

Food-web composition affects cross-ecosystem interactions and subsidies

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Summary

1. Ecosystems may affect each other through trophic interactions that cross ecosystem boundaries as well as via the transfer of subsidies, but these effects can vary depending on the identity of species involved in the interaction.

2. In this study, we manipulated two terrestrial bromeliad-living spider species (*Aglaoctenus castaneus*, *Corinna* gr. *rubripes*) that have variable hunting modes, to test their individual and combined effects on aquatic invertebrate community structure and ecosystem processes (i.e. decomposition rate and nitrogen cycling). We predicted that these terrestrial predators can affect aquatic invertebrates and nutrient dynamics within water-filled bromeliads.

3. *Aglaoctenus* spiders reduced the richness, abundance and biomass of aquatic insect larvae via consumptive or non-consumptive effects on ovipositing terrestrial adults, but effects of the two spider species in combination were usually the linear average of their monoculture effects. In contrast, invertebrates with entirely aquatic life cycles were unaffected or facilitated by spiders. Spiders did not affect either net detritivore biomass or the flux of detrital nitrogen to the bromeliad. Instead, *Corinna* spiders contributed allochthonous nitrogen to bromeliads.

4. Our results provide the novel observations that predators in one ecosystem not only directly reduce taxa whose life cycles cross-ecosystem boundaries, but also indirectly facilitate taxa whose life cycles are entirely within the second ecosystem. This compensatory response between cross-ecosystem and within-ecosystem taxa may have led to an attenuation of top-down effects across ecosystem boundaries. In addition, our results add to a growing consensus that species identity is an important determinant of community structure and ecosystem functioning. Thus, the composition of both terrestrial and aquatic food webs may affect the strength of cross-ecosystem interactions.

Key-words: allochthonous subsidies, density compensation, ecosystem functioning, indirect facilitation, predator hunting mode

Introduction

Regulation of food-web structure and dynamics is a central theme in ecology (Polis & Strong 1996; Shurin, Gruner & Hillebrand 2006). However, studies have traditionally emphasized only regulatory processes within an ecosystem, with limited integration among adjacent ecosystems. Recent studies have shown that aquatic and terrestrial food webs can strongly influence each other. For instance, aquatic ecosystems can influence terrestrial ecosystems in at least two differ-

ent ways: via allochthonous subsidies (Marczak, Thompson & Richardson 2007; Leroux & Loreau 2008), or via trophic links in which aquatic predators consume organisms whose life cycles cross the water–air interface (Knight *et al.* 2005; McCoy, Barfield & Holt 2009). In contrast, allochthonous subsidies dominate the reported effects of terrestrial ecosystems on aquatic food webs, such as the passive transport of detritus from uplands to streams (e.g. Vannote *et al.* 1980). To date, little is known about how terrestrial organisms influence aquatic ecosystems via trophic links such as predation.

Predators that forage in ecosystem boundaries often intercept cross-ecosystem organisms (Murakami & Nakano 2002; Marczak & Richardson 2007). Cross-ecosystem organisms are those whose life cycles involve multiple ecosystems, such as insects and amphibians that spend their larval life stages in

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the water but their adult life stages on land. Recent studies have demonstrated that organisms with complex life cycles are among the most common and important connectors linking the dynamics of different ecosystems (Knight *et al.* 2005; Marczak & Richardson 2007; Schreiber & Rudolf 2008). However, most food webs contain a combination of species both with and without cross-ecosystem life cycles. Therefore, predation on cross-ecosystem species may have indirect effects on species with within-ecosystem life cycles, and vice versa. For example, birds attracted to riparian borders by emerging stream insects also prey on terrestrial insects, an example of apparent competition (Murakami & Nakano 2002). Fish predation on aquatic damselfly larvae reduces predation on pollinators by terrestrial damselfly adults, an example of a trophic cascade (Knight *et al.* 2005). We believe that our study is among the first to examine how predation in one ecosystem affects, in another ecosystem, the relative abundance of species at the same trophic level.

Predation has long been considered as one of the most important biotic process structuring communities and food webs (e.g. Schmitz, Hambäck & Beckerman 2000; Halaj & Wise 2001; Shurin, Gruner & Hillebrand 2006). There is mounting evidence that interactions among predators can also indirectly affect prey communities (see Sih, Englund & Wooster 1998; Huxel 2007) via linear and nonlinear effects. Linear effects arise when predator species in combination have similar per capita impacts on their prey as their monoculture average, i.e. they are 'substitutable'. Nonlinear effects result in lower (risk reducing) or higher (risk enhancing) per capita predation rates when predators co-occur, and may result from interference or synergism between predator species or intraguild predation (Finke & Denno 2004; Schmitz 2007). The strength of predation effects on prey populations can also depend on the functional traits of predators, such as hunting mode (Beckerman, Petchey & Warren 2006; Straub & Snyder 2006; Preisser, Orrock & Schmitz 2007; Schmitz 2007; Otto *et al.* 2008). In addition, although predator traits and inter-predator interactions are important in determining predator identity effects on food-web dynamics (e.g. Griswold & Lounibos 2006), community structures (e.g. Schmitz 2006) and ecosystem processes (Schmitz 2008), this has not yet been examined in a cross-ecosystem context.

Terrestrial predators are most likely to intercept emerging aquatic organisms in aquatic systems with a high edge : volume ratio. Phytotelmata such as bromeliads and pitcher plants have exceptionally high edge : volume ratios, acting as tiny aquatic habitats in a terrestrial matrix (Fig. 1a). The invertebrate fauna of phytotelmata is typically dominated by aquatic insect larvae that emerge as winged terrestrial adults (Richardson 1999; Armbruster, Hutchinson & Cotgreave 2002; Srivastava *et al.* 2004; Srivastava 2006). Other aquatic invertebrates (e.g. leech, worms, small crustaceans) complete their life cycle inside the phytotelmata, and thus have more isolated populations linked only by phoresy (Lopez, Rodrigues & Rios 1999) or passive dispersal. Schreiber & Rudolf (2008) predicted that cross-ecosystem dynamics will be primarily transmitted by organisms with cross-ecosystem life

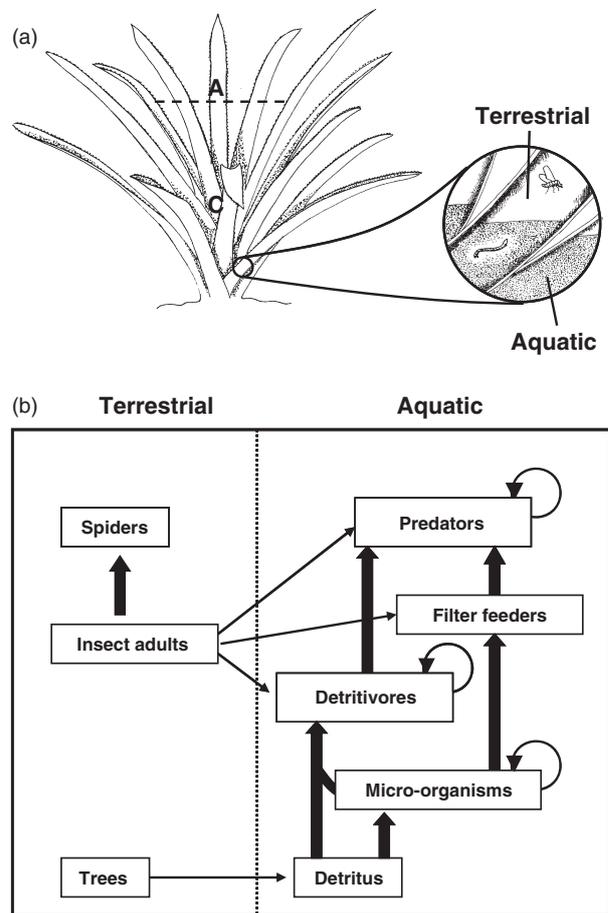


Fig. 1. Bromeliads contain both aquatic and terrestrial ecosystems. (a) Aquatic habitat is formed when water pools at the base of bromeliad leaves. Non-submerged parts of bromeliad leaves provide terrestrial habitat, inhabited by spiders including the web-spinning *Aglaoctenus castaneus* (common position shown with 'A') and the hunting *Corinna gr. rubripes* (common position shown with 'C'). (b) Organisms and organic matter (mainly dead leaves from trees) move across the aquatic-terrestrial interface (straight thin arrows), including the oviposition of aquatic eggs by terrestrial insect adults. Species with such cross-ecosystem life cycles can transmit the effect of trophic interactions (thick arrows) between organisms in one ecosystem to the other ecosystem. Other aquatic taxa are maintained by *in situ* reproduction (circular thin arrows), and so have predominantly within-ecosystem life cycles. To simplify the figure, longer term processes such as insect emergence and invertebrate phoresy are not shown.

cycles, which in this system are the insects. Terrestrial predators, such as spiders, often inhabit the terrestrial portions of phytotelmata (Richardson 1999; Armbruster, Hutchinson & Cotgreave 2002; Romero 2006) and their consumption of emerging or ovipositing adult insects is potentially important as a cross-ecosystem trophic link (Fig. 1b). Any effect of terrestrial predators on the aquatic invertebrate food web within phytotelmata could have important repercussions for ecosystem processes. For example, bromeliads are often epiphytic, and so rely on allochthonous sources of nitrogen, such as detritus or invertebrate carcasses and feces (Ngai & Srivastava 2006; Romero *et al.* 2006), which they absorb from the water column through specialized leaf trichomes (Benzing 2000). If terrestrial predators reduce aquatic detritivores, which aid in

releasing nitrogen from detritus (Ngai & Srivastava 2006), then terrestrial predators can indirectly reduce bromeliad nutrition. Alternatively, bromeliad nutrition may be improved by terrestrial predators that provide allochthonous subsidies. For example, spiders have been shown to add nitrogen to dry bromeliads in the form of fallen insect carcasses and guanine-rich spider feces (Romero *et al.* 2006), but it is not yet clear if water-filled bromeliads also benefit from spider-derived nitrogen.

In the field experiment, we report here, we manipulated two terrestrial spider species living on water-filled bromeliads to test their individual and combined effects on invertebrate community structure and ecosystem processes (decomposition rate and nitrogen cycling). Specifically, we addressed the following questions: (i) Do terrestrial predators directly reduce the abundance of species with cross-ecosystem life cycles (bromeliad-dwelling insects)? (ii) Do terrestrial predators indirectly affect the abundance of species with entirely aquatic life cycles (non-insect invertebrates)? (iii) Do terrestrial predators influence ecosystem processes (decomposition and nitrogen flux) either through allochthonous inputs or top-down effects on the aquatic food web? (iv) Do the above effects of terrestrial predators depend on predator identity?

Materials and methods

STUDY AREA AND BROMELIAD FOOD WEB

This study was conducted in a closed restinga forest in Parque Estadual da Ilha do Cardoso (25°03' S, 47°53' W), an Atlantic island of 22.5 ha located off the south coast of São Paulo state, Brazil. The understory of the restinga 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. A diverse arthropod fauna is associated with this bromeliad species (more than 47 species; Appendix S1, Supporting Information), composed of aquatic insect larvae of several functional groups, including predators (Zygoptera, Tabanidae, Syrphidae, Tanypodinae, leeches), filter feeders (Culicidae), detrital shredders (Tipulidae, Trichoptera), detrital scrapers (Scirtidae) and collectors (Chironomidae, Syrphidae, Psychodidae). The fauna also includes small non-insect invertebrates, such as Oligochaeta, Ostracoda (both detritivores), Hirudinea (predator), aquatic Acari (multiple trophic levels) and Turbellaria (collector of microscopic particles). The terrestrial parts of the bromeliad are inhabited by the spiders *Aglaoctenus castaneus* (Lycosidae) and *Corinna gr. rubripes* (Corinnidae).

The foraging mode of these spiders clearly differs from each other: *Aglaoctenus* construct a large horizontal funnel-like web in the centre of the rosette of bromeliad leaves. The spider exhibits a sit-and-wait foraging mode, motionless on its web, but is active both day and night (Fig. 1a). On average, *Aglaoctenus* spiders spend 22.4 days (± 1.31 SE, $n = 25$ spiders observed for 26 days each) in a particular bromeliad. In contrast, *Corinna* exhibits both sit-and-wait (day) and motile (night) foraging modes, and does not forage using a web; during the day it waits for prey in the base of an external leaf and at night it forages on all parts of the bromeliad rosettes (Fig. 1a). In our experiment, *Corinna* individuals were adult or subadult (mean body length in mm \pm SE = 16.3 ± 0.53) and *Aglaoctenus* individuals were juveniles (12.1 ± 0.36).

EXPERIMENTAL DESIGN FOR SPIDER MANIPULATIONS

To determine the effect of spider identity on the aquatic food web, we conducted a factorial experiment, crossing *Aglaoctenus* presence with *Corinna* presence in a randomized block design ($n = 12$ blocks). This resulted in four treatments: a control (no spiders), an *Aglaoctenus*-only treatment (one individual per bromeliad), a *Corinna*-only treatment (one individual) and a treatment with both *Aglaoctenus* and *Corinna* (one individual of each species). The influence of multiple predators could have been evaluated either with an additive design, in which the density of the focal species is held constant, or a substitutive design, in which the total abundance of predators is held constant. We chose an additive design for our experiment, as this design is able to isolate the absolute effect of interspecific from intra-specific interactions (Sih, Englund & Wooster 1998), and because bromeliads typically shelter only a single individual of each spider species; when species were together, *Aglaoctenus* was vertically displaced by *Corinna*, whereas no similar effect was seen on *Corinna* position within bromeliads (see Appendix S2).

To set up the experiment, we collected from the restinga 48 small-to medium-sized *Q. arvensis* bromeliads (maximum tank capacity: 140–380 mL) on 11 January 2008. Each bromeliad was washed in spring water for 10 min to remove detritus and invertebrates. We estimate that we removed 94% of existing individuals from bromeliads by washing. The few individuals (6.7 ± 1.2 , $n = 4$) which remained in the bromeliad served as founders for non-insect invertebrate populations, or as background levels for colonizing insects. Over the next month, total abundances increased by an order of magnitude in most bromeliads. Each bromeliad was planted in the sandy substrate of the restinga in 12 blocks of four bromeliads each. A distance of c. 0.2–0.4 m separated bromeliads within each block, and each block was 8–30 m apart. The bromeliads in each block were randomly assigned to the four spider treatments. The tanks were naturally filled by rainwater from the rain that fell in the first day of the experiment. An open cylinder (55 cm tall, 50 cm diameter) made from white PVC was fitted over each bromeliad and dug into the substrate to prevent dispersal of the spiders (especially *Corinna*) from the experimental bromeliads and to avoid entry of other non-flying terrestrial arthropods (jumping spiders, ants) into the cylinders. We periodically applied solid petroleum jelly (Rioquímica®, São José Do Rio Preto, Brazil) to the top edge of the cylinder as a further barrier. The cylinder apparently did not interfere with invertebrate colonization of bromeliads, since the fauna surveyed in the experimental bromeliads was similar to those surveyed from neighbouring field bromeliads (G.Q. Romero & D.S. Srivastava, unpublished). The bromeliads in the experiment were no taller than 45 cm, and thus the entire plant was below the height of the cylinder. All spiders were collected from nearby bromeliads. All the experimental spiders had established (e.g. constructed their webs in the case of *Aglaoctenus*) within a few hours of introduction. Spiders on each bromeliad were inspected daily, and in the rare case of a missing or additional spider (3–4 instances), the appropriate species was added or removed according to the treatment.

SPIDER EFFECTS ON AQUATIC INVERTEBRATES

We assessed invertebrate community assembly in bromeliads after 1 month (10–13 February, staggered by block), the approximate residence time of *Aglaoctenus* on an individual bromeliad. We carefully dissected and washed each leaf of each bromeliad. All detritus and water were collected in white trays, and fractionated with two soil sieves (125 and 800 μ m) to aid in detecting

invertebrates. We recorded the size, abundance and morpho-species of all aquatic invertebrates visible to the naked eye (> 0.5 mm). Voucher specimens of each morphospecies were later identified to the lowest possible taxonomic level by specialized taxonomists (see Acknowledgements). The functional group of each taxon was determined through consulting the literature (especially Merritt & Cummins 1996), as well as by direct observation (see Appendix S1). Invertebrate biomass was estimated from body length mainly using family or species-specific allometric equations developed at the field site, but also through allometric equations developed for similar Costa Rican bromeliad fauna (D. Srivastava, unpublished data).

ECOSYSTEM RESPONSES TO SPIDER MANIPULATIONS

We examined two important ecosystem processes: breakdown of detritus and flux of detrital nitrogen into new bromeliad leaves. In addition, we evaluated the influence of allochthonous input (i.e. spider feces) on total nitrogen content of new bromeliad leaves.

Detrital breakdown was measured as mass loss of detritus [fallen *Eugenia uniflora* L. (Myrtaceae) leaves] from litter bags. Prior to the experiment, *Eugenia* leaves were oven-dried at 70 °C and their dry mass determined ($\pm 10^{-4}$ g). Leaves were then conditioned by immersion in spring water for 12 h. Two *Eugenia* leaves were placed in a 3 × 5 cm litter bag (mesh size 3 mm). We added two litter bags to each bromeliad, with litter bags at opposite sides of the plant and completely submerged in water. The mesh diameter was large enough to enable detritivores to enter and leave the litter bags (G.Q. Romero, pers. obs.), but small enough to retain larger leaf fragments. At the end of the experiment (10–13 February), the contents of each litter bag were dried and their mass determined to estimate detrital loss.

We also added a total of 0.5 g of ^{15}N labelled bean leaves (*Phaseolus vulgaris* L.) to each bromeliad in order to measure nitrogen flux from detritus to new bromeliad tissue. The labelled bean leaves were distributed amongst leaf axils in the beginning (12 January) and middle of the experiment (26 January). Bean plants were grown from seeds in a greenhouse and watered for 10 days with 300 mL of solution ($5 \text{ g L}^{-1} \text{ day}^{-1}$) of labelled ammonium sulphate ($^{15}\text{NH}_4$)₂SO₄ (10 atom % excess, from Cambridge Isotope Laboratories, Andover, MA, USA). Labelled bean leaves were oven-dried at 70 °C before their mass was determined. At the end of experiment (10 February), we clipped two new bromeliad leaves from the innermost node of each experimental bromeliad for isotopic (^{15}N) and nitrogen concentration (μg of total N mg^{-1} of dried plant tissue) analyses. Stable isotope ratios of ^{15}N and N concentrations were determined in the Stable Isotope Facility laboratory (UC Davis, CA, USA) using continuous flow isotope ratio mass spectrometer (20–20 mass spectrometer; PDZ Europa, Sandbach, England) after sample combustion to N₂ at 1000 °C by an on-line elemental analyser (PDZ Europa ANCA-GSL).

STATISTICAL ANALYSES

The experiment was designed as a three-way ANOVA with two fixed factors (*Aglaoctenus* presence and *Corinna* presence) and one random factor (block). A significant *Aglaoctenus* × *Corinna* interaction in our design would suggest that spiders are acting either antagonistically (> expected prey surviving) or synergistically (< expected prey surviving). Following recommendations by Sih, Englund & Wooster (1998), data were either log transformed or linked to a log function for analysis; this ensures that the absence of an interaction represents multiplicative effects of predation probabilities.

Invertebrate response variables included abundance and biomass at the community, functional group and family levels. We were unable to identify functional groups for several invertebrates (aquatic mites, Turbellaria and a few Diptera larvae), so these were considered only in the total biomass analysis. We also separated species based on whether they completed their entire life cycle within bromeliads (i.e. non-insect invertebrates) or had both aquatic and terrestrial stages (i.e. insects). Although there are bromeliad-dwelling insects in Ilha do Cardoso that have both aquatic larvae and adults (Dytiscid beetles), these species were not encountered during our experiment. Ecosystem response variables included detrital mass loss, bromeliad uptake of ^{15}N from bean leaves, and total nitrogen concentration in bromeliad leaves. Depending on the error structure of models, we used either log transformations with a linear mixed effects model or log-link functions with a Poisson or quasi-Poisson generalized linear model. We checked for normality of residuals and absence of outliers with standard diagnostic plots and metrics. All ANOVAs were fitted using the statistical language R, version 2.6.2 (R Development core team, <http://www.r-project.org>).

We tested the influence of treatments on invertebrate community composition using an analysis of similarity (ANOSIM) procedure (PRIMER version 5; Plymouth Marine Labs, Plymouth, UK). ANOSIM uses a randomization test (999 permutations) to test the significance of 'Global R', the standardized difference between treatments vs. within treatments in mean pairwise dissimilarities (Clarke & Warwick 1994). Global R is scaled to be between +1 and -1; values > 0 mean that communities are more dissimilar between treatments than within treatments.

Results

SPIDER EFFECTS ON AQUATIC INVERTEBRATES

We first examine effects of spiders on the invertebrate community as a whole. Whereas *Aglaoctenus* reduced the species richness of all invertebrates by 45% (Table 1, Fig 2a) and total invertebrate abundance by 31% (Table 1, Fig 2b), *Corinna* did not affect these community parameters (Table 1, Fig. 2a,b). These negative effects of *Aglaoctenus* on the richness and abundance of all invertebrates were largely driven by reductions of the insect larvae (insect larvae have similar responses as total invertebrates: Table 1). There was no negative impact of spiders on non-insect invertebrates, all of which completed their entire life cycle within the bromeliad (Table 1, Fig. 2). When both spider species co-occurred, insect richness was reduced less than expected from multiplicative effects (Table 1, Fig. 2a), or even from additive effects ($F_{1,33} = 5.92, P = 0.02$).

Total invertebrate biomass was unaffected by spiders (Table 1, Fig. 2c). The biomass of non-insect invertebrates was unaffected by spider treatments (Table 1), but the biomass of just the insect larvae was reduced by 70% by *Aglaoctenus* (Table 1). This suggests that the response of the non-insect invertebrates simply added enough noise to the total biomass estimates to render spider effects for total biomass non-significant.

Spiders significantly affected the composition of invertebrate morphospecies (ANOSIM, Global R = 0.079, $P = 0.007$), and tended to also affect the composition of higher

Table 1. Two-way randomized block ANOVAs summarizing the main and interactive effects of two spider species (*Aglaoctenus* and *Corinna*) on the invertebrate community, detrital decomposition and nitrogen uptake by bromeliads. Degrees of freedom for all *F*-tests = 1,33. The interaction tests for deviance from multiplicative effects of the spiders, achieved by either log transformation (most data) or by using a log link within a generalized linear model (data on richness and abundance of non-insect invertebrates, and biomass of total invertebrates, total predators, predatory larvae and filter feeders). Significant effects ($P < 0.05$) are in bold face.

| Response variable | <i>Aglaoctenus</i> | | <i>Corinna</i> | | <i>Aglaoctenus</i> × <i>Corinna</i> | |
|-------------------------|--------------------|-----------------|----------------|-----------------|-------------------------------------|-----------------|
| | <i>F</i> | <i>P</i> -value | <i>F</i> | <i>P</i> -value | <i>F</i> | <i>P</i> -value |
| Invertebrate richness | | | | | | |
| Total | 22.9 | < 0.0001 | 2.58 | 0.12 | 2.96 | 0.09 |
| Insect larvae | 29.1 | < 0.0001 | 1.39 | 0.25 | 5.20 | 0.03 |
| Other invertebrates | 0.056 | 0.81 | 0.89 | 0.35 | 0.045 | 0.83 |
| Invertebrate abundance | | | | | | |
| Total | 4.02 | 0.05 | 0.58 | 0.45 | 1.54 | 0.22 |
| Insect larvae | 14.95 | 0.0005 | 0.99 | 0.33 | 2.35 | 0.13 |
| Other invertebrates | 0.97 | 0.33 | 0.25 | 0.62 | 0.85 | 0.36 |
| Invertebrate biomass | | | | | | |
| Total | 0.34 | 0.57 | 0.33 | 0.57 | 2.90 | 0.10 |
| Insect larvae | 11.5 | 0.002 | 0.77 | 0.39 | 0.62 | 0.44 |
| Other invertebrates | 0.39 | 0.54 | 0.77 | 0.39 | 0.65 | 0.43 |
| Total predators | 1.94 | 0.17 | 0.83 | 0.37 | 0.001 | 0.97 |
| Total detritivores | 0.49 | 0.49 | 1.83 | 0.18 | 0.35 | 0.56 |
| Total filter feeders | 6.76 | 0.014 | 1.99 | 0.17 | 2.62 | 0.12 |
| Predatory larvae | 4.89 | 0.034 | 2.95 | 0.10 | 1.28 | 0.27 |
| Detritivore larvae | 6.18 | 0.018 | 3.69 | 0.06 | 0.52 | 0.47 |
| Detritus decomp. rate | 2.34 | 0.14 | 0.77 | 0.39 | 0.52 | 0.47 |
| ¹⁵ N atoms % | 1.56 | 0.22 | 1.11 | 0.30 | 0.36 | 0.55 |
| Total N concentration | 0.02 | 0.90 | 15.1 | < 0.001 | 1.54 | 0.22 |

taxonomic groups (families and higher: Global $R = 0.050$, $P = 0.067$). When only insect larvae were considered, effects of spider treatments on composition were even stronger (morphospecies: Global $R = 0.103$, $P = 0.001$; families: Global $R = 0.088$, $P = 0.011$). These differences in composition reflected significant differences between controls and either *Aglaoctenus*-only treatments or *Aglaoctenus* + *Corinna* treatments (morphospecies and higher taxa: pairwise Global $R \geq 0.1$, $P < 0.05$), rather than between controls and *Corinna*-only treatments (morphospecies and higher taxa: pairwise Global $R < 0.06$, $P > 0.15$). Indeed, *Aglaoctenus* significantly reduced the abundance of the five most common insect families, and tended to also reduce the abundance of the less-common insect families, Cecidomyiidae and Scirtidae (Fig. 3). *Corinna* significantly reduced only the most common insect family, Psychodidae, although it tended to reduce four out of the six next most common insect families. Detritivorous but not predacious chironomids had higher abundance in treatments with both spider species than predicted by multiplicative effects of the spiders (detritivorous chironomids: *Aglaoctenus* × *Corinna* $F_{1,33} = 11.4$, $P = 0.002$; predacious chironomids: *Aglaoctenus* × *Corinna* $F_{1,33} = 0.05$, $P = 0.82$, results not shown).

In contrast, non-insect invertebrates often showed neutral or positive responses to spiders. Oligochaetes represented about half of total abundances and total biomass, and were unaffected by either spider species, alone or in combination (Fig. 3). Ostracods accounted for 20% of total abundance but only 2% of total biomass, and increased sevenfold in the

presence of *Corinna* (Fig. 3). Predacious leeches (< 5% of total abundance or biomass) increased substantially in the presence of *Aglaoctenus* but decreased in the presence of *Corinna* (Fig. 3).

These changes in composition have implications for the trophic structure of the invertebrate community (Table 1, Fig. 4). Total predator and detritivore biomass were unaffected by spiders, primarily because reductions in insect components of both trophic levels (78% of predator biomass, 38% of detritivore biomass) by *Aglaoctenus* were compensated by increases in non-insect invertebrates such as predacious leeches and detritivorous ostracods (Table 1, Fig. 4). Filter feeder biomass was entirely composed of mosquito (*Culicidae*) larvae and so was significantly reduced by *Aglaoctenus* (Table 1, Fig. 4).

ECOSYSTEM RESPONSES TO SPIDER MANIPULATIONS

Spiders had no effect on either the rate of detrital breakdown or the uptake of ¹⁵N from submersed bean leaves (Table 1). Total nitrogen concentration in bromeliad leaves was significantly higher in the presence of *Corinna* but not *Aglaoctenus* (Table 1, Fig. 5).

Discussion

The results from this study show that terrestrial predators can have strong effects on an aquatic ecosystem, affecting not only organisms with cross-ecosystem life cycles but also

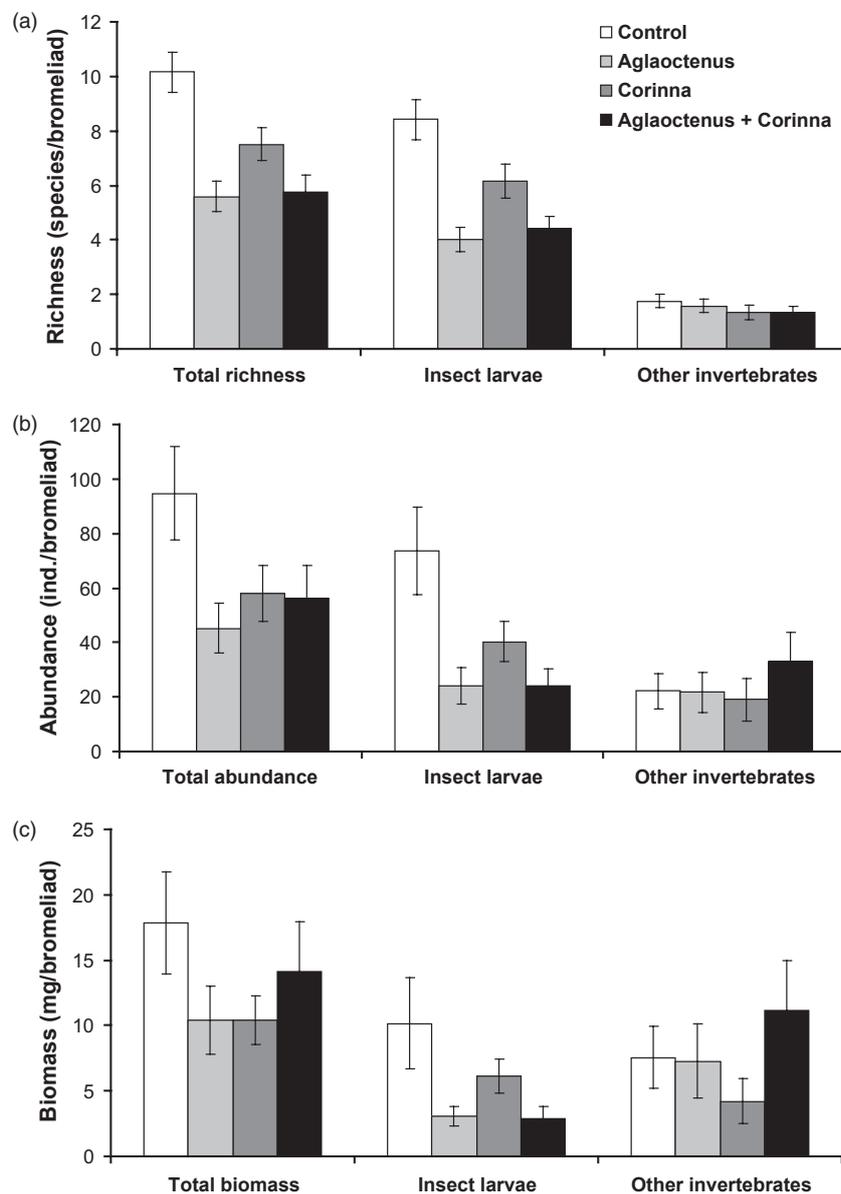


Fig. 2. Mean (a) richness, (b) abundance and (c) biomass of all invertebrates, insect larvae (cross-ecosystem life cycle), and other invertebrates (within-ecosystem life cycle). Error bars represent \pm SE.

indirectly affecting certain taxa with entirely aquatic life cycles. Spiders substantially reduced aquatic invertebrate diversity and abundance, and changed invertebrate composition from an insect-dominated food web to one dominated by non-insect invertebrates. We also found that such cross-ecosystem effects depend on the foraging mode of the terrestrial predators. However, contrary to our initial expectation, these negative effects of terrestrial predators on aquatic insects did not affect nitrogen release from detritus, and so there was no indirect effect of spiders on nitrogen uptake by bromeliads. Instead, one of the spider species appeared to directly increase nitrogen concentrations in bromeliad leaves. These results are some of the first to show that the strength of cross-ecosystem effects depends on features of both the aquatic food web (relative abundance of species with cross-ecosystem life cycles) and the terrestrial food web (predator identity).

The two spider species differed in their individual effects on the invertebrate community. *Aglaoctenus* and *Corinna* exhibit contrasting foraging modes. For example, *Aglaoctenus* constructs a large horizontal sheet web across the top of bromeliads, and is active both day and night. These two features ensure that the foraging of this species is extensive in both space and time, and maximize the likelihood of capturing prey. Moreover, terrestrial insects that detect the web prior to capture may avoid the bromeliad altogether, amplifying the negative effect of *Aglaoctenus* on insect oviposition. As a result, *Aglaoctenus* substantially reduced aquatic invertebrate richness and abundance of almost all insect families. In contrast, *Corinna* does not use web entrapment, and explores bromeliad surfaces only at night; during the day it is a sit-and-wait predator at the base of the bromeliads. *Corinna* had small and often non-significant effects on invertebrate communities. These results highlight the importance of pred-

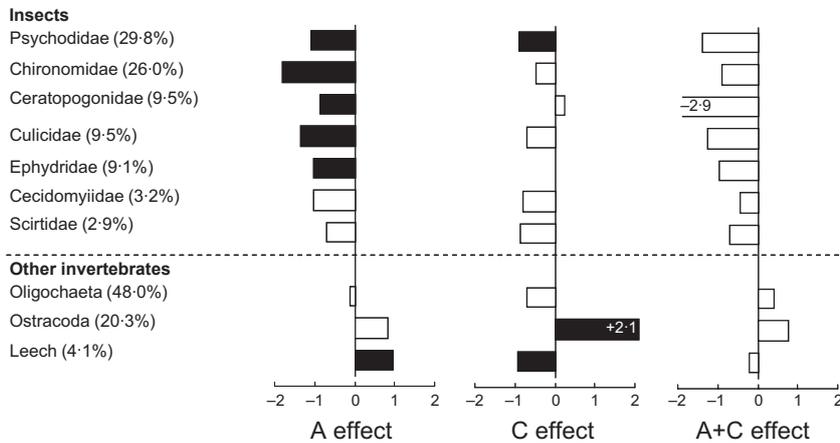


Fig. 3. Log-ratio effect magnitude [$\ln(N_{\text{predator}}/N_{\text{control}})$] of *Aglaoctenus* (A), *Corinna* (C) and both species (A + C) on abundance of common invertebrate taxa within bromeliads. Solid bars indicate significant effects, open bars non-significant effects, within generalized linear models (log-link function, Poisson or quasi-Poisson errors). Numbers in parentheses refer to the percent of total invertebrate abundance represented by each taxa.

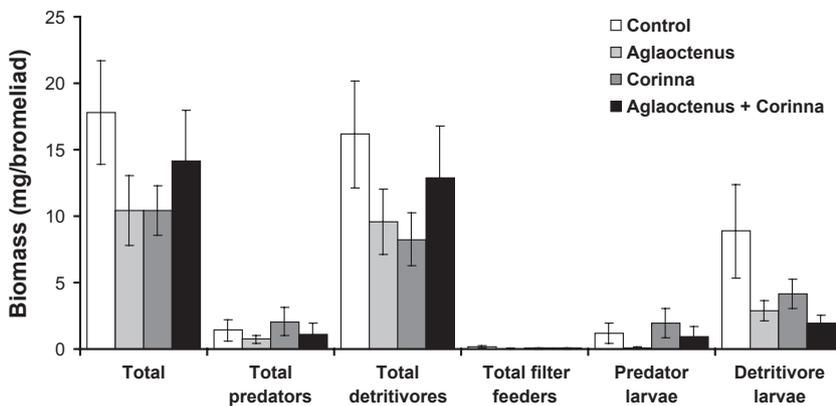


Fig. 4. Mean biomass of all invertebrates, all predators, all detritivores, all filter feeders, as well as predator larvae and detritivore larvae. Error bars represent \pm SE.

ator functional traits in community structure and food-web studies, and add to a growing consensus that species identity is an important determinant of community structure and ecosystem functioning.

Given that the predator species studied here forage in different parts of the bromeliads, at different times of day, and using different strategies (web entrapment vs. hunting), synergistic effects might be expected. However, the effects of spider co-occurrence on insects were either neutral or antagonistic ($>$ expected prey survival, as in the case of insect richness and detritivorous chironomid abundance). Neutral interactions are expected when one predator has a minor impact, as *Corinna* often does, but are trivial in terms of understanding interference between predators (Sih, Englund & Wooster 1998). Antagonistic effects of predators have previously been reported when similarity in foraging niches between predators results in high interspecific competition (Otto *et al.* 2008), or when one predator also preys upon other predators (intraguild predation). It is probable that indirect effects of intraguild predation explain the pattern of predator interference in our system. We observed a few cases of *Corinna* preying on *Aglaoctenus* in our experiment (*Aglaoctenus* was immediately replaced when lost to predation, so direct effects of intraguild predation were minimized). This risk of intraguild predation is likely responsible for the observed increase in *Aglaoctenus* foraging height

when it co-occurred with *Corinna* (Appendix S2). Higher foraging sites may be suboptimal in terms of prey capture, so this behavioural change may have reduced the efficiency of *Aglaoctenus*. Antagonistic effects arising directly from intraguild predation or interspecific competition have been frequently explored theoretically and empirically, but indirect trait-mediated mechanisms for such antagonistic effects have been largely ignored (see Huxel 2007).

The influence of spiders (e.g. *Aglaoctenus*) on different aquatic invertebrate taxa depended on whether the underlying population dynamics of the invertebrates were open (cross-ecosystem), represented by insects with aquatic larvae but terrestrial adults, or relatively closed (within-ecosystem), represented by non-insect invertebrates that are aquatic for all life stages. We predicted that spiders would reduce oviposition by terrestrial insect adults in bromeliads, but not reduce colonization of taxa with within-ecosystem life cycles (such taxa likely increased in numbers from the few individuals that escaped washing). When cross- and within-ecosystem taxa were analysed separately, we found that primarily cross-ecosystem taxa were reduced by spiders. Within-ecosystem taxa either increase variation in total invertebrate parameters (e.g. Oligochaeta) or are indirectly facilitated by one spider species (e.g. ostracods and, in the case of *Aglaoctenus*, leeches) with the result that overall invertebrate biomass is relatively insensitive to spiders. Other studies also highlight

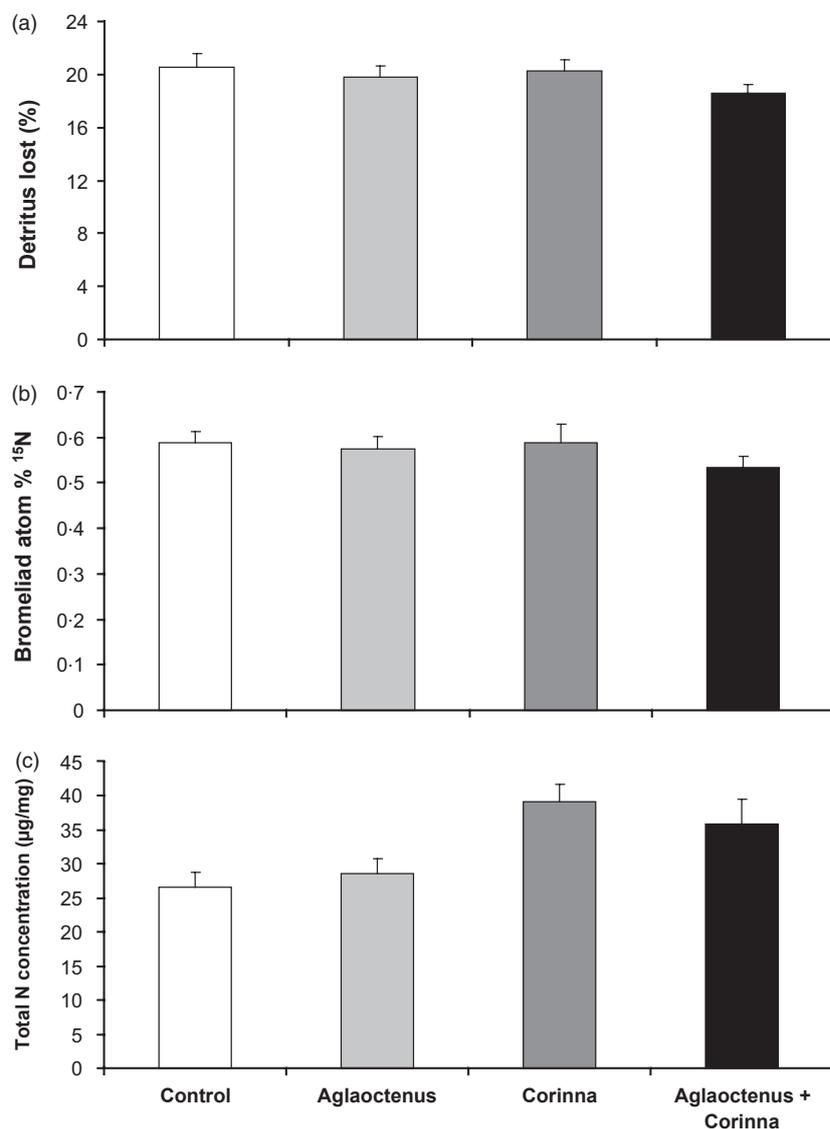


Fig. 5. Mean (a) decomposition rate, (b) ¹⁵N atoms percent of bromeliad leaves and (c) total nitrogen concentration (¹⁵N + ¹⁴N) in bromeliad tissues. Error bars represent \pm SE.

the role of species with cross-ecosystem dynamics in transmitting trophic effects between ecosystems (e.g. Knight *et al.* 2005; McCoy, Barfield & Holt 2009). However, our study additionally shows that terrestrial predators may mediate interactions between cross-ecosystem and within-ecosystem taxa. For example, reduction in detritivorous insects by spiders may have released other detritivorous taxa like ostracods from resource competition.

We expected spiders to decrease detritivore biomass and therefore detrital decomposition including the release of labelled nitrogen from detritus. This did not occur, presumably because spiders had no net effect on detritivore biomass despite marked effects on most insect taxa. The attenuation of terrestrial predator effects on the aquatic ecosystem can therefore be attributed in large part to the fact that not all detritivores had cross-ecosystem life cycles, and that compensation may have occurred between detritivores with within- vs. cross-ecosystem life cycles. In addition, the majority (98%) of detritivore biomass in our experiment was represented by collectors (taxa that sweep tiny debris particles into their

mouthparts) rather than the more efficient scrapers and shredders (taxa that use their mouthparts to chop or scour the surface of dead leaves). In bromeliads, shredders and scrapers are entirely cross-ecosystem taxa such as tipulids and scirtid beetle larvae. As the relative proportion of collectors vs. shredders and scrapers often changes with assembly time in phytotelmata (Richardson & Hull 2000), indirect effects of spiders on detrital decomposition may switch from neutral to negative over longer timeframes. Spiders had strong negative effects on filter feeding mosquitoes, suggesting that spiders may have strong indirect effects on other ecosystem processes (e.g. persistence of ciliates and rotifers).

Although spiders did not affect bromeliad nutrition via changes in detrital breakdown, the spider *Corinna* increased total nitrogen concentrations in bromeliad leaves. The probable mechanism here is spider-mediated inputs of nitrogen-rich debris (e.g. spider feces, prey carcasses) into the bromeliad phytotelmata, thus reflecting a second route by which allochthonous nitrogen enters the system (shown earlier for non-phytelm bromeliads: Romero *et al.* 2006). Spider feces

are mostly composed of guanine, a nitrogen-rich compound that can be absorbed by bromeliad leaves (Romero *et al.* 2006). *Corinna* is able to hunt some of the larger ground insects that invaded the enclosures (e.g. crickets), and so may be particularly effective in adding nitrogen-rich feces and carcasses. To date, the effects of predator-mediated nutrient inputs on aquatic ecosystems are largely unstudied (but see Marczak, Thompson & Richardson 2007) despite substantial interest in the converse process of trophic aquatic subsidies to terrestrial productivity (e.g. Maron *et al.* 2006). The effects of such allochthonous inputs on microbial growth and therefore nutrient cycling would be an interesting theme for future research.

Although the small size of bromeliads makes them particularly likely to show cross-ecosystem effects (see Introduction), the results of our study should not be viewed as specific to bromeliads. Many ecological communities consist of a mix of competing species both with and without complex life cycles that cross ecosystem boundaries, and compensatory effects between these two types of species are to be expected. For example, terrestrial predation on frogs could reduce tadpole densities in ponds and so indirectly affect one of their competitors: freshwater snails. Similarly, aquatic predation on dragonfly nymphs could reduce adult dragonflies and so indirectly affect one of their competitors: terrestrial spiders. We hope this study inspires more of these types of indirect cross-ecosystem effects to be explored.

In conclusion, this study stresses the importance of considering predator foraging strategies, as well as potential interference or synergism between foraging predators, when predicting their cross-ecosystem effects. In addition, this study demonstrates the importance of integrating trophic processes across ecosystem boundaries to understand variation in community structure and ecosystem processes. Our results provide empirical support for the prediction (Schreiber & Rudolf 2008) that organisms with cross-ecosystem life cycles will be those primarily responsible for connecting ecosystems in terms of fluxes of energy and matter. However, our results also highlight the need to consider not only direct consumption of cross-ecosystem taxa by predators, but also the indirect facilitation of within-ecosystem taxa by allochthonous predators.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Morphospecies.

Appendix S2. Habitat segregation amongst spiders.

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