paths and alter processes inherent to the functioning of the ecosystems via trait-mediated indirect interactions (TMIIs; Ohgushi et al. 2012).

For decades, ecologists have studied and compared the roles played by TMIIs and DMIIs in aquatic or terrestrial ecosystems separately (see Preisser et al. 2007; Romero and Srivastava 2010; Schmitz 2010; Ohgushi et al. 2012). However, ecosystems are rarely closed and are therefore influenced by adjacent ecosystems in several ways, such as through the passive and active transport of matter between the donor and receptor ecosystems (Polis et al. 1997; Recalde et al. 2016) and via top-down control (Knight et al. 2005; McCoy et al. 2009). In addition, it is known that predators can have remote effects on prey populations that are connected via metapopulations (i.e., by dispersal) because changes induced by predators in prey behavior and abundance effectively transmit the impact of predators into predator-free prey populations (Orrock et al. 2010). Therefore, a separate set of studies have reported that predators that forage at the boundaries between ecosystems can affect organisms from adjacent ecosystems, thereby triggering consumptive and nonconsumptive cascade effects across the ecosystems via DMIIs or TMIIs (e.g., Silliman et al. 2002; Knight et al. 2005; McCoy et al. 2009; Romero and Srivastava 2010; Suraci et al. 2016).

Trophic cascades that cross ecosystem boundaries are typically triggered by predators that intercept cross-ecosystem organisms (Marczak et al. 2007). Cross-ecosystem organisms are those whose life cycles involve multiple ecosystems, such

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as insects and amphibians that spend their larval life stages in the water but their adult life stages on land. For instance, ovipositing terrestrial adults can detect aquatic predator cues (visual and olfactory stimuli) in freshwater ecosystems and avoid laying eggs in these ecosystems, thus protecting their offspring from predation (Kats and Sih 1992; Resetarits 2001; Åbjörnsson et al. 2002; Blaustein et al. 2004; Binckley and Resetarits 2005; Binckley and Resetarits 2008). Therefore, colonization and oviposition behavior strongly affect the assembly of individual aquatic communities and are key processes linking communities across habitat boundaries and spatial scales in complex landscapes (Binckley and Resetarits 2008). However, most studies reporting indirect effects across ecosystem boundaries show only a small fraction of the extent to which a trophic cascade occurs in the ecosystem and comprise only a small portion of the assembly of predators and consumers. To our knowledge, no study has investigated the effects of terrestrial vertebrate predators on the oviposition of organisms with complex life cycles and

the consequences for the functioning of the whole aquatic ecosystem.

In the present study, we demonstrate trophic cascades across ecosystems via TMIIs through the manipulation of stuffed models of terrestrial insectivorous birds (i.e., visual stimuli from great kiskadee; app. A; apps. A–C are available online). We show the effects of these models on the structure of the aquatic invertebrate community and, consequently, on ecosystem processes (i.e., decomposition rate, nitrogen cycling, and productivity) in bromeliad aquatic environments. We predict that the presence of insectivorous birds would be sufficient to trigger antipredator behavioral responses by adult damselflies, resulting in a decrease in the abundance and/or biomass of their larvae inside the phytotelmata via nonconsumptive effects (prediction 1; fig. 1). Adult damselflies are known to have high visual acuity and would be able to detect predation risk (Frye 2013). Because damselfly larvae are top predators in bromeliad systems (Ngai and Srivastava 2006; Petermann et al. 2015; Romero
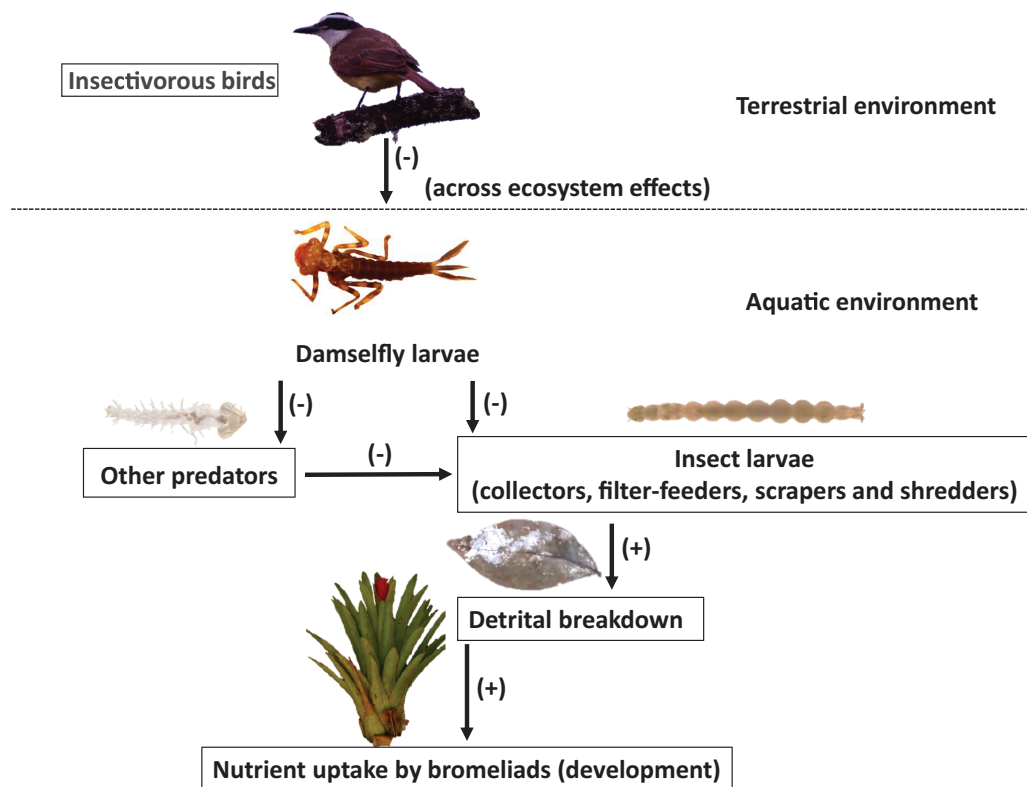

Figure 1: Across-ecosystem effects of insectivorous birds (great kiskadee) observed in bromeliad systems. The arrows show the direction of the effects, which are identified as positive (+) or negative (−). The presence of terrestrial insectivorous bird models foraging close to the bromeliads can decrease the abundance and biomass of damselfly larvae on the bromeliads by predation risk (via egg laying by females; prediction 1). These alterations in the top predator communities can affect the composition and other parameters of the prey communities, including mesopredators and detritivores; we predicted that detritivorous insects and mesopredator larvae would increase in abundance, biomass, and richness in smaller densities of damselflies (prediction 2), resulting in an increase in detrital breakdown rates (prediction 3). Thus, bromeliads would benefit from the greater supply of nutrients made available by the consumption of detritus by detritivores and from their feces and carcasses (prediction 4).

et al. 2016), a decrease in their abundance and biomass would change the composition and other parameters (richness, abundance, and biomass) of the bromeliad-dwelling invertebrate community (prediction 2). We thus predict an increase in richness, biomass, and/or abundance of detritivorous organisms caused by the decrease in damselflies. We predict that the change in the invertebrate community would accelerate ecosystem functioning (e.g., the breakdown of organic matter) via TMIIs across ecosystems (prediction 3). The acceleration of ecosystem functioning by detritivorous organisms would provide a higher supply of soluble nutrients derived from the decomposed organic matter to the bromeliads, which can obtain these nutrients via specialized trichomes (Romero et al. 2006). Finally, we predict that the presence of terrestrial birds would indirectly benefit the development and growth of the bromeliads via TMIIs across ecosystems (prediction 4).

Methods

Study Area

The present study was performed in an open restinga habitat at the Parque Estadual da Ilha do Cardoso (PEIC), situated along the southern shore of the state of São Paulo (25°03′S, 48°53′W), Brazil. PEIC covers an area of ∼151 km^2, has a predominantly mountainous topography (Bernardi et al. 2005), and has a megathermal superhumid climate without a well-defined dry season and with a mean yearly rainfall of 3,000 mm. The vegetation present on the island is a mixture of formations found on the southeastern shore of Brazil, characterized by seven types of vegetation: dunes, restingas (open and closed), mangroves, flat land and slope rain forests, mountaintop tree formations, and secondary vegetation (C. P. B. Breviglieri, personal observations).

The present study was performed exclusively among the vegetation characterized as open restinga, an area composed mainly of woody plants of the genera *Baccharis*, *Dodonaea*, *Psidium*, and *Calophyllum*. Bromeliad species commonly found are representatives of the genera *Vriesea*, *Tillandsia*, *Aechmea*, *Ananas*, *Canistrum*, *Catopsis*, and *Nidularium*. However, *Quesnelia arvensis*, the focal species of the present study, is the most dominant and is densely distributed throughout the sampling area (C. P. B. Breviglieri, personal observations). Throughout the study, *Q. arvensis* was observed to partially dominate open areas, sand strips, mangrove border stretches, and undergrowth and was present in the tops of the highest trees (C. P. B. Breviglieri, personal observations).

Organisms

The bromeliad *Q. arvensis* can accumulate more than 2.8 L of rainwater in tanks made by individual leaves, which are able to host a diverse fauna of aquatic and terrestrial arthropods (more than 140 species of aquatic invertebrates; G. Q. Romero, G. C. O. Piccoli, and P. M. de Omena, unpublished data). The aquatic fauna is mainly composed of invertebrate larvae of various functional groups, including top predators (*Leptagrion andromache* and *Leptagrion macrurum*), mesopredators (*Corethrella* spp., *Omicrus* spp., *Monopelopia* spp., *Phytotelmatocladius* spp., *Stibasoma* spp., *Bezzia* spp., and *Copelatus* spp.), filter feeders (*Wyeomyia* spp. and *Culex* spp.), shredders (*Trentepohlia* sp. and *Phylloicus* sp.), scrapers (*Scirtes* spp., *Lejops* sp., and *Copestilum* sp.), and detritivores/collectors (*Corynoneura* sp., *Stenochironomus* sp., *Polypedilum* spp., *Atrichopogon* sp., *Chironomus* spp., and Ephydridae spp.). According to Romero and Srivastava (2010), the aquatic community also includes small noninsect invertebrates, such as Oligochaeta, Ostracoda (both detritivores), Hirudinea (leech, predator), Acari (multiple trophic levels), and Turbellaria (microscopic particulate collector). Most of them (Ostracoda, leech) can reach the bromeliad via phoresy (frogs). Whereas the small invertebrates (detritivores and mesopredators) have a short life cycle (2 weeks to 2 months), large predators (damselflies, Tabanidae) have a long life cycle and can stay in bromeliads as larvae for more than 6 months (G. Q. Romero, personal observations).

The terrestrial fauna is mainly composed of spiders (such as *Aglaoctenus castaneus* [Lycosidae] and *Corinna demersa* [Corinnidae]; see Romero and Srivastava 2010), ants, and small amphibians (such as *Scinax argyreornatus*, *Scinax alter*, and *Aparasphenodon bokermanni* [Hylidae]; C. P. B. Breviglieri, personal observations).

Great Kiskadee as an Insectivorous Predator Model

In PEIC, 416 bird species have been recorded (Willis and Oniki 2003). Of these, tyrant flycatchers are predominantly insectivorous passerine birds that show multiple prey-capture techniques (Fitzpatrick 1981; Sick 1997), such as perch gleanings, upward hover gleanings, and short aerial hawkings (Fitzpatrick 1985; Sick 1997). Typically, these behaviors start after the visual detection of potential prey moving in midflight or over the vegetation. From this moment, the bird takes flight toward the prey, which is captured and consumed after the bird returns to the perch (Fitzpatrick 1981; Traylor and Fitzpatrick 1982; Sick 1997). Great kiskadee (*Pitangus sulphuratus*, Linnaeus 1766; Tyrannidae) consume large prey items, for example, caterpillars, dragonflies, small lizards, small birds, and bats (Sick 1997; Munin et al. 2012). Thus, the presence of this species of predatory bird can represent a potential risk for large insects, which, with good visual acuity, may be able to identify them in the landscape (e.g., Odonata; Frye 2013). Within the study area, this bird species was observed trying to capture (or capturing) dragonflies, damselflies, frogs, and even small vespertilionid bats

at twilight (C. P. B. Breviglieri, personal observations), proving its feeding plasticity and focusing on large prey, as described by Sick (1997). Therefore, we consider the combination of the wide geographic distribution of *P. sulphuratus* (i.e., including the area where we performed our study) and the species' elaborate hunting behaviors as indicators that this species is an ideal model with which to answer the questions addressed in the present study.

Experimental Design

To test the cascade effects across ecosystems of predation risk from avian predators on the structure of aquatic communities and the functioning of bromeliad ecosystems, we developed a randomized block experimental design ($n = 5$). Each block consisted of the following treatments: (i) a stuffed individual of *P. sulphuratus* (predatory bird) on a 1-m perch placed 30 cm away from the pot with the bromeliad (app. A); (ii) a fixed butterfly of the species *Heraclides thoas* (Papilionidae; the butterfly treatment), installed in the same conditions as for the previous treatment; and (iii) only the perch (the control treatment), installed in the same conditions as for the other treatments. Stuffed great kiskadee models were perched to suggest typical foraging behavior. Fixed models of butterflies *H. thoas* were placed in a resting position on the perch but with open wings. We used the *H. thoas* butterfly as the butterfly treatment because this species is not a predator and shows the same natural color pattern (i.e., black and yellow) as the bird *P. sulphuratus* and because when the fixed butterfly is placed on the perch with wings open it is similar in size to the predator bird. Thus, we identified whether adult Zygoptera avoid models due to predation risk caused by the presence of avian predators or whether they simply avoid any object or organism placed around the plants (see Romero et al. 2011). Once the Zygoptera larvae are climbers (Corbet 1962), they may migrate and colonize new bromeliads; to avoid colonization of our experimental bromeliads, we set them up at least 10 m apart from the naturally growing bromeliads. Each of the blocks was placed along the open restinga, at 50-m intervals, and the treatments were placed randomly at a distance of 20 m apart from each other inside each of the blocks (app. A). To avoid prey conditioning in the face of the avian predator models and other treatments, perches were rotated daily clockwise around the plant at about 5:40 a.m. (app. A).

Our *P. sulphuratus* models were realistic enough to confuse visually oriented vertebrate predators. During the field experiment, one of our models was attacked by a hawk (*Rupornis magnirostris*, Gmelin 1788). Two other model predation events also occurred involving *Cerdocyon thous* (Linnaeus 1766), at about 6:00 p.m. These events prove that our models were realistic and that adult damselflies could potentially recognize them.

In preparation for the experiment, 15 bromeliads of the species *Q. arvensis* were collected from the open restinga on January 6, 2014; these bromeliads were then meticulously cleaned and replanted in 25-L pots and allowed to remain exposed for natural colonization by the invertebrate community for 60 days from January 11 to March 11, 2014 (see details in Romero and Srivastava 2010). An attempt was made to standardize the plants used in the present study according to physical structure and size. For this purpose, before the beginning of the study we used an analysis of variance (ANOVA) to assess the following characteristics of the bromeliads used in the different treatments: maximum volume (mL) of rainwater each plant is able to store (mean ± SD; birds, 1.47 ± 0.13; butterflies, 1.26 ± 0.10; control, 1.41 ± 0.19; $F = 0.14$, $P = .179$), real volume (mL; birds, 727 ± 183; butterflies, 562 ± 190; control, 627 ± 136; $F = 0.15$, $P = .363$), rosette diameter (cm; birds, 51 ± 13; butterflies, 44 ± 3.14; control, 45 ± 6.57; $F = 0.84$, $P = .464$), plant height (cm; birds: 52 ± 5.89; butterflies, 52 ± 2.34; control, 52 ± 2.70; $F = 0.04$, $P = .952$), and total number of leaves per plant (birds, 41 ± 5; butterflies, 36 ± 2; control, 43 ± 7; $F = 0.41$, $P = .151$). All plants were placed below restinga trees to avoid drying. Therefore, we also needed to analyze the rate of sunlight incidence through the canopy because this variable could interfere with plant development; the openness of the canopy did not differ between treatments (mean ± SD; birds, 93 ± 2; butterflies, 89 ± 6; control, 93 ± 4; $F = 0.15$, $P = .364$).

Stuffed birds might influence the local density of conspecifics (or other insectivorous birds) around bromeliads, leading to biased predation pressure on damselfly among the treatments. However, field observations made over the 60-day experiment (180 h during the first 3 h of the day and 180 h during the last 3 h before twilight) with the help of a camera (300 mm), four common video cameras (Sony Camcorder DCR 610 on 1.5-m-tall tripods, totaling 1,440 hours of filming for 6 h every morning), and four digital camera traps (Bushnell, totaling 2,880 hours exposed for 12 h every day) set up among the blocks did not detect any presence, aggregation, or other interactions among birds and other vertebrates during the experiment (except the predation event by a hawk). Moreover, we did not observe any live birds foraging on the experimental bromeliads, only on the bromeliads of the natural populations (those aggregated in the forest borders).

Effect of Treatments on the Structure of the Invertebrate Community

At the end of the experiment, we carefully dissected and washed each leaf of each bromeliad to collect all of the aquatic invertebrates (adult and larvae) present in the bromeliad. The method used for bromeliad screening after the

conclusion of the experiment has been used before (for details, see Romero and Srivastava 2010). We recorded the size, abundance, and richness of the morphospecies of all of the aquatic invertebrates visible to the naked eye (>0.5 mm). Morphospecies were later identified to the lowest possible taxonomic level by specialized taxonomists and/or on the basis of specialized literature. The functional group for each taxonomic group was determined by consulting the literature (e.g., Merritt and Cummins 1996; Romero and Srivastava 2010; Hammill et al. 2015; Petermann et al. 2015) and by bioassays developed for other purposes. The dry invertebrate biomass was estimated from body length, mainly using allometric equations based on the family or species collected in the field but also using allometric equations developed for the fauna of similar bromeliads of Costa Rica (D. Srivastava, unpublished data).

Ecosystem Responses to Treatment Manipulation

We examined two important ecosystem processes: the detrital breakdown and nitrogen flux from detritus to new bromeliad leaves. To analyze the decomposition rate of the detritus contained in the bromeliad tanks, on the first day of the experiment we inserted two sets made of three *Eugenia uniflora* (Myrtaceae) leaves, connected to each other by a 0.25-mm-diameter nylon thread (mean ± SD weight of each set, 0.22 ± 0.03 g; weighed with the aid of a high precision scale [0.0001 g]), into each bromeliad. These two detritus sets were placed in different tanks in the middle portion of the bromeliads. At the end of the experiment, each of the sets were recovered and weighed again for comparisons. To analyze the effects of treatments on the flow of nitrogen acquired by bromeliads via the detritus that had decomposed in their phytotelmata, we deposited portions of *E. uniflora* leaves (mean ± SD weight per portion, 0.52 ± 0.01 g) enriched with a nitrogen isotope (^{15}N). To monitor the absorption of ^{15}N by the bromeliad, at the end of the experiment we removed three new leaves from the submerged portion of each bromeliad. These leaves were processed according to the sample preparation protocol of the Stable Isotope Facility, University of California, Davis, and sent there for determinations of isotope ^{15}N.

To produce enriched debris, we cultivated 10 small saplings (~60 cm in height) of *E. uniflora* in a greenhouse with an automatic irrigation system. Enrichment with ^{15}N was done by applying 5 mL of a 2.5 g/L concentration of ammonium sulfate ($[^{15}NH_4]2SO_4$) solution enriched with 10% excess of ^{15}N atoms (Cambridge Isotope Laboratories, Tewksbury, MA) every 2 days. This procedure took place over 60 days. Later, the saplings were cut at the base of the stems, and these stems were placed in a tray for collection; after senescence of all of the leaves, the leaves were dried in an incubator with air circulation (Marconi) at 70°C for 48 h.

Additionally, at the beginning of the experiment we measured the total length of the three youngest bromeliad leaves and quantified the total number of leaves for comparison at the end of the experiment.

Statistical Analyses

To analyze the effect of the treatments (i.e., presence of avian predators, presence of butterflies, and control) on the composition of the aquatic invertebrate community, we used permutational multivariate ANOVA (PERMANOVA), with the Bray-Curtis dissimilarity coefficient and 999 permutations. Next, we performed a nonmetric multidimensional scaling (NMDS) analysis to graphically represent the species composition among the three treatments; we plotted the graph as a spider graph using the ordispider function in the vegan package to emphasize the community centroid in each of the treatments.

To test the effects of the treatments on species richness (i.e., other than the damselfly larvae, which were mostly represented by *L. andromache*) and the abundance and biomass of the damselfly larvae and organisms in larval stage belonging to the various functional groups (e.g., mesopredators, collectors, filter feeders, scrapers, and shredders), we used a one-way ANOVA with a fixed factor (i.e., treatments, three levels) and a random factor (i.e., blocks); we used Tukey post hoc tests for paired comparisons. We also analyzed the effects of the treatments on the decomposition rate of *E. uniflora*, on the isotopic values of the nitrogen (^{15}N) accumulated in the bromeliad leaves, on the total nitrogen concentration in the young leaves, on leaf growth, on the number of new leaves, on rosette diameter, and on plant height.

PERMANOVA, NMDS, and mixed ANOVAs were performed using R software (ver. 3.1.2; R Development Core Team 2015). The established significance level was α = .05. We verified variance heterogeneity, normality, and outliers via graphical inspections (e.g., quantile-quantile plots, Cook's distance, and influence) and statistical tests (e.g., Levene's test). Data were log transformed when necessary; however, the data were back transformed to build the figures.

Results

The presence of insectivorous birds near the bromeliads strongly affected the occurrence of damselfly larvae. Both the abundance and the biomass of the damselfly larvae were ~30% lower inside the bromeliad tanks in the presence of birds compared with values for the butterfly and control treatments (table 1; fig. 2a, 2b).

The total community of invertebrates collected comprised 1,007 individuals divided into three orders: Diptera, Coleoptera, and Odonata (app. B). The presence of avian

Table 1: Analyses of variance examining the effects of the treatments (i.e., presence of avian predators, presence of butterflies, and control) on the global community of bromeliad-dwelling insects and of each functional group separately

Source of variation	Richness		Abundance		Biomass	
	F ratio	*P*	*F* ratio	*P*	*F* ratio	*P*
Total	8.79	<.009	.51	.617	.62	.558
Zygoptera	…	…	7.89	.012	6.68	.019
Other predators	6.15	.024	.65	.545	.49	.629
Collectors	1.10	.377	.06	.941	.12	.887
Filter feeders	.32	.732	.30	.742	.191	.829
Scrapers	…	…	.52	.613	97.61	<.001
Shredders	…	…	8.22	.011	1.90	.210

Note: Response variables analyzed included species richness, abundance, and biomass. Damselfly richness was not analyzed because only two species were recorded (*Leptagrion andromache* and *Leptagrion macrurum*; app. B). The richness of scrapers and shredders functional groups were not analyzed because of the low number of species (see app. B).

predators strongly affected several parameters of the aquatic community. Birds altered the morphospecies composition of the aquatic invertebrates (PERMANOVA; treatments, $R^2 = 0.20$, $P = .019$; see app. C for NMDS analyses). In the presence of birds (and with a decrease in Zygoptera), the total aquatic invertebrate richness was 33% greater than that in the butterfly treatment (e.g., in the presence of *Heraclides thoas*) and was ~25% greater than that in the control treatment (table 1; fig. 2*c*). In addition, we also observed that, in the presence of avian predators, greater mesopredator richness was found than in either the butterfly or the control treatment, representing an increase over each of 81% and 100%, respectively (table 1; fig. 2*d*). Mesopredators showed a greater increase in species of the genera *Stibasoma*, *Corethrella*, and *Bezzia*; their abundance per bromeliad varied from 1 to 18, with an average of 8.7 mesopredators per bromeliad regardless of treatment. The mean abundance of the shredder functional group was ~200% higher in the presence of birds compared with that in the butterfly treatment and was ~150% higher compared with that in the control treatment (table 1; fig. 2*e*). In contrast, the mean biomass of the scrapers functional group was ~53% smaller in the presence of birds compared with that in both the butterfly and the control treatment (table 1; fig. 2*f*). The other functional groups (i.e., collectors and filter feeders) were not significantly influenced by the treatments (table 1; app. C).

The presence of the avian predators (and the decrease in damselflies) decreased detritus processing by 27% compared with the butterfly treatment and by 31% compared with the control treatment ($F = 8.19$, $P = .012$; fig. 2*g*). There was also a decrease of 20% in new leaf production by bromeliads in the presence of birds compared with that in the butterfly treatment and a decrease of 24% compared with that in the control treatment ($F = 13.21$, $P = .003$; fig. 2*h*). The other variables analyzed (i.e., the amount of isotopic nitrogen [15N] accumulated in the bromeliad leaves, total concentration of nitrogen in young leaves, leaf growth, rosette diameter, and plant height) were not significantly affected by the treatments (app. C). Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2bq8g (Breviglieri et al. 2017).

Discussion

Our results demonstrate that the presence of terrestrial avian predator models decreased the abundance and biomass of damselfly larvae in bromeliad aquatic systems through nonconsumptive effects. The decrease in these aquatic apex predators changed the composition of the invertebrate community, most dramatically due to an increase in mesopredator richness and decreased scraper biomass. In the absence of birds, we observed higher decomposition rates; we attribute this phenomenon to the increase in detritivore biomass (i.e., scraper) and/or the increase in top predator abundance and biomass, which may have subsidized aquatic microorganisms with nutrients from debris (feces, prey carcass), thus accelerating detritus decomposition. Higher detritus decomposition likely made more nutrients available for bromeliads, which increased their growth. These results highlight that nonconsumptive effects of apex predators across ecosystems can cascade down to lower trophic levels (e.g., Odonata, detritivores, and mesopredators) and bromeliad ecosystem functioning (detrital decomposition and bromeliad growth) via a TMII. This reveals that the nonconsumptive effects of terrestrial predators can influence food web composition and structure and, consequently, the functioning of aquatic ecosystems, including the development of these living ecosystems (i.e., bromeliads).

The abundance and biomass of damselfly larvae inside the phytotelmata decreased in the presence of avian predator models, confirming our first prediction (fig. 1). Because these avian predators capture only large diurnal and twilight
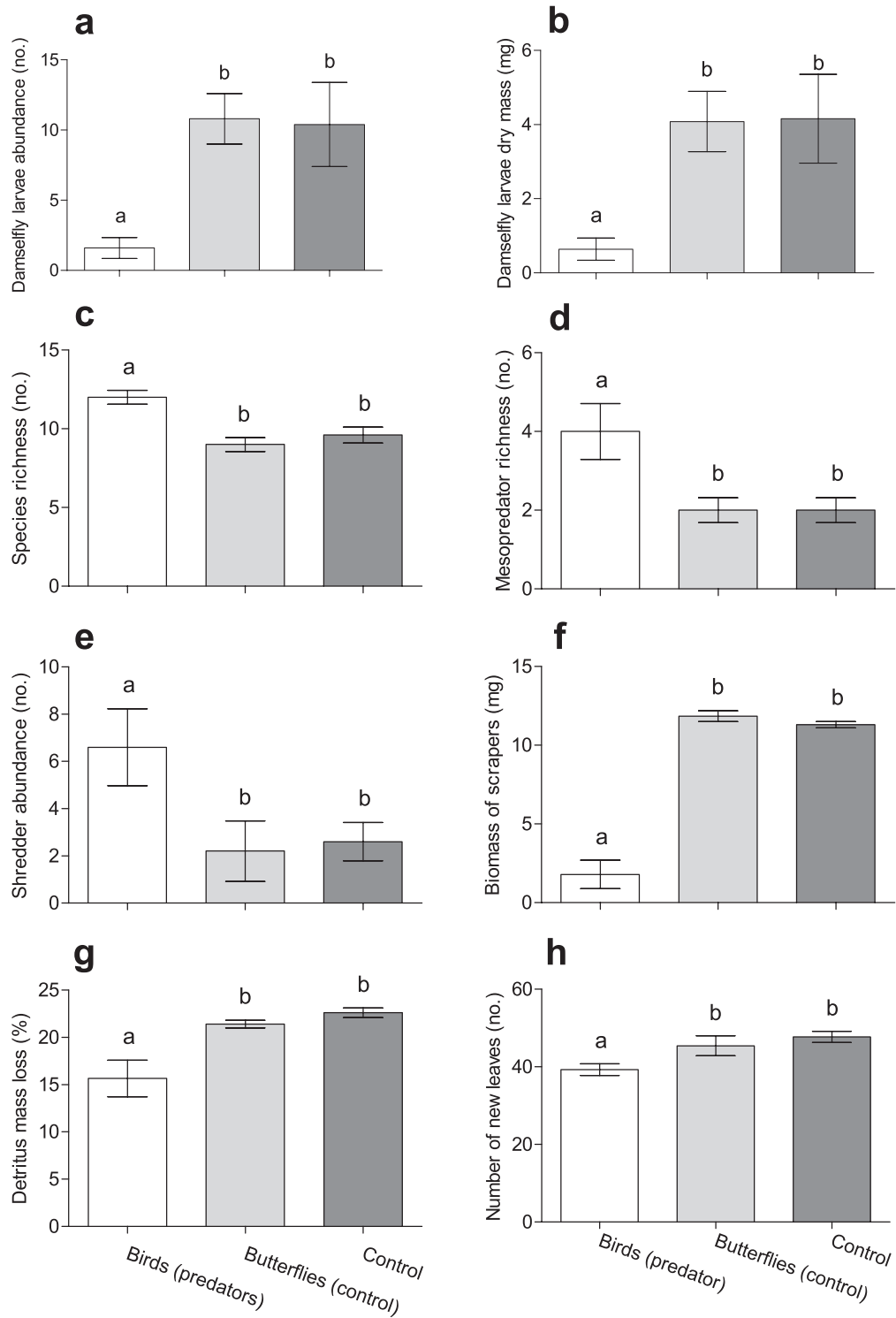
Figure 2: Abundance (*a*), dry mass of damselfly larvae (*b*), total species richness (*c*), richness of mesopredators (*d*), abundance of shredders (*e*), scraper dry mass per bromeliad (*f*), percentage of detritus mass loss (*g*), and mean number of new leaves per bromeliad (*h*) among the treatments (i.e., presence of avian predators, presence of butterflies, and control). Error bars represent 1 SE. Different letters indicate significant differences ($P < .05$, analyses of variance/Tukey post hoc test; $\alpha = .05$).

prey (Sick 1997), such as those of the order Odonata (damselflies and dragonflies), we believe that this effect is related to the visual, cognitive, and learning capacity of the adult damselflies to recognize possible predators near their egg-laying sites (bromeliads). Indeed, it is known that damselflies are vulnerable to avian predators during emergence; thus, they typically emerge at night. Moreover, they move fast to protected areas among dense vegetation in the presence of avian predators (Corbet 1962). Invertebrates constantly exposed to predation risk are known to learn to detect and recognize predator characteristics via visual stimuli (e.g., predator behaviors, colors, and shapes; see Sendoya et al. 2009; Romero et al. 2011). Dragonflies and damselflies strongly depend on their visual senses to capture their prey and to identify partners or possible aggressors (Frye 2013; Futahashia et al. 2015). These organisms are able to distinguish their prey of possible predators (i.e., wasps) through body shape and color (i.e., black and yellow; Rowe 1999; Kauppinen and Mappes 2003). Therefore, we suggest that the damselflies studied here were able to differentiate the stuffed birds from butterflies on the basis of the color and shape of the models, decreasing the oviposition rate in response to possible predators (i.e., insectivorous birds). In addition, these organisms can learn to avoid predators on the basis of attacks to members of their own species and by avoidance of those places that present a high risk of predation (Wisenden 1997). Although we did not observe antipredatory behaviors of adult damselflies under predation risk (through several hours of video recording and direct observations in the field; see details in "Experimental Design"), the presence of avian predators capturing invertebrates close to damselflies can warn them about a potential risk.

The decrease in abundance and biomass of the damselfly larvae changed the structure (composition, richness) of the aquatic invertebrate community, confirming our second prediction. Aside from an increase in overall species richness, we also saw an increase in the richness of mesopredators (genera *Stibasoma*, *Corethrella*, and *Bezzia*), an increase in the abundance of the shredders (i.e., *Trentepohlia* sp. and *Phylloicus bromeliarum*), and a decrease in the biomass of the scrapers (i.e., *Scyrtes* beetles). In contrast, other functional groups were not affected (e.g., Culicidae). These results are likely due to several different mechanisms; behavior, life span, and the interaction strength in predator-prey relationships are quite variable among the taxa involved and may explain the results. For example, adult females of prey species (e.g., *Wyeomyia*) that come to bromeliads to lay eggs can recognize and avoid bromeliads with a high concentration of top aquatic predators (Hammill et al. 2015). The absence of some species and the low abundance or richness of others (e.g., mesopredators, shredders) under higher densities of damselfly larvae can be mediated by consumptive effects (e.g., Hammill et al. 2015). Mesopredator larvae (e.g., Corethre-

llidae and Cecidomyiidae) are known to actively forage in search of prey and, therefore, become vulnerable to predation by damselfly larvae, which adopt a sit-and-wait behavior. Damselflies interact strongly with culicids, that is, they can feed on many mosquito larvae per hour (G. Q. Romero, personal observations); however, since the life cycle of these filter feeders is very fast (i.e., up to 20 days) and their biomass turnover via new colonizers is likely very high (Romero et al. 2016), we expect no influence of predators on populations of this functional group. On the other hand, the scrapers *Scyrtes* sp. move in the water column and spend a long time (∼2 months) to complete their development, thus becoming more vulnerable to predation (e.g., by mesopredators). In contrast, the shredders *P. bromeliarum* and *Trentepohlia* sp. are larger detritivores, and, like *Scyrtes*, they spend longer in the bromeliads to complete life cycle. In addition, *P. bromeliarum* are protected by their shelters (built using leaf fragments), and *Trentepohlia* sp. forage inside dead leaves or below the detritus; thus, they are likely less vulnerable, at least to mesopredators. Alternatively, the decrease in scraper biomass can also be explained by the increase in mesopredator diversity via two distinct mechanisms: an increase in diversity (i) can increase the chance of including a more efficient predator within the community (i.e., selection effect) or (ii) can increase overall predator foraging efficiency due to a mixture of species occupying different niches, with each species foraging in different compartments of the bromeliad (i.e., complementarity; Duffy et al. 2007).

Contrary to our third prediction (see fig. 1), the presence of terrestrial birds decreased detrital decomposition, an important aspect of bromeliad ecosystem functioning. The explanations are twofold: first, top predators may have directly facilitated microorganism activity. Debris derived from damselflies (prey carcass and feces) could enhance nutrient availability to microorganisms, which in turn could have accelerated detrital processing. At our field site, bacteria were proven to be very important in detrital decomposition, surpassing the role played by macroinvertebrates (Lecraw et al. 2016). Second, scrapers may have improved detritus processing. Birds decreased damselfly abundances, which increased mesopredator richness, which decreased the abundance of scrapers. The feeding guild of scrapers is particularly important for facilitating the decomposition of organic matter and cycling of nutrients in bromeliad ecosystems, as also observed in other studies (P. M. de Omena, unpublished data). Although shredders (mostly *Trentepohlia* sp.) increased in the presence of birds and are efficient in detritus processing, their feeding activities may have been inhibited by the increase in mesopredator richness. The presence of predators may decrease detritivore abundance in bromeliad studies (Hammill et al. 2015). These results highlight the importance of considering the role that top predators (damselflies) play in the functioning of bromeliad ecosystems via facilita-

tion of microorganism activities and/or as mediators of the interactions between mesopredators and detritivores.

Bromeliads also grew less in the presence of terrestrial birds, rejecting our fourth prediction. This should be expected given that detrital decomposition decreased in the presence of avian predators due to the decrease in damselfly abundance and biomass. Bromeliaceae have trichomes that are able to absorb water, minerals, and even amino acids present in the tank (e.g., Romero et al. 2006) and would have absorbed more nitrogen with the increase in detrital breakdown rates. Since the bromeliad tanks are formed by leaf axils, an increase in nitrogen availability allows the plants to invest in vegetative structures (Gonçalves et al. 2016); by producing new leaves, these plants provide larger surface areas to absorb more nutrients. In this sense, avian predators and damselflies can mediate complex interactions between detritivores and mesopredators as well as bromeliad nutrition. In addition, predators can also directly feed bromeliads via deposition of feces and prey carcasses (Ngai and Srivastava 2006; Romero et al. 2006). Damselflies can minimize the migration of detritivores out of the aquatic system of bromeliads, preventing the nutrients that are assimilated from the detritus by these detritivores from leaving the system; thus, they can increase the nutrients available in the system and facilitate their absorption by bromeliads (Ngai and Srivastava 2006). Despite this, we did not detect variations in the flux of ^{15}N to the bromeliad leaves. This can be explained by the fact that nitrogen is labile and prone to easily volatilize under higher temperatures (Rubenstein and Hobson 2004). Other ways it can leave the system are through leaching (by rainfall; S. G. Benavides, V. Farjalla, A. González, et al., unpublished data) and carriage out of the system via detritivorous insects, which pupate relatively rapidly and constitute a loss of litter-derived N for bromeliads when they emerge (Ngai and Srivastava 2006). Therefore, we did not discount the possibility that bromeliad growth may have been determined by direct effects of the increase in top aquatic predators (making more carcasses and feces available) as well as by indirect effects via detrital breakdown. Finally, we believe that nutrients leached out of the bromeliads through rainfall can subsidize terrestrial organisms (e.g., other plants, microorganisms). Since the terrestrial top predators decreased decomposition and nutrient inputs inside the bromeliads, this would represent a negative feedback of terrestrial predators to terrestrial ecosystems. As such, decreased decomposition and nutrient inputs inside bromeliads caused by terrestrial top predators would generate a negative feedback to the terrestrial ecosystem.

In summary, our results suggest that adult damselflies can react to the visual presence of their predators (i.e., birds) and alter their oviposition behavior (i.e., avoidance). Given their role as apex predators in these aquatic systems, this indicates that terrestrial predators influence the composition of the aquatic invertebrate community. In addition, our findings indicate that the cascading effects generated by terrestrial avian predators can alter ecosystem processes in bromeliad aquatic systems (via multiple trophic levels across ecosystems) and can interfere in the development of these living ecosystems (i.e., the bromeliads). Organisms cross ecosystem borders all the time, and any time this happens there is the potential for cross-ecosystem trophic cascades and behavioral indirect effects. While it is probably especially common in species with complex life cycles involving multiple habitats (e.g., insects, frogs), this is not necessary for cross-ecosystem TMIIs to occur. A number of ecosystems are inhabited by apex predators, such as aquatic birds (e.g., kingfishers) and giant otters (*Pteronura brasiliensis*), which feed on fishes; Nile crocodiles (*Crocodylus niloticus*), which feed on large terrestrial mammals (e.g., during wildebeest migration); or Brazilian felids (*Panthera onca*), which feed on crocodiles. All of these and other ecosystems not mentioned are prone to experience similar processes described here and remain to be investigated. For instance, fear triggered by Nile crocodiles might increase the waiting time of wildebeest in the river margins during migrations; in turn, these herbivores can impact plant communities at the margins by grazing and/or improving plant nutrition and terrestrial productivity via their feces. Our results from a simple ecosystem provide insights into how apex predators can potentially trigger trait-mediated trophic cascades across land-water boundaries (such as other microcosms, ponds, lakes, streams, rivers, and seas) by impacting lower trophic levels via nonconsumptive effects and indirectly affecting ecosystem functions, such as productivity, decomposition, and nutrient cycling.

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Top, the great kiskadee (*Pitangus sulphuratus*) foraging in the restinga. *Bottom, Myiarchus swainsoni* (Tyrannidae) perched after catching an insect in a coastal forest. Photo credit: Crasso Paulo B. Breviglieri.