Bidirectional trophic linkages couple canopy and understorey food webs

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Summary

1. Cross-system resource flux is a fundamental component of ecological systems. Allochthonous material flows generate trophic linkages between adjacent food webs, thereby affecting community structure and stability in recipient systems.

2. We investigated cross-habitat trophic linkages between canopy and understorey food webs in a terrestrial, wooded, ecosystem in South Florida, USA. The focal community consisted of three species of *Anolis* lizards and their prey. We described interspecific differences among *Anolis* species in the strength and routing of these cross-habitat flows using stable isotope analysis, stomach content analysis and habitat use data.

3. All three *Anolis* species in this study consumed different prey and occupied vertically distinct arboreal habitats. Despite these differences, carbon isotope and stomach content analysis revealed strong integration with understorey and canopy food webs for all *Anolis* species. Modes of resource flux contributing to the observed cross-habitat trophic linkages included prey movement and the gravity-driven transport of detritus.

4. Our study shows that terrestrial systems are linked by considerable bidirectional cross-system resource flux. Our results also suggest that considering species-specific interactions between predator and prey is necessary to fully understand the diversity of material and energy flows between spatially separated habitats.

Key-words: allochthonous, *Anolis*, cross-habitat linkages, food webs, reciprocal linkage, resource subsidy, terrestrial ecosystem

Introduction

Ecological systems are often characterized by cross-system linkages by which considerable quantities of materials and energy flow across system boundaries (Polis & Hurd 1995; Nakano & Murakami 2001; Cole *et al.* 2011). These allochthonous fluxes, in the form of organisms, detritus or nutrients, can have strong effects on ecological structure and dynamics in recipient systems (Polis, Anderson & Holt 1997). As a result, understanding the causes and consequences of allochthonous flux has emerged as an important area of empirical and theoretical investigation (Huxel & McCann 1998; Polis, Power & Huxel 2004; McCann 2012).

Many studies focus on allochthonous flows that are driven by physical forces such as gravity and currents; movements that are largely unidirectional (e.g. Spiller *et al.* 2010; Cole *et al.* 2011). Animal movement (migration, foraging

movements or dispersal events) is another obvious vector of material transport across system boundaries (Sanchez-Pinero & Polis 2000; Nakano & Murakami 2001; Moore *et al.* 2007). Physically driven flows and animal movements can vary in direction culminating in diverse reciprocal linkages among neighbouring systems (Nakano & Murakami 2001; Vadeboncoeur, Vander Zanden & Lodge 2002; Raffaelli *et al.* 2003; Vander Zanden & Gratton 2011).

The investigation of cross-system flux has largely been an aquatic endeavour, with studies focusing on fluxes within aquatic ecosystems or between aquatic and terrestrial systems (e.g. Polis, Power & Huxel 2004; Marczak, Thompson & Richardson 2007); fewer attempts have been made to explicitly incorporate flux among terrestrial habitats using a food web approach (but see Magnusson *et al.* 2001; Pringle & Fox-Dobbs 2008). In forested systems, much like aquatic systems, the majority of material flux is driven by prevailing physical forces such as gravity, which tends to generate unidirectional flows of material such as detritus from

canopy to understorey habitats (Frost & Hunter 2004; Moore *et al.* 2004; Pringle & Fox-Dobbs 2008). While examples of understorey to canopy flows are known (e.g. Yang 2004), empirical evidence for bidirectional linkages in terrestrial ecosystems is largely absent from food web literature (e.g. Polis, Power & Huxel 2004).

Here, we investigated cross-habitat trophic linkages between canopy and understorey food webs in a wooded park in South Florida. The focal study system was a community of small, arboreal, vertebrate predators (*Anolis* lizards) and their prey. Our goal was to determine whether and how resources move between understorey and canopy habitats. Secondarily, we sought to determine whether different *Anolis* species integrate resource pools differently. We hypothesized that because *Anolis* species occupy distinct, vertically partitioned microhabitats (Schoener 1968), interspecific variation in the degree of integration of allochthonous resources would vary according to distance from donor habitats (Baxter, Fausch & Saunders 2005; Paetzold, Lee & Post 2008). Specifically, we expected the incorporation of understorey material to be inversely related to perch height; that is, canopy-dwelling *Anolis* would consume small amounts of understorey resources relative to ground and trunk-perching *Anolis*.

Materials and methods

STUDY SYSTEM

Our study took place in a 14-ha wooded park on the campus of Florida International University in North Miami, Florida. This ecosystem is characterized by isolated strangler fig trees (*Ficus aurea*; hereafter *Ficus*) with an extensive understorey of St. Augustine grass (*Stenotaphrum secundatum*; hereafter *Stenotaphrum*). The dominant vertebrate predators in our study system are three species of *Anolis* lizards, as well as several species of small passerine birds. *Anolis* vertically partition arboreal habitats, which can be roughly categorized into ground, trunk and canopy habitats (Schoener 1968). Brown anoles (*Anolis sagrei*) typically perch on the lowest portions of trees and forage in adjacent ground habitats. Bark anoles (*Anolis distichus*) utilize the vertical trunk and lower, large diameter branches of mature trees. Knight anoles (*A. equestris*) inhabit tree canopies including the outer branches and limbs. Most *Anolis* lizards exhibit generalist diets composed of invertebrates with a minor component of fruit, yet differences in diet do exist among species (Schoener 1968; Lister 1976). These differences may be attributable to different prey communities that each species encounters in their respective microhabitat, variation in body (gape) size or diet specialization at the species level (Schoener 1968). One of the species in our focal community, *A. distichus*, is a known ant specialist; however, the diets of *A. sagrei* and *A. equestris* are more general, consisting primarily of invertebrates, and possibly small vertebrates.

SAMPLING

Anolis were hand-captured during daylight hours from the canopy and trunks of *Ficus* trees between October 2010 and July 2011. The microhabitat of each lizard was recorded upon capture (perch height, perch width). Our capture methods permitted sampling of lizards up to 4 m above the ground. Samples were restricted to sexually mature individuals. Stomach contents were removed by

dissection and identified to the lowest taxonomic level (for most items, this resolution was to Order or Family). The length (*L*) and width (*W*) of each prey item were measured and prey volume (*V*) estimated following Magnusson *et al.* (2003):

$$V = \frac{4}{3}\pi\left(\frac{L}{2}\right)\left(\frac{W}{2}\right)^2 \qquad \text{eqn 1}$$

Diet overlap between *Anolis* species was analysed using two different approaches. First, we generated a population-level estimate of diet overlap using Schoener's (1968) proportional similarity index (*D*). Schoener's index uses diet data, pooled by group, to estimate the proportional importance of each prey taxa to generate an estimate of overlap between two species,

$$D = 1 - 0 \cdot 5 \sum |p_{xi} - p_{yi}| \qquad \text{eqn 2}$$

where p_{xi} and p_{yi} are the proportions of prey taxa *i* in the diet of predator species *x* and *y*. A value of 1 indicates complete overlap and 0 indicates no overlap. Values >0·6 typically are used to infer a significant overlap in diet. Proportions (p_{xi} and p_{yi}) were calculated from the pooled diets of all individuals within a species. Thus, this metric provides a population-level analysis of diet similarity between *Anolis* species.

Our second approach also used Schoener's index, but unlike a population-level analysis in which all diet data are averaged within a species, we estimated diet overlap by calculating *D* for 1000 randomly selected pairs of individuals from the focal species (e.g. comparing *A. distichus* with *A. equestris*). This individual-level analysis provides bootstrapped confidence intervals for diet similarity (*D*) among individuals from two species. As with population-level analyses, *D* = 0·6 was used as the cut-off to assess significant diet overlap. We bootstrapped *D* for all pairwise species comparisons to estimate diet overlap among all three species.

ISOTOPE ANALYSIS

The distal 1·5 cm of *Anolis* tails was clipped, dried to constant mass and homogenized. Whole animals were used to analyse prey taxa. Invertebrate prey were collected from around tree bases, trunks and canopies using sweep nets, aspirators and forceps. Individuals of each prey taxa were pooled for each sample. If enough material was available, pooled samples were analysed in duplicate to assess variability. *Ficus* leaves were sampled from several trees, and *Stenotaphrum* were collected from areas around the base of *Ficus* trees.

To assess flow of material and energy between different habitats, we capitalized on different photosynthetic pathways present in our primary producers to distinguish between carbon fixed by *Stenotaphrum* (C_4) in the understorey and *Ficus* (C_3) in the canopy. In our wooded ecosystem, the terrestrial, grass-based food web is distinguished by an enriched signature in carbon isotopes that results from the C_4 metabolic pathway of *Stenotaphrum*. The arboreal source of carbon in our case, *Ficus*, is distinguished by a relatively depleted isotope signature characteristic of the C_3 metabolic pathway (see Results). To approximate the importance of *Ficus*- and *Stenotaphrum*-based production fixation in the diets of *Anolis* and their prey, we employed IsoError mixing models (Phillips & Gregg 2001) and chose the two-end members to be the two dominant primary producers in our ecosystem, *Stenotaphrum* and *Ficus*. Mixing models estimate the contribution of two or more dietary sources to the composition of consumer tissues from one or more elemental isotopes. Because we were interested in the relative ratio of C_3 to C_4 carbon in consumer tissues, we restricted our mixing model analysis to $\delta^{13}C$. Our employment of a two-end member model reflects the simple structure of the producer community in our ecosystem. Although other species of primary producers are present in the study area, the understorey is extensively

Stenotaphrum, a ubiquitous ground cover species in S. Florida. In addition, we restricted our consumer sampling to the dominant tree in our study site, *Ficus aurea*, to isolate these two isotopically distinct producers as the primary basal resources for this study.

Isotope samples were dried to constant mass at 60 °C and homogenized with mortar and pestle. Carbon (%C) and nitrogen (%N) content and stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) were estimated using a Shimadzu C/N analyzer. Stable isotope values are reported in the δ notation where $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$ and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. We focused on ratios of $\delta^{15}N$ and $\delta^{13}C$ because each reveals a distinct aspect of the consumer's long-term trophic niche. $\delta^{15}N$ exhibits stepwise enrichment with trophic transfers and can thus be used to estimate an organism's trophic position relative to that of others in a food web. $\delta^{13}C$ varies substantially among primary producers with different photosynthetic pathways (e.g. C_3 vs. C_4 plants), but changes relatively little with trophic transfers, and can thus be used to infer sources of dietary carbon (Layman *et al.* 2012).

We corrected data for isotope signature shifts associated with diet-to-tissue discrimination factors. To correct our $\delta^{13}C$ isotope data for trophic shifts (a consequence of fractionation with each trophic transfer), we used a prey-specific approach to calculate a trophic correction factor (TC). This correction factor was then added to the raw $\delta^{13}C$ values to account for trophic shifts before entered into the mixing models. To estimate TC, we used *Anolis* diet data and published estimates for $\delta^{13}C$ fractionation constants for prey and predators. We assumed a 0·5 % fractionation constant for invertebrates (Spence & Rosenheim 2005) and a 1·35 % constant for our lizard predators (Warne, Gilman & Wolf 2010). To estimate TC, the following equation was employed:

$$TC = \left[\sum(P_i F_i T_i)\right] + F_p \qquad \text{eqn 3}$$

where P_i is the proportion, by volume, of prey taxa i in the stomach contents of each lizard species, F_i is taxa-specific trophic fractionation of prey, and T_i is the estimated number of trophic transfers between primary producer and prey (herbivores = 1, omnivores/detritivores = 1·5 and predators = 2). F_p is the trophic fractionation of the predator (1·35%), *Anolis* in this case.

STATISTICAL ANALYSIS

Due to the non-normality of perch height data, we used sequential pairwise Mann–Whitney tests to examine interspecific variation in microhabitat use. Differences among *Anolis* species in coupling strength were evaluated with pairwise t-tests using summary statistics (mean, variance) calculated from IsoError mixing model outputs (Phillips & Gregg 2001). All results are evaluated at $\alpha = 0.05$. Analyses were performed in JMP (Version 9. SAS Institute Inc., Cary, NC, USA) and R v2.14 (R Development Core Team, Vienna, Austria, 2012).

Results

HABITAT USE

Habitat use in *Anolis* was primarily arboreal. Only six individuals, all *A. sagrei*, were observed on the ground. *Anolis equestris* showed significantly higher perches than either *A. distichus* or *A. sagrei* ($\chi^2 = 13.2$, $P < 0.001$; $\chi^2 = 18.1$, $P < 0.001$; Table 1). *Anolis distichus* showed significantly higher perches than *A. sagrei* ($\chi^2 = 5.0$, $P = 0.026$; Table 1). For *A. distichus* and *A. equestris*, estimates of perch height are likely underestimates as sighting and capturing individuals in the canopy is difficult. Despite this limitation, the distribution of the different species in our study matches other studies showing that sympatric *Anolis* species predictably partition perch habitats vertically (Schoener 1968).

STOMACH CONTENTS

We examined stomach contents for 24 *A. distichus*, 32 *A. sagrei* and 21 *A. equestris*. Only one individual, an *A. equestris*, had an empty stomach. All 1056 prey items were either invertebrates or fruit, encompassing 57 taxa, four Phyla and six Classes. Prey included primary producers, herbivores, predators and detritivores (see Table S1, Supporting Information). Also, each *Anolis* species consumed prey found in arboreal and understorey habitats (Fig. 1). Diets differed significantly between each pair of *Anolis* species. Schoener's similarity index showed low degrees of overlap between species (*A. equestris* and *A. distichus*, $D = 0.09$; *A. equestris* and *A. sagrei*, $D = 0.18$; and *A. sagrei* and *A. distichus*, $D = 0.39$). The bootstrapped estimates of diet similarity also showed low levels of overlap for each species [mean (95% CI) for each species-wise comparison: *A. equestris* and *A. distichus*, 0·03 (0–0·59); *A. equestris* and *A. sagrei*, 0·04 (0–0·48); and *A. sagrei* and *A. distichus*, 0·07, (0–0·64)]. Distributions of bootstrapped estimates were extremely right skewed for each comparison with a majority of values at zero. Fewer than 5% of bootstrapped similarity indices were >0·6 for any species comparison. Therefore, all pairwise proportional similarity values were significantly <0·6 ($P < 0.05$) further supporting interspecific differences in *Anolis* diets in our study system.

Some of the distinct differences in diet were that *A. equestris* primarily consumed *Ficus* fruits, *Euphoria* beetles and *Schistocerca* grasshoppers. *Anolis sagrei* consumed

Table 1. Summary of microhabitat and isotope data for each *Anolis* species. Microhabitat use is displayed as median with first and third quantiles

| Species | Perch height (cm) | | | $\delta^{15}N$ | $\delta^{13}C$ | |
	Median	25%	75%	Mean ± SD	Mean ± SD	Mean*
Anolis equestris	306	190	360	7·4 ± 0·77	−22·2 ± 1·86	−24·5
Anolis distichus	71	42	111	7·7 ± 0·70	−24·3 ± 1·84	−26·3
Anolis sagrei	45	0	103	7·9 ± 0·74	−22·6 ± 1·80	−25·4

*Values adjusted for trophic shift using species-specific trophic correction values.
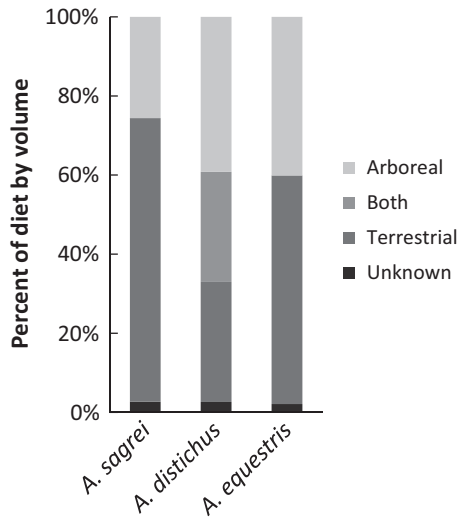
Fig. 1. Stomach contents by volume for each *Anolis* species categorized by the primary habitat of each prey taxa. In several cases, prey taxa (*Camponutus* and *Pheidole* ants) were observed using both arboreal and terrestrial habitats and were categorized as 'Both'. Prey taxa for which habitat use data were unknown include several species of small snails, several unidentified Coleoptera, an unidentified spider, chironomids and several species of ant. All of these unknown prey taxa were minor components of diet by volume (each unidentified taxa was <3% of total volume for each *Anolis* species).

Parcoblattta roaches, Lycaenid seed bugs and Lepidopteran larvae. And, as expected, *A. distichus* specialized on ants. Although 14 different ant species were recovered from bark anole stomachs, only *Camponotus* sp. ants comprised >10% of diet by volume. While *A. distichus* exhibit what looks to be a clear specialization on ants, other important diet taxa include Lycaenid seed bugs and Lepidopteran larvae.

ISOTOPE ANALYSIS AND MODEL RESULTS

Carbon isotope values for *Ficus* leaves were depleted ($\delta^{13}C = -30 \cdot 06$, SD = 0·08) relative to *Stenotaphrum* ($\delta^{13}C = -13 \cdot 18$, SD = 1·14; Fig. 2). Among invertebrate prey, the majority of taxa analysed showed relatively depleted $\delta^{13}C$ signatures, indicative of a heavy reliance on arboreal-derived carbon (see Table S2, Supporting information). Few invertebrates showed carbon signatures that suggested strong integration with the grass-based food web (Fig. 3). Among these, fire ants (*Solanopsis invicta*), dark flower scarabs (*Euphoria sepulcralis*), carpenter ants (*Camponotus* sp.), long-legged flies (*Condostylus* sp.), sheet-web spiders (*Neriene* sp.), citrus root weevils (*Pachnaleus litus*), American grasshoppers (*Schistocerca americana*) and crickets (*Gryllus* sp.) were the only prey that showed $\delta^{13}C$ values that suggested >25% integration with the *Stenotaphrum*-based food web (see Table S2, Supporting information).

Using the IsoError mixing model to quantify the contribution of *Stenotaphrum* and *Ficus* based carbon, we show that the mean proportion of grass-based food items in the diet was highest for *A. equestris*, followed by *A. sagrei* and
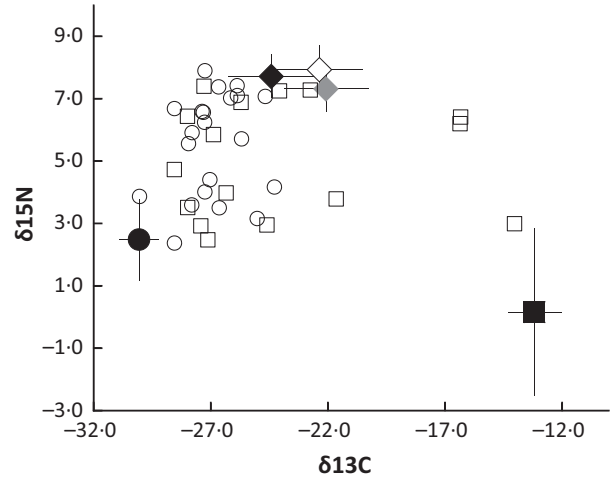

Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ bi-plot of isotope values from organisms constituting the wooded park ecosystem. Organisms are labelled as follows: ♦ = *Anolis distichus*, ◆ = *A. sagrei*, ◇ = *A. equestris*, ● = *Ficus aurea*, ■ = *Stenotaphrum secundatum*, ○ = arboreal invertebrates, □ = terrestrial invertebrates. Primary producers and *Anolis* are displayed as means (±SD). Invertebrate values are pooled samples of multiple individuals for each prey taxa. Right panel: Results of IsoError mixing models showing mean proportions (±SD) of grass-based carbon in *Anolis* tissues.

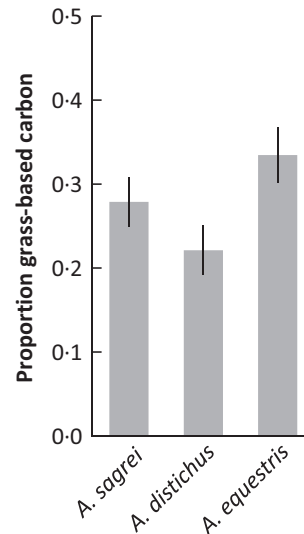**Fig. 3.** Results of IsoError mixing models showing mean proportions (±SD) of grass-based carbon in *Anolis* tissues.

A. distichus (mean ± SD: 0·33 ± 0·03, 0·28 ± 0·03, and 0·22 ± 0·03, respectively; Fig. 3). However, there were no significant differences among *Anolis* species in the proportion of grass-based carbon in their tissues (pairwise Z-tests, *P* > 0·05 for all comparisons).

Discussion

Trophic linkages generated by the movement of energy and material across habitat boundaries are recognized as a fundamental component of food webs and ecological

systems (Polis, Power & Huxel 2004). In this study, we illustrate multiple routes of cross-habitat resource flux in a wooded ecosystem. As predicted, *Anolis* species differentially integrated carbon from understorey and canopy food webs. However, the degree of integration did not appear to depend on habitat variables such as distance from the resource (i.e. perch height). Rather the degree of integration was presumably determined by species-specific interactions between *Anolis* lizards, arthropod prey and different primary producers. Combined, the interactions between each *Anolis* species and their prey generate diverse and distinct trophic linkages that result from the bidirectional flux of material between canopy and understorey habitats (Fig. 4). These results suggest that considering species-specific interactions between predator and prey is necessary to fully understand the diversity of energy flow pathways between spatially distinct habitats.

The isotope data are consistent with our prediction of two distinct sources of energy in our ecosystem, one based on understorey grass (*Stenotaphrum*) and the other based on canopy-derived resources (*Ficus*: Figs 2 and 4). In many cases, we found that the spatial distribution of organisms specializing on each resource was not always correlated with the location in which the primary resources were based. For example, consumers deriving a high proportion of their energy from *Ficus* could be found in understorey habitats. The disjunction between the location of consumers and their resource base evinces a significant amount of cross-habitat energy and material flow in this ecosystem.

We found several cases of strong trophic linkages that were mediated by the consumption of insect prey that moved vertically, from understorey to canopy habitats. One of the most significant vectors of understorey to canopy flux was *Schistocerca americana*, a large grasshopper that feeds in the understorey and migrates to tree canopies at night to roost (Kuitert & Connin 1952). This roosting behaviour generates an apparently important trophic linkage when these mobile prey are consumed by the canopy specialist lizard *A. equestris*. Another strong linkage was created by the movement of the beetle, *Euphoria sepulcralis*, which feeds in arboreal and terrestrial vegetation as an adult but feeds on grass roots (presumably *Stenotaphrum*) during the larval phase. Movements of foraging carpenter ants (*Camponotus* sp.) between understorey and canopy habitats (Koptur 1992) also generate allochthonous flows when consumed by *A. distichus*, a trunk specialist. The other major flux of allochthonous material apparent in this system is the more passive, gravity-driven flow of detritus from the canopy to the understorey. This detritus fall supports a diverse community of terrestrial arthropods including cockroaches (*Parcoblatta* sp.), darkling beetles (*Alphitobius laevigatus*), isopods (*Armadillium* sp.) and earwigs (*Euborellia annulipes*). These prey are consumed by *A. sagrei*, which use *Ficus* trees to perch, but forage in the understorey (Lister 1976; Adolph & Roughgarden 1983).

These trophic linkages illustrate several features of wooded ecosystems that may be relevant for other ecosystems. First,
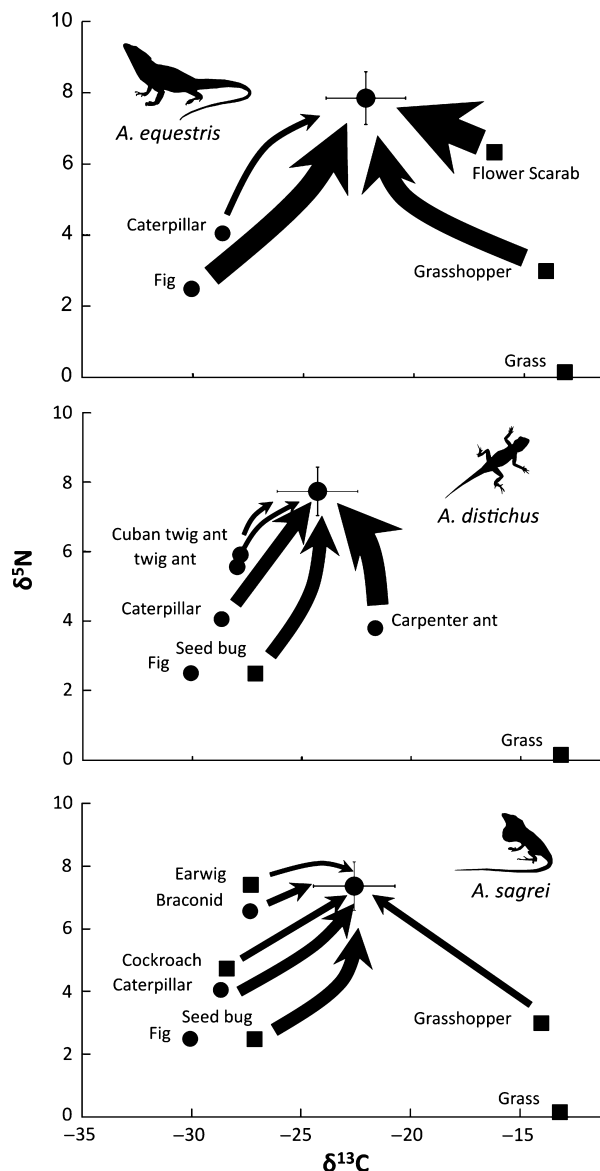

Fig. 4. Major energetic pathways leading to bark anoles, brown anoles and knight anoles. Positions of prey items and lizard predators on each biplot were determined from stable isotope analysis, and raw values are displayed here. The width of arrows is proportional to the volume in stomach contents. Only prey representing more than 5% of the total volume for each *Anolis* species are plotted. For each prey taxa, symbols designate its primary habitat: ■ = terrestrial, ● = arboreal.

prey movement and detritus falls generate extensive habitat coupling. Second, distinct predator–prey interactions can result in unique trophic linkages between canopy and understorey habitats. Third, the magnitude of habitat coupling does not appear to be correlated with distance from the location of resource production. Fourth, terrestrial ecosystems, much like benthic-pelagic flux in aquatic ecosystems, can exhibit extensive bidirectional material flows.

Each of the allochthonous flows in our ecosystem is generated by the unique ecologies of species, that is, habitat use and the diet of predators and prey. These results are relevant for understanding the potential effects of species

diversity on food web structure and ecological stability (Rooney & McCann 2011) because in concert, these species-specific interactions generate multiple trophic linkages that result in the coupling of adjacent food webs. We believe that multiple linkages are probably quite common among spatially distinct systems, yet several approaches to illustrating the biological vectors of allochthonous flux might mask important underlying diversity in trophic linkages. For example, organisms are often lumped into groups of functionally and/or taxonomically similar species such as 'seabirds', or 'waterbirds' (e.g. Sanchez-Pinero & Polis 2000). Another common approach is to focus on individual species, while not examining the larger community (e.g. examining a single species of salmonid where several may coexist; Holtgrieve & Schindler 2011). The results we present here suggest that the taxonomic scope and resolution used when studying food web linkages, whether lumping organisms into mixed taxa groups or taking a narrow perspective on community level analysis, may mask important diversity in trophic interactions.

Acknowledgements

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Supporting Information

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

Table S1. Stomach contents of *Anolis* lizards.

Table S2. Summary of habitat use and isotope data for primary producers and prey organisms in our study system.