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Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs

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Abstract. Recent advances in food-web ecology highlight that most real food webs (1) represent an interplay between producer- and detritus-based webs and (2) are governed by consumers which are rampant omnivores; feeding on varied prey across trophic levels and resource channels. A possible avenue to unify these advances comes from models demonstrating that predators feeding on distinctly different channels may stabilize food webs. Empirical studies suggest many consumers engage in such behavior by feeding on prey items from both living-autotroph (green) and detritus-based (brown) webs, what we term "multichannel feeding," yet we know little about how common such feeding is across systems and trophic levels, or its effect on system stability. Considering 23 empirical webs, we find that multichannel feeding is equally common across terrestrial, freshwater, and marine systems, with >50% of consumers classified as multichannel consumers. Multichannel feeding occurred most often at the first consumer level, indicating that most taxa at the herbivore/detritivore level are more aptly described as multichannel consumers, and that such feeding is not restricted to predators. We next developed a simple four-compartment nutrient cycling model for consumers eating both autotrophs and detritus with separate parameter sets to represent aquatic vs. terrestrial ecosystems. Modeling results showed that, across terrestrial and aquatic ecosystems, multichannel feeding is stabilizing at low attack rates on autotrophs or when attack rates are asymmetric (moderate on autotrophs while low on detritus), but destabilizing at high attack rates on autotrophs, compared to herbivory- or detritivory-only models. The set of conditions with stable webs with multichannel consumers is narrower, however, for aquatic systems, suggesting that multichannel feeding may generally be more stabilizing in terrestrial systems. Together, our results demonstrate that multichannel feeding is common across ecosystems and may be a stabilizing force in real webs that have consumers with low or asymmetric attack rates.

Key words: attack rates; brown world; detritus; food webs; green world; multichannel; stability.

INTRODUCTION

Reconciling the complexity of food webs with their apparent stability over time, and in response to disturbance, has driven a large body of research in theoretical community ecology (Pimm 1982, Polis 1998). Much of this work has used models of (living-autotroph-based) grazing chains and webs (the "green world"; Hairston et al. 1960) that include strong top-down control (Pimm 1982, McCann and Hastings 1997). Such models have found that many factors common in natural systems can destabilize systems (Holt and Lawton 1994, Tanabe and Namba 2005). For example, feeding on multiple prey items (omnivory) in its many forms can be highly destabilizing (Pimm and Lawton 1978, Pimm 1979, Holt and Lawton 1994). In contrast, work focusing on detrital or "brown world" chains, often using aspects of donor-control (sensu Pimm 1982), shows comparatively consistent stability (Moore et al. 2004, Blanchard et al. 2011). Models linking green and brown webs have traditionally done so by incorporating nutrient cycling, where dead materials from the green chain transfer to a detrital pool, which mineralizes into nutrients that limit the basal autotrophs of the green chain (DeAngelis et al. 1989, DeAngelis 1992). Empirical food-web studies, however, underscore that nutrient cycling is not the only connection between grazing and detrital webs.

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Multichannel (Marples 1966, Odum 1969, Moore and Hunt 1988, Polis and Strong 1996) or multichain (Vadeboncoeur et al. 2005) feeding, where consumers link distinct resource channels, has been noted, if not described as such, for some time (Lindeman 1942, Swift et al. 1979, Azam et al. 1983, Coleman et al. 1983, Odum and Biever 1984, Coleman 1985, Hairston and Hairston 1993). Many omnivores are actually multichannel consumers that link grazing and detrital channels, including species such as scorpions (Polis and McCormick 1987), predaceous nematodes and mesostigmatid mites (Moore and Hunt 1988), wolf spiders (Fagan 1997), salamanders (Whitaker and Rubin 1971), gizzard shad (Nowlin et al. 2008), and rocky littoral fish species (Pinnegar and Polunin 2000). In freshwater systems, multichannel consumers that link mainly autotroph-based pelagic webs with highly detritus-based benthic webs appear common and may drive trophic cascades (Vadeboncoeur et al. 2002, 2005). Similar links between grazing- and detrital-based chains have been found in terrestrial soils (Hunt et al. 1987), crop systems (Settle et al. 1996), and forests (Miyashita et al. 2003).

Given its prevalence in many systems, understanding how multichannel feeding affects food-web stability, especially in comparison to the more commonly used models that have only grazing or detrital chains, may aid in explaining how complex natural food webs return to similar conditions following disturbance. Multichannel consumers that link grazing and detrital resource channels may be especially important because they provide a unique way for detrital biomass to reenter and affect the grazing web (Polis and Strong 1996). Such cross-chain feeding allows consumers to access detritus directly (by eating detritus) and/or indirectly (by eating lower consumers that are themselves detritivores or multichannel consumers). This key link between predation and the resource pool that is critical to nutrient cycling may complicate the effect of multichannel feeding on food-web stability, given differences in the dynamic properties of the different channels. Models of grazing food chains typically start with a primary producer or consumer with density-dependent growth and death (May 1973, Pimm 1982). Models of detrital chains start with dead organic material with donor-controlled inputs (Pimm 1982, Polis and Strong 1996, Moore et al. 2012) from allochthonous or autochthonous sources and density-dependent loss via consumption (Moore et al. 1993). While detritus is often stabilizing when included in simple food-web models (Neutel et al. 1994, Moore et al. 2004), its role may change when predator dynamics with top-down control are linked to more than one resource (Pimm 1979, Holt and Lawton 1994, Post et al. 2000).

Here, we examine the prevalence of multichannel feeding in real systems, and its role in the stability of modeled food webs. First, we examine whether multichannel feeding is prevalent within and across real systems, using 23 empirical food webs. Theoretical studies make mixed predictions regarding the prevalence of multichannel feeding, particularly whether it is more common at higher vs. lower trophic levels. Recent theory suggests that predators linking distinctly different energy sources (i.e., fast and slow channels) should occur at higher trophic levels in food webs (Rooney et al. 2006) and should derive their energy equally across energy sources; this is supported by numerous empirical studies showing carnivores that feed across grazing and detrital energy channels (Whitaker and Rubin 1971, Polis and McCormick 1987, Fagan 1997, Vadeboncoeur et al. 2005). However, earlier work suggested that distinct energy channels based on living autotroph vs. detrital resources basically break down after the first (basal) trophic level (Odum and Biever 1984, Moore et al. 1988, Moore and Hunt 1988) as taxa consume both living autotrophs and detritus. The sparse results to date are equivocal: in freshwater systems, the diets of pelagic fish vary strongly by species, with some species deriving less than 10% of their diet from alternative energy channels and others consuming considerable amounts of benthic diet items (Vander Zanden and Vadeboncoeur 2002). The empirical food-web data used here, however, allow tests of the commonness or rarity of multichannel feeding and its general trophic position in food webs across a wide array of ecosystem types. Next, we develop a simple food-web model with nutrient recycling to assess whether multichannel feeding is a stabilizing or destabilizing component of food webs, in comparison with grazing-only or detrital-only models.

PREVALENCE OF MULTICHANNEL FEEDING IN REAL FOOD WEBS

Methods

We first examined data from real food webs to quantify the prevalence and variation of multichannel feeding across ecosystems and trophic levels. Described food webs are inherently simplified versions of all actual feeding relationships in a system, and using such food webs to look for actual ecological trends requires care (Martinez 1991, Dunne et al. 2004). Here, we attempted to control for possible bias by using the best data available and choosing webs that have well-resolved feeding relationships derived from robust sampling (Martinez et al. 1999); this yielded 23 webs based on observation and gut content analysis. Total taxa per web ranged from 21 to 200 and all webs included both detrital and living autotroph taxa at the base. All webs gave links between predators and prey (binary link data), while 13 also reported estimates of the flows occurring between each resource and its consumers. We classified webs as terrestrial, freshwater, emergent vegetation (wetlands and mangroves), or marine based on their taxa. A complete list of the webs used, and their sources, is given in Appendix A.

We estimated the trophic level and diet specificity for each consumer taxon in each web. We computed the trophic level according to the flow information (Levine 1980), when present. For binary food webs, we began by assuming that each of the X consumers of a given resource receives the same fraction ε/X of the flow originating from the resource (where ε is the efficiency of transformation) and that all plants received an equal input from detritus. We constructed from an adjacency matrix ($\mathbf{A}$) $\mathbf{A}'$ such that each row sums to the efficiency of transformation (ε). We added one column of $1 - \varepsilon$ for all species except top predators, which were given a value of 1. The eigenvector associated with the dominant eigenvalue of the resulting matrix measures the "PageRank" (Allesina and Pascual 2009): each coefficient can be interpreted as the total amount flowing through the corresponding node. With this information we then computed the trophic level as for the flow-based food webs. For the figures reported here, we chose $\varepsilon = 0.15$, but our analysis is not sensitive to the particular value chosen for the efficiency of transformation (Appendix B). For living autotrophs and detritus we assigned a trophic level of 1. We then calculated the proportion of diet derived from detritus vs. living autotrophs for each consumer on a scale of 0 to 1, with 0 representing a diet derived solely from detrital-based sources and 1 representing a completely green-web diet; this metric included diet flows from feeding directly on living autotrophs or detritus as well as diet flows from feeding on consumers that themselves feed on both channels. We operationally defined multichannel consumers as taxa at or above the second trophic level with diets falling between 0.1 and 0.9 on this scale (results are not sensitive to this criterion, Appendix B). All other taxa were then defined as detritus, living plants, or autotroph or detritus specialists depending on trophic level and diet. We then determined the percentage of taxa in each category for each web, and tested for whether the prevalence of multichannel consumers varied by system type (terrestrial, freshwater, marine, emergent vegetation) via a one-way ANOVA.

We then tested the prediction that consumers derive their food resources more equally from brown and green channels (i.e., are more omnivorous) as trophic level increases. Using our diet specificity index, we calculated the distance of each consumer from equal consumption of brown and green resources as distance from equally derived diet $= |\text{diet index} - 0.5|$. Thus taxa that derive their energy equally from both channels would have a diet index of 0.5 and their distance from an equally derived diet (diet-distance) would be 0. This metric allowed us to test for patterns in diet specialization with a mixed-effects ANOVA model that included a linear effect of trophic level, a fixed categorical variable for system type, and a random effect for food-web identity (accounting for the nonindependence of multiple taxa within each web). Because we had an incomplete set of systems within each web type (for flow data we had no terrestrial webs, and for binary data we had no emergent vegetation webs), we did not include web type (binary/flow) in the analyses. We explored alternative variance–covariance structures and error distributions (Wolfinger 1996, Bolker et al. 2009) and selected a Gaussian distribution with autoregressive heterogeneous variances based in Akaike's information criterion (AIC) and examination of residuals.

We used R version 2.12.0 for all analyses (R Development Core Team 2010), and report all summary statistics as mean ± standard error unless otherwise noted.

Results

We found that multichannel consumers were prevalent across all ecosystems (Fig. 1), comprising 42.1% ± 5.3% of taxa (53.5% ± 6.4% of all consumers) and were far more prevalent than taxa feeding only on living autotrophs (16.8% ± 3.6%) or detritus (17.5% ± 4.4%). These trends were consistent across systems (one-way ANOVA: $F_{3,19} = 1.42$, $P = 0.27$).

Multichannel consumers were more common at higher trophic levels (Fig. 2, mixed-effects model, a linear effect of trophic level: $F_{1,1130} = 45.0$, $P < 0.0001$). This relationship did not vary by system type ($F_{3,1130} = 1.17$, $P = 0.32$), and system type alone did not explain diet ($F_{3,19} = 0.77$, $P = 0.53$). As predicted by Rooney et al. (2006), multichannel consumers were the most common consumer type at the highest trophic levels: 63.6% of taxa in trophic level 3 and above were multichannel consumers consuming at least 10% of each resource, as compared to 41.3% of taxa between the second and third trophic levels. However, when considering where the majority of multichannel consumers occurred, we found that most occupied the first to second heterotrophic levels: 58.6% ± 5.7% of all multichannel consumers occupied trophic levels 2–3, and nearly three-quarters of these taxa (74.7%), occurred between trophic levels 2 and 2.5. This suggests that most multichannel consumers directly link basal detrital and autotroph channels.

EFFECT OF MULTICHANNEL FEEDING ON SYSTEM STABILITY

Methods

Since nearly 60% of all multichannel consumers in our empirical food webs occupied trophic levels 2–3, we next evaluated how multichannel feeding low in the food web affects system stability. We developed a four-compartment nutrient-recycling predator–prey model (Fig. 3) that captured the three features we highlighted in *Introduction*; a compartmentalized multichannel structure, primary producers and detritus as basal resources, and consumers (X) that have the ability to derive energy from both autotrophs (A) and detritus (D). We then linked these compartments to a plant-

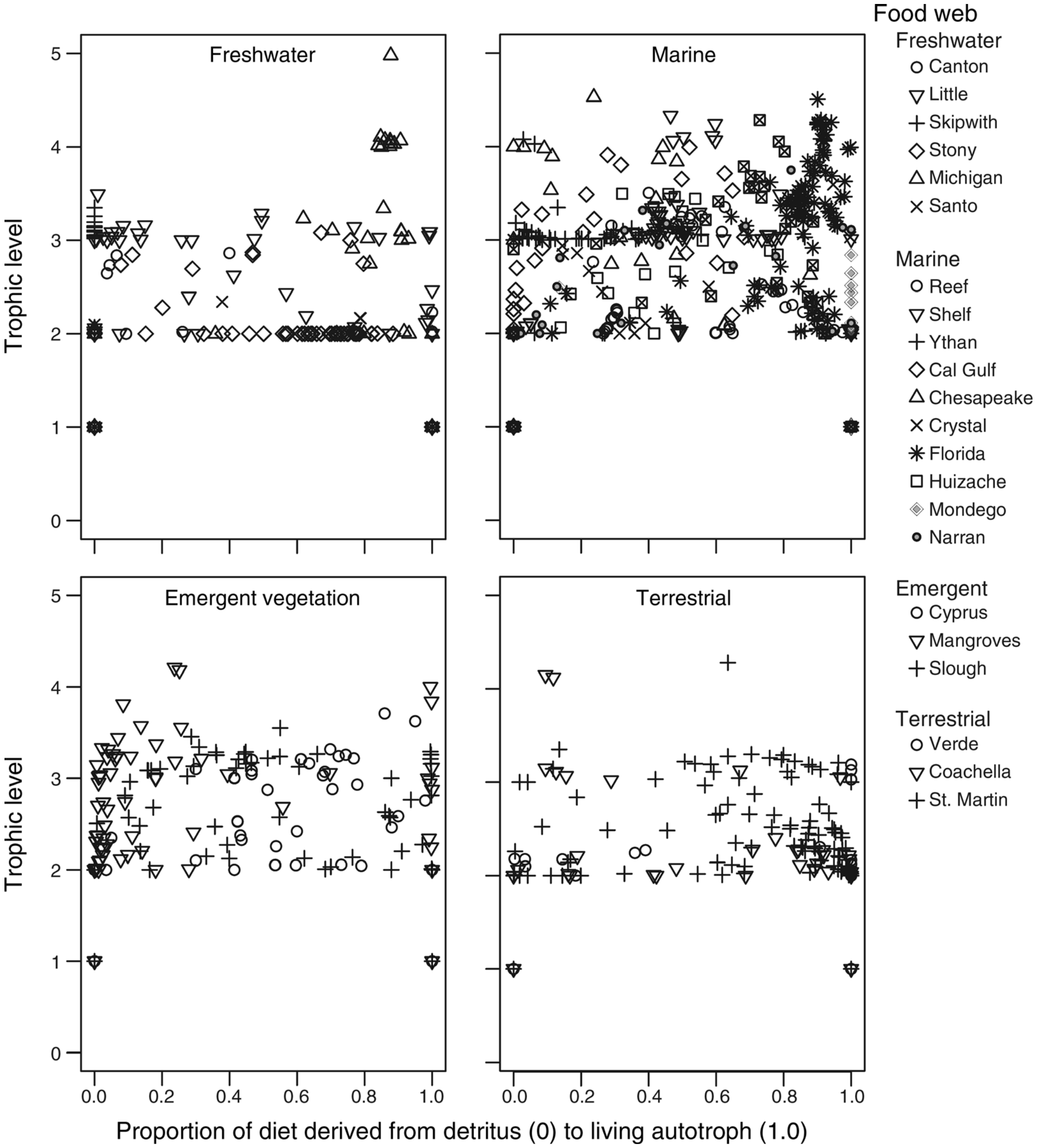

FIG. 1. All 23 food webs we examined, grouped by environment (see Appendix A for more detail). All food webs were based on both detritus (trophic level = 1 and diet = 0) and living autotrophs (trophic level = 1 and diet = 1). Contrary to expectations, there were many taxa at the second trophic level that mixed their diet between detrital- and living-autotroph-derived resources.

available nutrient pool (N). We used a nutrient-recycling model because we wanted to evaluate the unique ability of multichannel feeding to directly bring detrital-web nutrients into the grazing web, which would otherwise occur only via nutrient recycling from the detritus pool.

In all model formulations, autotrophs take up nutrients from a plant-available nutrient pool. The nutrient pool increases via external inputs and mineralization from the detrital pool. The detrital pool increases due to external inputs, sloppy feeding by herbivores, and death from the autotroph and consumer pools. In the multichannel feeding form of the model, the consumer feeds on both the autotroph and detrital pool with a Type II functional response following Chesson (1983)

$$\frac{dA}{dt} = \mu NA - \frac{a_{\mathrm{AX}}AX}{1 + a_{\mathrm{AX}}h_{\mathrm{AX}}A + a_{\mathrm{DX}}h_{\mathrm{DX}}D} - d_{\mathrm{A}}A - e_{\mathrm{A}}A$$

$$\frac{dN}{dt} = I_{\mathrm{N}} + \frac{(1-\delta_{\mathrm{AX}})a_{\mathrm{AX}}\gamma_{\mathrm{AX}}AX}{1 + a_{\mathrm{AX}}h_{\mathrm{AX}}A + a_{\mathrm{DX}}h_{\mathrm{DX}}D} + \frac{(1-\delta_{\mathrm{DX}})\gamma_{\mathrm{DX}}a_{\mathrm{DX}}DX}{1 + a_{\mathrm{AX}}h_{\mathrm{AX}}A + a_{\mathrm{DX}}h_{\mathrm{DX}}D} + mD - \mu NA - e_{\mathrm{N}}N$$

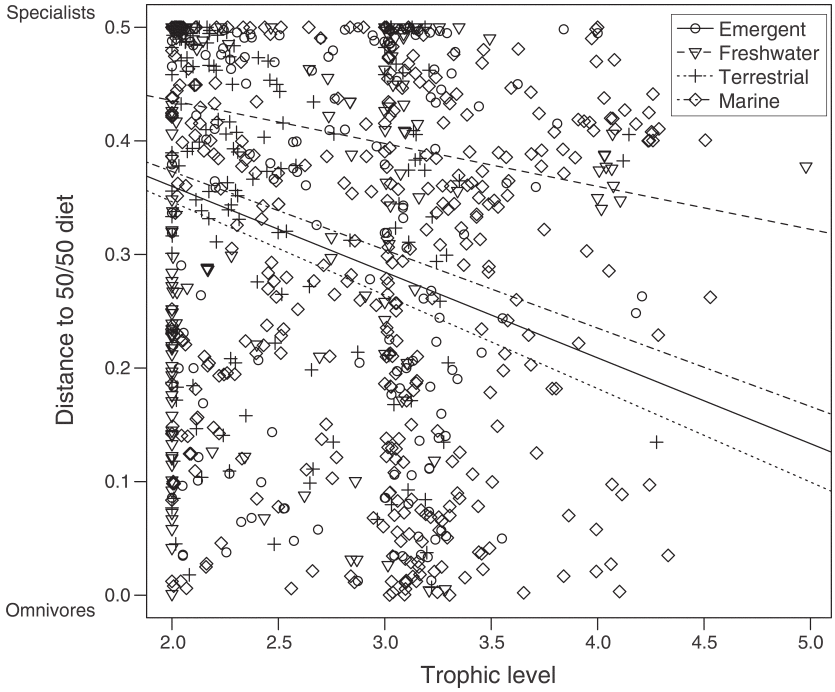

FIG. 2. Data from 23 food webs support the hypothesis that higher trophic levels have less specialized (more omnivorous) diets than lower trophic levels. Trophic level starts at 2 (since trophic level 1 is constrained to being detritus or living autotrophs). Distance to a 50/50 diet ranges from 0 (eating 50% from the brown [detrital] web and 50% from the green [autotroph-based] web) to 0.5 (eating completely from either the detrital or autotroph-based resources). Lines represent fits from the mixed-effect model presented in *Results, prevalence of multichannel feeding in real food webs.*

$$\frac{dD}{dt} = I_D + \frac{(1-\gamma_{AX})a_{AX}AX}{1+a_{AX}h_{AX}A+a_{DX}h_{DX}D} - \frac{\gamma_{DX}a_{DX}DX}{1+a_{AX}h_{AX}A+a_{DX}h_{DX}D} - mD + d_AA + d_XX - e_DD$$

$$\frac{dX}{dt} = \frac{a_{AX}\gamma_{AX}\delta_{AX}AX}{1+a_{AX}h_{AX}A+a_{DX}h_{DX}D} + \frac{a_{DX}\gamma_{DX}\delta_{DX}DX}{1+a_{AX}h_{AX}A+a_{DX}h_{DX}D} - d_XX - e_XX.$$

The model simplifies to pure detritivory when the attack rate of the consumer on autotrophs (a_{AX}) is set to zero, and to pure herbivory when the attack rate of the consumer on detritus (a_{DX}) is set to zero. We used a Type II functional response for realism and because Type I functional responses did not allow analytical solutions (due to the nutrient recycling and omnivory aspects of the model).

We defined parameters for the model (Table 1) for two of our four system types, freshwater and terrestrial. These systems are distinctly different endpoints along a continuum, varying in key attributes that may be important to how multichannel feeding affects web stability. Specifically, freshwater systems tend to have smaller standing stocks of all pools, higher-quality detritus, and faster nutrient

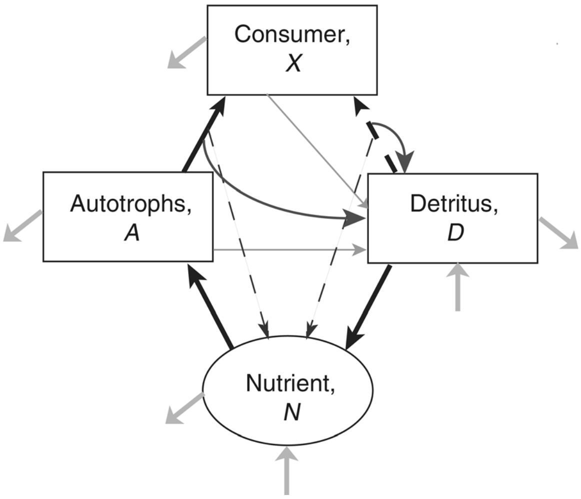

FIG. 3. Conceptual model of the four-compartment nutrient recycling model we used to examine how multichannel feeding may affect food-web stability. The model varied whether or not the consumer ate detritus (thick dashed arrow). Thick black arrows represent internal flows, while thick gray arrows represent inputs and outputs; thinner arrows show flows to the detrital pool via death (solid light-gray lines) and sloppy feeding (solid dark-gray lines) and to the nutrient pool via excretion (dashed lines).

Table 1. Parameter values used for four-compartment nutrient cycling model.

Parameter	Description	Terrestrial parameters: Units	Terrestrial parameters: Values evaluated	Freshwater parameters: Units	Freshwater parameters: Values evaluated
I_N	inputs to nutrient pool	g N·m^{-2}·yr^{-1}	0.05–10 (0.5)	μg P·L^{-1}·d^{-1}	0.001–10 (0.5)
I_D	inputs to detrital pool	g N·m^{-2}·yr^{-1}	0.5–20 (1.5)	μg P·L^{-1}·d^{-1}	0.00005–5 (0.01)
e_N	loss rate of inorganic nutrient	yr	0.005–1.5 (0.01)	d	0.00001–1 (0.05)
e_A	loss rate of autotrophs	yr	0.005–1.5 (0.05)	d	0.00001–1 (0.05)
e_D	loss rate of detritus	yr	0.005–1.5 (0.01)	d	0.00001–1 (0.05)
e_X	loss rate of consumers	yr	0.001–1.5 (0.1)	d	0.00001–1 (0.05)
μ	uptake rate of nutrients by plants	m^2·y^{-1}·g^{-1}	0.5–10 (3)	d	0.0001–5 (0.5)
d_A	death + metabolic rate of autotrophs	yr	0.001–4 (0.02)	d	0.0001–1 (0.01)
d_X	death + metabolic rate of consumers	yr	0.001–5 (0.01)	d	0.0001–1 (0.05)
γ_{AX}	assimilation efficiency feeding on autotrophs	unitless	0.2–0.9 (0.3)	unitless	0.1–0.9 (0.5)
γ_{DX}	assimilation efficiency feeding on detritus	unitless	0.2–0.9 (0.5)	unitless	0.1–0.9 (0.5)
δ_{AX}	production efficiency feeding on autotrophs	unitless	0.3–0.7 (0.35)	unitless	0.3–0.7 (0.4)
δ_{DX}	production efficiency feeding on detritus	unitless	0.3–0.7 (0.5)	unitless	0.2–0.9 (0.4)
a_{AX}	attack rate on autotrophs	m^2·y^{-1}·g^{-1}	0.05–5 (1.5)	μg P·L^{-1}·d^{-1}	0.0001–6 (0.1)
a_{DX}	attack rate on detritus	m^2·y^{-1}·g^{-1}	0.05–5 (varied)	μg P·L^{-1}·d^{-1}	0.0001–6 (varied)
m	detritus mineralization rate	yr	0.3–10 (1.5)	d	0.001–5 (0.05)
h_{AX}	handling time on autotrophs	yr	0.0000001–1 (0.1)	d	0.01–100 (0.1)
h_{DX}	handling time on detritus	yr	0.0000001–1 (0.1)	d	0.01–200 (0.1)

Notes: An extended version of this table including literature values and references for all parameters is given in the supplementary material (Appendix C). Values evaluated give the range examined for most results, with the value used to test sensitivity to attack rates in parentheses.

cycling as compared to terrestrial systems (Cebrian and Lartigue 2004).

We designed the equations to be in expressed in units of the most limiting nutrient (here, g N·m^{-2}·y^{-1} for a terrestrial system and μg P·L^{-1}·d^{-1} for a freshwater system). We used literature values from grassland systems and North American temperate lakes and background knowledge to develop possible ranges for each parameter (Table 1), then explored parameter space around these ranges. While some studies have found that higher-quality detritus in aquatic systems results in higher assimilation and production efficiencies compared to terrestrial systems (Cebrian and Lartigue 2004, Cebrian et al. 2009), our values do not reveal such a pattern.

We ran separate sets of 100 000 simulations to randomly explore both terrestrial and freshwater parameter space for the three models: multichannel feeding (consumption of both detritus and autotrophs by the consumer), detritivory only, and herbivory only. For each simulation we generated random parameter sets within uniform distributions between our minimum and maximum values (Table 1), allowing an examination of a large parameter space. For each parameter set, we calculated the equilibrium and assessed whether it was feasible (i.e., all pools had positive equilibrium values, sensu Roberts [1974]). For systems with feasible equilibria, we calculated dominant eigenvalues and then used them to estimate stability (whether the system will return to the equilibrium if disturbed) and resilience (the rate of recovery) following classical procedures (May 1973). While the ecological literature is rife with definitions and calculations of stability (Grimm and Wissel 1997), we chose to use classical procedures because the dominant eigenvalue has both a clear theoretical definition (that is easily measurable in the model) and a relationship to empirical measurements of a system's response to perturbation (Cottingham and Carpenter 1994, Jorgensen et al. 2000).

We further explored the effect of multichannel feeding on food-web stability by examining in more detail how system return times changed with attack rates on the autotroph and detrital pools. We focused on attack rates because they allowed us to vary how strongly the omnivore fed on one resource or the other. For this, we used one parameter set for each system type (Table 1), chosen because it was realistic biologically; results were robust to the choice of external input rates for both the nutrient and detrital pools. All model simulations were done in Mathematica 7.0 (Wolfram Research, Champaign, Illinois, USA) and analyzed in R 2.12.0.

Results

Our models suggest that the degree to which multichannel feeding affects system stability and return time depends on the system type (terrestrial or freshwater, as reflected by the parameter sets) and the rates at which omnivores attack living autotrophs vs. detritus. In both system types, models with multichannel feeding produced fewer parameter sets generating stable models compared to herbivory-only and detritivory-only models (Table 2).

The effect of multichannel feeding on system resilience varied by system type. In terrestrial systems, multichannel feeding tended to produce systems with intermediate resilience between the least-resilient detritivory-only models and the most-resilient herbivory-only models. Additionally, in terrestrial systems, multichannel feeding produced only a small destabilizing effect. For freshwater systems, however, the destabilizing effect was far greater (Table 2). In freshwater parameter sets with equilibria, multichannel feeding generally produced less

TABLE 2. Parameter search results.

Model	Freshwater		Terrestrial	
	Stable systems (%)	Mean return time	Stable systems (%)	Mean return time
Detritivory only	100	5.0	100	2.6
Herbivory only	54.5	3.5	80.8	1.9
Multichannel feeding	45.8	7.5	71.6	2.4

Notes: We give the percentage of systems with negative critical eigenvalues (stable systems) and their mean return times for freshwater and terrestrial parameter sets. Return times are in years for terrestrial models, and days for freshwater models.

resilient systems, compared to models without multichannel feeding. Return times in models with multichannel feeding were twice as long as herbivory-only models (which tended to produce systems with the shortest return times) and 50% higher than detritivory-only models (Table 2).

Across both terrestrial and freshwater parameter space, multichannel feeding was stabilizing at low attack rates on the autotroph, and destabilizing at high attack rates on the autotroph (Fig. 4a–d). When the omnivore attacked autotrophs at a high rate, the attack rate on detritus had to be comparatively much lower to produce a stable system (Fig. 4a–d). In models with multichannel feeding, across both system types, the transition from a stable to unstable system with higher attack rates resulted from system dynamics entering limit cycles, not from the extinction of any pool. Additionally, declines in stability with multichannel feeding were not explained by a slow–fast stabilization mechanism (Appendix D).

DISCUSSION

Across 23 food webs and four ecosystem types, we found that most consumers were multichannel consumers, deriving their diets from both autotrophs and detritus, especially at the top of the food web. The majority of multichannel consumers, however, occurred as primary consumers (e.g., *Daphnia*, see Plate 1), indicating most taxa at the herbivore/detritivore level are more aptly described as multichannel consumers.

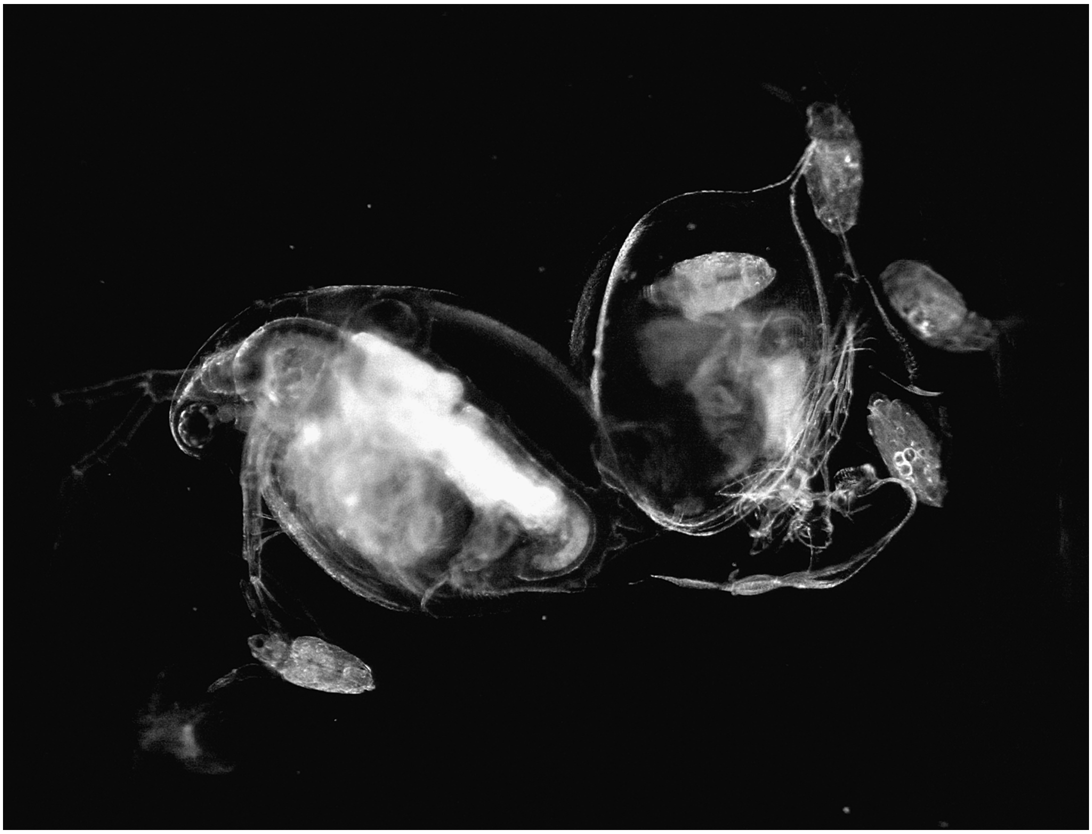

PLATE 1. Empirical food web data showed that primary consumers, such as *Daphnia pulex* (shown here releasing neonates during a molt), are often multichannel consumers. Photo credit: Samuel Fey.

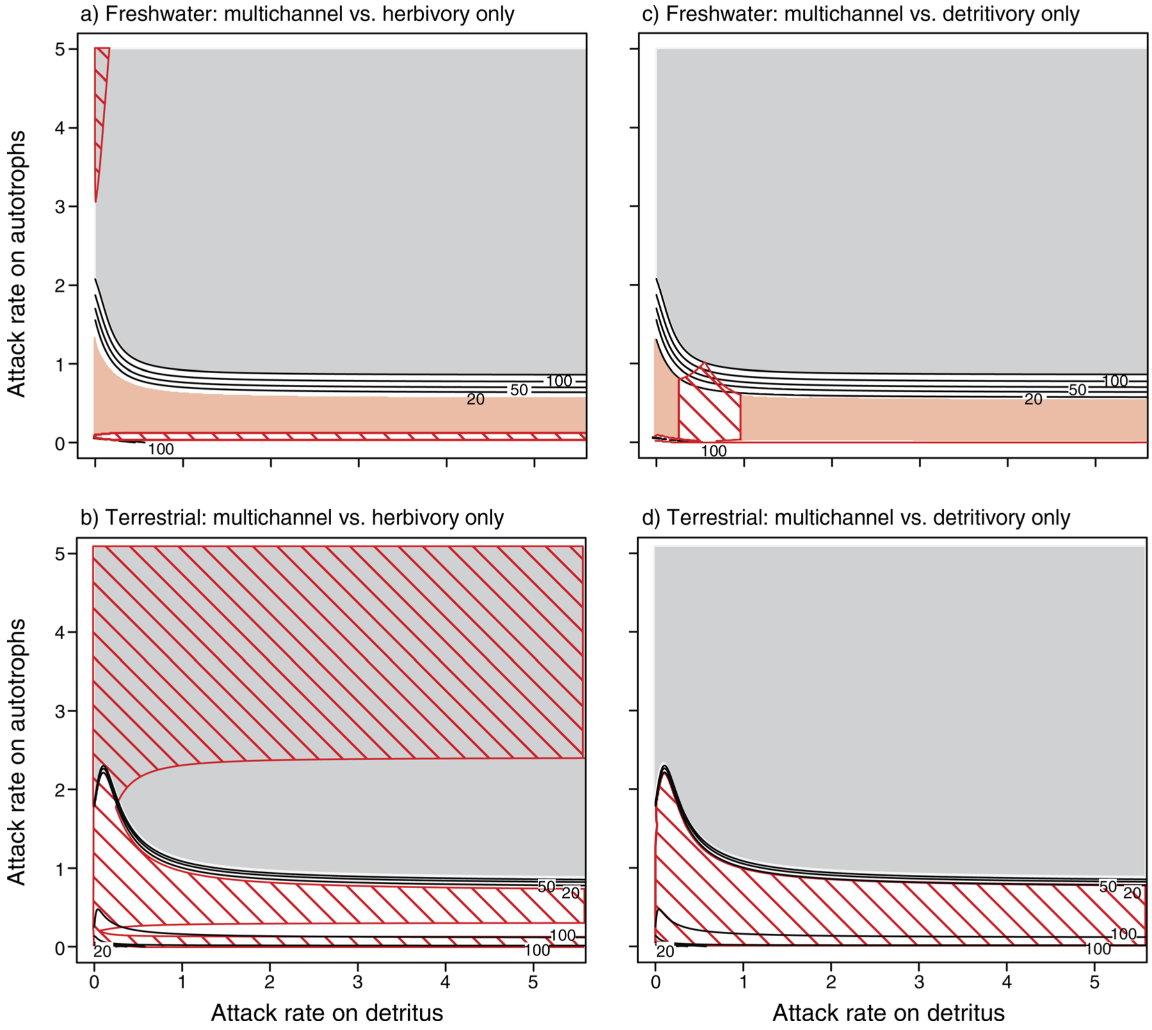

Fig. 4. Contour plots of return times depending on attack rates on autotrophs vs. attack rates on detritus by a multichannel consumer within (a and c) freshwater and (b and d) terrestrial parameter sets (attack rates defined in Table 1). Return times are in years for terrestrial models, and days for freshwater models. Black contour lines show return times, with return times of 20, 50, and 100; the shaded gray areas represent parameter space where systems were unstable while remaining areas represent parameter space where systems were stable. Overlay areas with diagonal red lines represent parameter space where multichannel feeding is stabilizing (instead of destabilizing) compared to (a and b) an herbivory-only or (c and d) a detritivory-only model, while light red shading represents areas where there was no effect of multichannel feeding.

Moreover, our models show that multichannel feeding, though generally destabilizing when simplistically compared to herbivory- or detritivory-only models, can be stabilizing, when occurring with low attack rates on autotrophs (Fig. 4).

Prevalence and position of multichannel consumers in empirical webs

Past research has routinely suggested that multichannel feeding and detrital resources may be both more common and more important in terrestrial compared to aquatic ecosystems (Polis and Strong 1996). In contrast, we found that multichannel feeding is as common in freshwater lakes and oceanic shelves dominated by pelagic species as in terrestrial systems. Consumers in all four system types derived substantial amounts of energy from both autotroph and detrital channels. This challenges the traditional view that food webs can be abstracted into simple grazing channels of plants, herbivores, and predators (Pimm 1982, Holt 2006), and suggests that the real world is far messier, echoing recent work on intraguild predation (Rudolf 2007). While our 23 food webs are still a small sample, our results suggest that current webs capture highly connected systems. Grazing chains exist only as one part of webs heavily subsidized by widespread consumer interactions with the detrital web (Coleman 1985, Moore et al. 2004). Thus, while our modeling work showed detritivory-only or herbivory-only systems may be the most stable (Table 2), our empirical web findings suggest that such systems are rare, and are not representative of real systems.

Stability and multichannel feeding in modeled webs

Our modeling results show that integration between the brown and green worlds may stabilize food webs, but only under certain conditions. Using a simple food-web model with nutrient cycling and considering stability as assessed by return times calculated from the dominant eigenvalue, we found models with multichannel feeding often produced stable webs. Such models, however, produced the fewest stable systems; in contrast, herbivory-only systems were consistently more stable, and all of the detritivory-only models were stable (Table 2). While return times were higher for multichannel consumer models compared to herbivory-only models, we found that multichannel feeding could have a stabilizing effect in both terrestrial and freshwater parameter sets, even without the stabilizing forces of predator-switching often used in other models that introduce this sort of omnivory (Rooney et al. 2006). In particular, we found multichannel feeding was stabilizing at low to moderate attack rates on autotrophs, however, high attack rates on both autotrophs and detritus led to highly unstable systems (Fig. 4).

We noted, however, distinct differences in the effects of multichannel feeding on the stability of terrestrial vs. freshwater systems, suggesting that multichannel feeding may be generally more stabilizing in terrestrial systems. Terrestrial systems with multichannel feeding had return times of intermediate length compared to the detritivory- and herbivory-only models (Table 2), and showed a peak in stabilizing effects when multichannel feeders attacked detritus at a low rate (Fig. 4b, d). In contrast, modeled freshwater systems with multichannel feeding produced longer return times and showed a larger range of parameter space in which detrital feeding by multichannel feeding destabilized systems (Fig. 4a, c). While this may initially seem incongruous with our finding that multichannel consumers are equally common across all ecosystem types, our modeling results suggest that the key difference may lie in attack rates between systems. Both systems can be stable with multichannel consumers and high attack rates on detritus, provided attack rates on autotrophs remain low.

Integrating results from empirical and modeled food webs

Combining our model predictions with empirical food-web data indicates that while multichannel consumers in real webs tend to consume a highly mixed diet (Figs. 1 and 2), a key for system stability may be asymmetric attack rates across resource channels. Thus, our results integrate the findings that (1) multichannel feeding can be stabilizing when weak (McCann et al. 1998, McCann 2012) and (2) prey preferences of predators that link food chains affect stability (Post et al. 2000), but also that (3) stable systems have omnivores which balance their resource needs across dichotomous resource channels (Rooney et al. 2006). Dichotomous resource channels can be critical to stability by allowing multiple pathways and rates of energy flow through webs (MacArthur 1955). Variation in how dichotomous the relative rates of these two channels are, particularly the rate of input of detritus relative to its consumption and whether the input is allochthonous or autochthonous, may explain differences between our terrestrial and freshwater parameterized models (see Neutel et al. 1994, Moore et al. 2012, Fig. 4). Freshwater systems tend to have higher-quality (C:N or C:P) living autotrophs, with resulting stronger herbivory and faster turnover times compared to terrestrial systems, while detritus in freshwater systems is often allochthonous, derived from the lower-quality plant materials of terrestrial systems (Cebrian and Lartigue 2004). Thus, the high ratio of edibility of autotrophs vs. detritus in freshwater systems may produce greater asymmetry in the attack rates of omnivores: across systems, this relative ratio of edibility between the brown and green webs may be key to predicting the relative asymmetry of attack rates.

Teasing out hypotheses related to how edibility affects food-web dynamics would also benefit from a more refined consideration of detritus that explicitly recognizes the varying qualities of detritus (Moore et al. 2004). While it is well recognized that turnover times for detritus can vary dramatically from slowly decaying recalcitrant litter (Cornwell et al. 2008) to rapidly decaying carrion (Polis 1991), the majority of food web data collection continues to consider detritus as only one pool (Wilson and Wolkovich 2011). This was true of our studied webs as well. Further, when multiple pools were identified in the webs we studied, they, with few exceptions (e.g., Polis 1991), only differentiated among groups of detritus (e.g., dead roots vs. leaves, or suspended vs. sediment detritus) that may be less important to highlighting and understanding the role of detritus quality and turnover to dynamics.

Our prediction of trade-offs between attack rates on autotrophs vs. detritus calls for improved data to more carefully estimate interactions between consumers and detrital resources, especially nutrient transfers. Testing our model predictions requires field estimates of attack rates, especially on detrital resources; particularly insightful may be data from open-water systems where autotrophs, consumers, and detritus are all mobile, and from systems that vary in the quality of their green vs. brown basal resources. Further, improved estimates of the pool sizes of detritus may be required to calculate accurate attack rates; many webs estimate only a single pool of detritus, while consumers may view and attack detrital pools of varying quality quite differently (Wilson and Wolkovich 2011).

Conclusions

Our results build on continued work demonstrating the importance of detritus to structuring food webs (Lindeman 1942, Azam et al. 1983, Odum and Biever 1984, Allesina and Pascual 2009). Further, while community ecology has generally conceptualized grazing and detrital webs as separate (Moore et al. 2004), our results, combined with increasing empirical and theoretical work (Moore and Hunt 1988, Vadeboncoeur et al. 2005, Anderson et al. 2008, Blanchard et al. 2011), suggest consumers across ecosystems ignore this distinction, drawing resources from both the brown and green worlds. Our findings demonstrate that key differences among ecosystems in the effects of multichannel feeding on stability and the rates of attack on autotrophs may affect trophic structure. Such differences could affect the flow of nutrients in food webs and webs' dynamical structure (see MacArthur 1955, Pimm 1979), with cascading community and ecosystem consequences.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/13-1721.1.sm