ARTICLES

Structural asymmetry and the stability of diverse food webs

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Untangling the influence of human activities on food-web stability and persistence is complex given the large numbers of species and overwhelming number of interactions within ecosystems. Although biodiversity has been associated with stability, the actual structures and processes that confer stability to diverse food webs remain largely unknown. Here we show that real food webs are structured such that top predators act as couplers of distinct energy channels that differ in both productivity and turnover rate. Our theoretical analysis shows that coupled fast and slow channels convey both local and non-local stability to food webs. Alarmingly, the same human actions that have been implicated in the loss of biodiversity also directly erode the very structures and processes that we show to confer stability on food webs.

May[1,2] ignited one of the most enduring debates in ecology when he proposed that there is no *a priori* mathematical reason to believe that greater species-diversity begets enhanced community stability, and further challenged ecologists to "…elucidate the devious strategies which make for stability in enduring natural systems". If increased diversity does not necessarily result in greater stability, why do diverse food webs seem to be more stable than depauperate ones? May noted that if the interactions among species within his models were arranged into 'blocks' rather than at random, stability was more likely, suggesting that the pattern of interactions in real food webs might impart stability in nature. This intuition has been supported by studies revealing that models structured from biologically plausible interaction strengths generate more stability than their randomly generated counterparts[3–5]. Although increased stability in real food webs has thus been documented, ecologists have yet to identify the ecological basis for these structures and the mechanisms that impart stability in nature.

Ecologists have pointed to the potential for both sub-assemblages of species or compartments within food webs and the concomitant structure of interaction strengths among species to have significant roles in the persistence of complex natural systems[1,2,4,6]. Whereas recent analyses have shown promise in analysing patterns of interaction strengths in nature to reveal the presence of compartments in large food webs[7], ecologists have vacillated on the roles of compartments and interaction strengths in nature[8–10]. Recent theoretical work, however, suggests that both may indeed have critical roles in ecosystem stability[11,12]. Despite theoretical[1,13,14] and empirical[15–18] advances, the complex tangle of interactions found in real food webs has made it difficult to link the patterns of interaction strengths in nature and the mechanisms that impart stability to food webs[19,20].

A primary goal for ecologists, therefore, should be to identify the overarching structures and processes in food webs that impart stability and persistence. Along these lines, soil ecologists have argued the existence of compartments in the form of fast and slow energy channels, ultimately coupled by mobile higher-order consumers in soil food webs[4,21–23]. Here, fast and slow channels refer to the turnover rates, or the production:biomass ratios, which are intimately related to energy or biomass flux definitions of interaction strength[6,23] (see Box 1). Turnover rates can be seen as a combination of interaction strength and the life history attributes of species or trophospecies—for example, birth rates, death rates and energetic efficiencies. Thus, if soil ecologists' suggestions are correct, fast channels are on average comprised of strong interactions and slow channels are comprised of weak interactions. This simple connection between turnover rate and interaction strength allows us to examine food-web turnover rates that emanate from distinct basal resources (source webs *sensu* Cohen[24]). If patterns of fast and slow energy channels exist in food webs, then in a sense we effectively have located strong and weak interaction chains. Here we expand on this suggestion of soil ecologists[4,12–14] by rigorously assessing the existence of distinct energy channels in a variety of ecosystems. We then assess if there is, in fact, any tendency towards characteristic turnover rates within channels. Finally, we synthesize our empirical results within recent theory and in doing so show that coupled fast and slow energy channels confer both potent local and non-local stability to food webs.

Empirical results

On the existence of energy channels. We began our empirical analysis with the identification of basal resources within aquatic and terrestrial ecosystems from published food-web data. For aquatic food webs, we analysed data from Chesapeake Bay[25,26], the Chilean upwelling[27], the Cantabrian Sea shelf[28], and the Bering Sea[29]. Terrestrial food webs included in the study were a North American grassland (shortgrass steppe, SGS-LTER Nunn, Colorado)[30], the Lovinkhoeve Experimental Farm (Integrated Management) in The Netherlands[31], moist acidic tundra (Arctic-LTER, Toolik Lake, Alaska)[32], and a European Scots pine forest (Werkerom, The Netherlands)[33]. In our examples, aquatic systems consisted of resource compartments based on phytoplankton and detritus. In three of the four detrital soil food webs studied, bacteria and fungi were the basal resources, whereas in the fourth terrestrial example, fungi and detritus were the basal resources (see Supplementary Notes for data sources). On the basis of feeding interactions, we calculated the per cent of carbon derived from each basal resource by any given consumer, and the trophic position of each food-web member (see Supplementary Methods for details). Figure 1 shows two examples of the general pattern that emerged from our analysis (see Supplementary Fig. 1a, b for six further examples). Lower-order consumers tended to derive the bulk

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of their carbon from one of the two resources, providing the basis for resource compartments or energy channels. As trophic level increased, so did the tendency to derive carbon from both source webs. Notably, analogous patterns of predatory fish coupling benthic and pelagic pathways have also been detected using stable isotope analysis in lake food webs[34]. Given the broad range of systems analysed, the consistency of the pattern among food webs is remarkable and, to our knowledge, novel.

On productivity and turnover rates. As strong and weak channels map to fast and slow turnover rates within compartments, we calculated or took from the literature production and biomass values for the channels (defined as groups that derived >60% of their carbon from a given basal resource). Our analysis substantiates previously suspected patterns of weak and strong energy flux through channels. Table 1 shows that for the example food webs presented in Fig. 1, the amount of production entering aquatic food webs is consistently higher in the pelagic channel. Similarly, within the example terrestrial web, the consumers of bacteria dominate the carbon influx. Strikingly similar patterns of asymmetrical energy flux into food webs are also seen in the remaining six food webs (Supplementary Table 1). The important point is that carbon influx into these food webs through primary consumers is not symmetrical, as one channel dominates.

Moving up trophic levels in the food webs, the production:biomass ratios within the pelagic channels are consistently higher than the benthic channels for aquatic systems (Table 1). This pattern reflects ecological and life history characteristics of the consumers within each channel. For example, pelagic primary consumers (zooplankton) are smaller and have much shorter generation times compared with their benthic primary consumer counterparts. By and large, bacterial channels showed higher production:biomass ratios than fungal channels in soil systems dominated by non-woody plants, such as the North American grassland.

The empirical analysis has detected remarkable similarities in food-web structure across a range of ecosystems. Food webs are constructed such that energy channels based on different basal resources are coupled by higher-order predators. Across systems, channels within food webs are consistently asymmetrical in both the amount of energy entering through basal resources (annual production) and the turnover rates of the energy channels (production: biomass ratios).

Box 1 | The relationship between turnover rate (P:B ratio) and interaction strength

Let us start with a generic consumer model where the consumer, C, feeds on resources, R_i, and is fed on by predators, P_j:

$$\frac{dC}{dt} = e\sum_{i\in R} CF_{CR_i} - mC - \sum_{j\in P} CF_{P_jC} \quad (1)$$

where F_{ji} is the functional response of consumer j on resource i, m is the rate of mortality, and e is the conversion efficiency. Assuming equilibrium conditions (that is, flux into C equals flux out of C), then consumer biomass turnover rates (ν_C) can be calculated from either the flux in or the flux out:

Flux in

$$v_C = \frac{e\sum_{i\in R} CF_{CR_i}}{C} \quad (2)$$

Flux out

$$v_C = \frac{\sum_{j\in P} CF_{P_jC} + mC}{C} \quad (3)$$

Using energy flow as a metric for interaction strength[23,31], the per capita interaction strength (IS) between any resource and its consumer can be defined as:

$$IS'_{CR} = -\frac{CF_{CR}}{C} \quad IS'_{RC} = \frac{eCF_{CR}}{R} \quad (4)$$

Similarly, the total interaction strength can be defined as:

$$IS_{CR} = -CF_{CR} \quad IS_{RC} = eCF_{CR} \quad (5)$$

Given estimates of biomass, then the magnitudes of equations (2) to (5) can easily be estimated.

Thus, the relationship between consumer biomass turnover rates (ν_C) and interaction strengths (IS) can be expressed as:

Flux in

$$v_C = \frac{e\sum_{i\in R} CF_{CR_i}}{C} = \frac{IS_{R_1C} + IS_{R_2C} + \ldots}{C} \quad (6)$$

Flux out

$$v_C = \frac{\sum_{j\in P} CF_{P_jC} + mC}{C} = \frac{-IS_{P_1C} - IS_{P_2C} - \ldots}{C} + m \quad (7)$$

It is clear that the speed of energy flow for a consumer ultimately depends on a number of traits of an organism. The speed of energy flow (v) can thus be envisioned as a general property of a food web (interaction strength is embedded within this property). Thus, a fast flow is, on average, composed of stronger interactions than a slow flow. Furthermore, fast pathways (for example, up a food chain), on average, are composed of stronger interactions than slow pathways.

Theoretical synthesis

Theoretical explorations of compartmented food webs have suggested that system dynamics can be stabilized by both higher-order predators coupling food webs in space, and the presence of weak and strong channels[10,11]. These results resonate with our empirical observations, so we sought to integrate them into a food-web model to analyse their influence on food-web stability. Our model consists of a top predator that couples two consumer–resource chains that exist in different habitats. The resources have access to exclusive nutrient pools, and also compete for a common pool of nutrients (see Supplementary Fig. 2 for model details and Supplementary Table 2 for parameter values). Within the model, we varied two central factors that mirrored our empirical observations. To reflect the observed differences in production:biomass ratios within channels, we simultaneously varied the attack rates of both predator on consumer and consumer on resource (attack rate ratio). Given the constant attack rates of one channel (constant channel), we varied the attack rates of the second channel (modified channel) by factors ranging from 0.5 to 2.5, thus forcing the modified channel to be both slower and faster than the constant channel. In preliminary model runs, we also modified channel speed using a variety of different parameters (for example, mortality (m)) without qualitatively changing the results that follow. To parallel the observed differences in basal production between energy channels, we independently varied the proportion of energy (p) that entered the food web though the resources of the modified channel. This metric essentially forced food-web production to be dominated by either the constant channel or the modified channel (see Supplementary Fig. 1 and Table 1 for further details).

Equilibrium results. First we considered the most straightforward scenario, where equal amounts of energy enter the food web through the two basal resources ($p = 50\%$) and then varied the attack rate ratio (Fig. 2a, solid line). The least stable food web configuration occurs when the attack rate ratio is 1:1, a similar pattern found in previously published work[11]. This symmetrical arrangement of energy flow essentially creates an unstructured food web, wherein the dynamics of the two channels are synchronized. Increasing or decreasing the attack rate ratio (analogous to increasing or decreasing the production:biomass ratio in the modified channel) confers local stability, as measured by the most negative eigenvalue (Fig. 2a). Stated biologically, we see that equilibrium stability is enhanced as energy flow between the channels becomes asymmetric. This change in energy flow is reflected in the dynamics of the consumers from the two different energy channels. Figure 2b shows that the correlation between consumers following a small perturbation decreases on

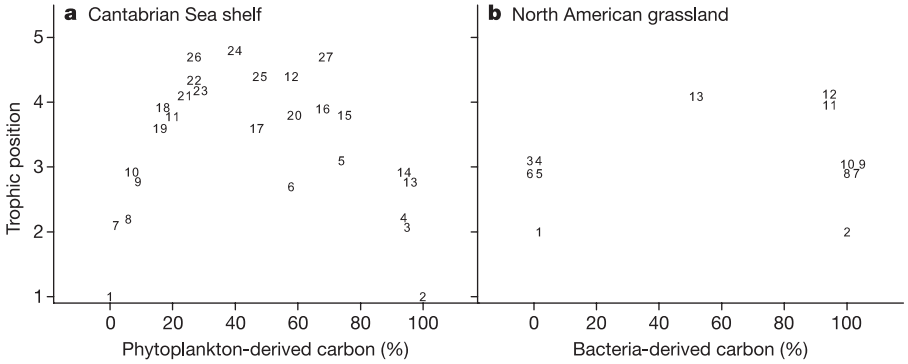

Figure 1 | Food webs are structured such that top predators couple distinct energy channels. **a**, **b**, Food-web representations based on estimations of the percentage of carbon derived from basal resources for the Cantabrian Sea shelf (**a**) and the North American grassland (**b**). Trophic position (based on feeding interactions) is shown on the *y*-axis. Taxonomic group names corresponding to the numbers can be found in Supplementary Table 4. Labels have been offset to allow for the identification of taxonomic groups.

either side of the symmetrical, or unstructured, case (when the attack rate ratio = 1.0 and $p = 50\%$). This implies that the two chains start to vary out of phase as the attack rate ratio is skewed (Fig. 2b, solid line). As recent theory has suggested, this asynchrony in prey (that is, the consumers) translates into a more stable prey base for the predator[12,35] and so can act as an important stabilizing mechanism in nature.

Mirroring our empirical results, we next asked how simultaneously varying both p and the attack rate ratio modified these results. Figure 2a (dashed line) plots the most stable configurations observed for any given attack rate ratio across the entire range in p. The local stability is greatly enhanced when we allow both factors to change (Fig. 2a), demonstrating that the most stable food web configurations occur when both attack rates and production (p) are skewed.

Increased stability of these food webs is reflected in lower correlation coefficients (greater asynchrony) between the consumer populations (Fig. 2b, dashed line). To unfold this pattern more clearly, we plotted the percentage of energy that flowed through the faster channel (remembering that the modified channel is fastest above an attack rate ratio of 1:1, and the constant channel is the faster below an attack rate ratio of 1:1) at the most stable scenario for each attack rate ratio (Fig. 2c). The first clear pattern that emerges is that food webs are always most stable when the majority of energy flows through the fast channel. Further, as the food webs become more asymmetric with respect to the attack rate ratio, more energy must flow through the fast channel to realize maximum stability.

Transient non-equilibrium results. Ecological systems are inherently variable and so it is worthwhile to consider how mechanisms that drive equilibrium stability act away from the equilibrium (for example, after a large perturbation). We allowed our model systems to reach equilibrium and then removed 10% of the top predator as a perturbation to the food web. To understand the dynamics within a transient non-equilibrium context, we looked at two dynamical properties that confer resilience and stability to food webs. First, we determined the rate at which the predator population densities return to the equilibrium value immediately following a perturbation ('global return speed', Fig. 3a). Second, we determined the degree to which the predator population overshoots its equilibrium during the transient phase ('overshoot', Fig. 3a), as a measure of the potential for compensatory responses to dampen food-web dynamics near the equilibrium. These two attributes are important, as often dynamic systems that return to equilibrium rapidly also tend to overshoot the equilibrium significantly. Using these metrics, we constructed a measure of non-local stability ('transient non-equilibrium stability', Fig. 3a) defined as global return speed divided by overshoot. Defined this way, stability away from the equilibrium is largest when global return speed is large and overshoot is simultaneously small. As illustrated in Fig. 3b, the regions of greatest local stability (most negative dominant eigenvalue, Fig. 2a) also have high degrees of transient non-equilibrium stability. Although we do not explore the influence of environmental fluctuations on the stability of our food web configuration, we argue that the very same factors that confer stability away from the system attractor in our example will do so in nature. Both the ability to respond quickly to changes and the capacity to dampen potentially destabilizing oscillatory fluctuations will confer overall stability to food webs in the face of fluctuating environmental conditions.

Summary

The phenomenon of population asynchrony resulting in community stability has been postulated in theoretical analyses[12,35] and observed in both experimental[36] and empirical[37] studies. Here we demonstrate that common empirical food-web structures have the potential to readily drive such a differential response. Encouragingly, this suggests that the weak interaction effect, heretofore demonstrated at the

Table 1 | Energy flow in a marine and a terrestrial food web

Cantabrian Sea shelf	Trophic level	Benthic channel			Pelagic channel		
		Production ($g\,C\,m^{-2}\,yr^{-1}$)	Biomass ($g\,C\,m^{-2}$)	P:B ratio	Production ($g\,C\,m^{-2}\,yr^{-1}$)	Biomass ($g\,C\,m^{-2}$)	P:B ratio
	2 +	130.38	35.15	3.71	537.30	22.68	23.69
	3 +	14.76	20.47	0.72	72.79	29.76	2.45
	4 +	1.10	2.49	0.44	0.31	0.38	0.82
North American grassland	**Trophic level**	**Fungal channel**			**Bacterial channel**		
		Production ($g\,C\,m^{-2}\,yr^{-1}$)	Biomass ($g\,C\,m^{-2}$)	P:B ratio	Production ($g\,C\,m^{-2}\,yr^{-1}$)	Biomass ($g\,C\,m^{-2}$)	P:B ratio
	2 +	11.00	6.30	1.75	54.55	30.40	1.8
	3 +	0.64	0.35	1.83	5.19	1.14	4.5
	4 +	–	–	–	0.032	0.016	2.0

Total production, biomass and production:biomass (P:B) ratios of species grouped by trophic position and basal energy resource for the two example food webs illustrated in Fig. 1. Values for the remaining six food webs can be found in Supplementary Information.

consumer–resource level[6], may be scaled to whole ecosystems if we recognize the presence of fast and slow energy channels coupled by higher-order predators (that is, the fast and slow channels can be envisioned as coupled strong and weak interaction chains). It is important to point out that this stabilizing result depends on the rapid behavioural response of the top predator to changing densities in the different channels[38]. As one channel increases and the other decreases (that is, the channels have asynchronous dynamics) the predator moves to regulate the increasing channel and in doing so frees the decreasing channel from strong predatory pressure. It is therefore the rapid predatory switching behaviour that balances such asynchrony. Although here we use a preference-based functional response in our model, optimal foraging models will give the same qualitative results as they too respond to the asynchrony in a way that balances such asynchronous dynamics[39,40].

Notably, our results also suggest that a food-web architecture based on multiple asymmetric energy channels provides ecosystems with a potent mechanism for responding to large perturbations (that is, dynamics far from the equilibrium). The asymmetry of energy flux in coupled channels provides top predators with prey bases that show characteristic and complementary dynamics. In the face of such large perturbations, a fast channel allows for the rapid recovery of predator populations, but would almost certainly result in overshoot and runaway consumption dynamics. The presence of a slow channel, however, enhances compensatory responses near the system attractor. These complementary functions produce a rapid yet stable recovery from a perturbation.

In summary, our results suggest that the stability of complex ecosystems depends critically on the maintenance of the heterogeneity of distinct energy channels, their differential dynamic properties (that is, differential productivity and turnover), and the mobile consumers that couple these distinct channels. A corollary to this general result is twofold: (1) any perturbations that destroys this heterogeneity (either through synchronizing or removing channels) ought to destabilize these systems relative to their heterogeneous counterparts; and, (2) removal of mobile higher-order consumers that couple these distinct zones ought to destabilize these systems relative to their coupled counterparts.

It is important to note that the same traits we identify as critical ecosystem structures are currently being undermined by human

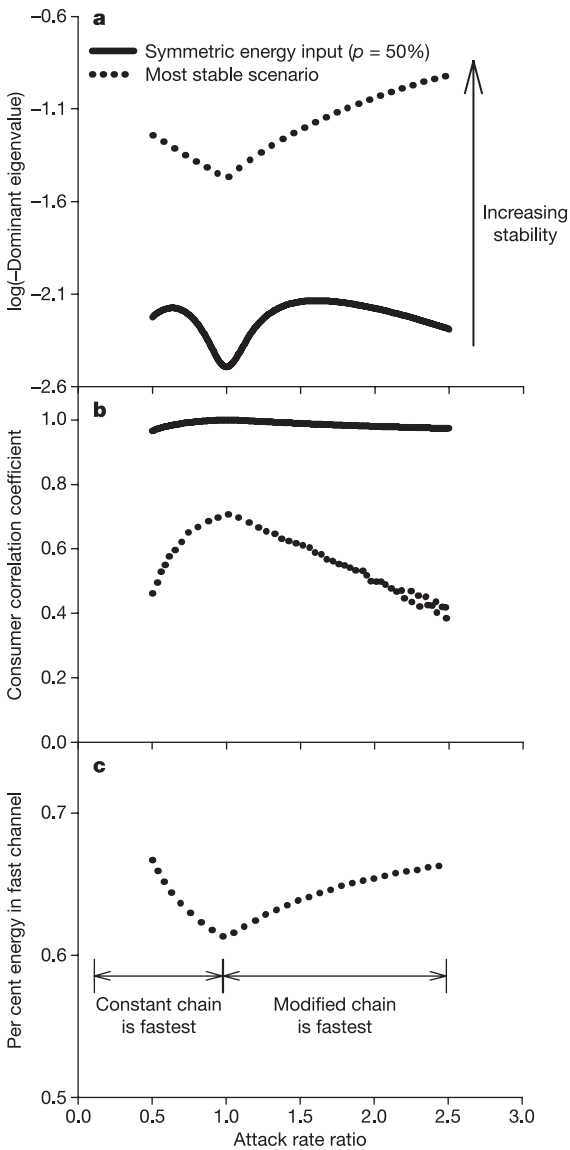

Figure 2 | Differing productivities and turnover rates between coupled energy channels result in increased local food-web stability and decreased consumer population synchrony. a–c, The relationship between attack rate ratio and: **a**, the local stability of the food webs (log(−dominant eigenvalue); solid line represents food-web stability when $p = 50\%$ and the dotted line is the most stable possible state given any p); **b**, the correlation coefficient of the two consumer populations during the transient phase of the food-web dynamics (legend same as in **a**); and **c**, the proportion of energy flowing through the faster channel that gives rise to the greatest stability as shown in **a**. See Supplementary Fig. 1 for model equations and parameter values used in the food-web model.

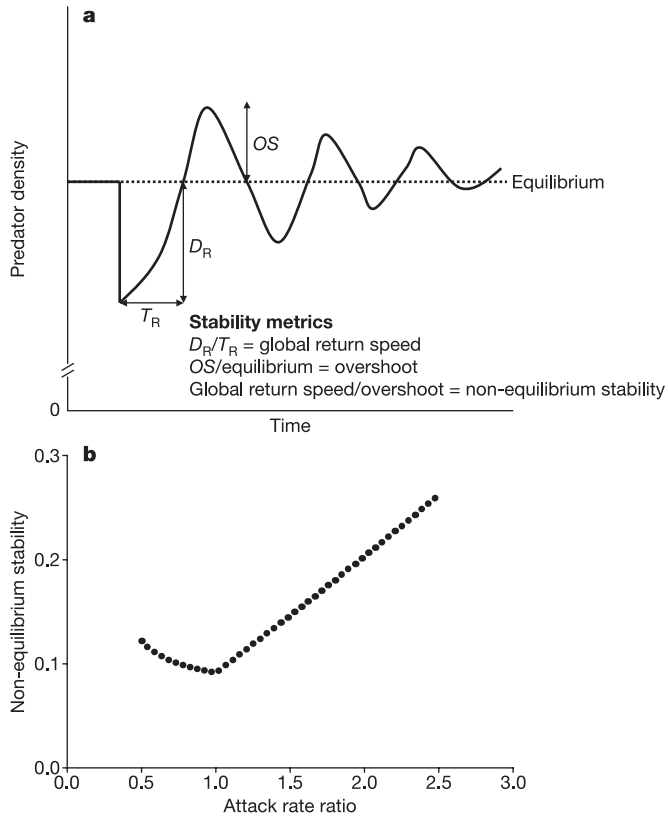

Figure 3 | Coupled fast and slow energy channels allow for non-local food-web stability. a, A schematic diagram assessing transient non-equilibrium stability using post-perturbation predator densities. After a perturbation, D_R is the increase in density required to reach equilibrium, T_R is the time required to reach equilibrium, and OS is the overshoot in predator density. The metrics measured quantify the rate at which food webs react to perturbations and the degree to which overshoot is dampened by food-web interactions. **b**, The relationship between attack rate ratio and the transient non-equilibrium stability of the food webs.

activities. For example, the literature is replete with documented losses of top predators (Supplementary Table 3a), and, in cases where ensuing food-web dynamics have been documented, diversity has abruptly and dramatically declined (termed 'ecological meltdown' by Terborgh and colleagues[41]). In addition, human activities have also frequently resulted in dramatic changes to both the flux of energy into food webs, and the process rates within energy channels (Supplementary Table 3b). Nutrient loading to ecosystems often drives almost complete dominance by a specific energy channel such that we effectively have homogenized production in such systems. Ecosystems can often resist such loading up to a point whereupon a catastrophic shift occurs, resulting in both the loss of diversity and stability of these ecosystems[42]. Thus, it seems that human actions are not only reducing the diversity of our natural ecosystems, but more importantly they are probably eroding the very structures that confer stability to food webs in nature.

METHODS

We used food-web data that contained consumption rates for all consumer–resource interactions. Within the soil food webs, only carbon derived from detrital sources was incorporated. Interactions within food webs were all converted to flux rates of $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Producers and detritus were assigned trophic positions of 1 and, where not reported directly, higher-order consumer trophic positions (TP_C) were calculated as:

$$TP_C = 1 + \sum_{1}^{n} P_C \times TP_R$$

where n is the number of resources consumed by the consumer, P_C is the proportion of the consumers' diet accounted for by a resource, and TP_R is the trophic position of the resource. In a similar manner, the proportion of carbon derived from basal resources ($\%BR_C$) was calculated as:

$$\%BR_C = \sum_{1}^{n} P_C \times \%BR_R$$

where n is the number of resources consumed by the consumer, P_C is the proportion of the consumers' diet accounted for by a resource, and $\%BR_R$ is the proportion of carbon derived from the basal resource in the resource being consumed. In some cases, for calculating both trophic position and the proportion of carbon derived from a basal resource, loops within food webs necessitated iterations of the calculations.

In cases where biomass production was not reported directly, production values were estimated by assuming equilibrium conditions using:

$$P_C = e \sum_{i \in R} CF_{CR}$$

where R is the basal resource, C is the consumer eating R, F_{CR} is the functional response of the consumer on the resource, and e is the conversion efficiency.

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