REVIEW AND SYNTHESIS

On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities

Douglas J. McCauley,[1]*,[†]
Gabriel Gellner,[2],[†] Neo D.
Martinez,[3] Richard J. Williams,[4]
Stuart A. Sandin,[5]
Fiorenza Micheli,[6] Peter J. Mumby[7]
and Kevin S. McCann[8]

Abstract

Classically, biomass partitioning across trophic levels was thought to add up to a pyramidal distribution. Numerous exceptions have, however, been noted including complete pyramidal inversions. Elevated levels of biomass top-heaviness (i.e. high consumer/resource biomass ratios) have been reported from Arctic tundra communities to Brazilian phytotelmata, and in species assemblages as diverse as those dominated by sharks and ants. We highlight two major pathways for creating top-heaviness, via: (1) endogenous channels that enhance energy transfer across trophic boundaries within a community and (2) exogenous pathways that transfer energy into communities from across spatial and temporal boundaries. Consumer–resource models and allometric trophic network models combined with niche models reveal the nature of core mechanisms for promoting top-heaviness. Outputs from these models suggest that top-heavy communities can be stable, but they also reveal sources of instability. Humans are both increasing and decreasing top-heaviness in nature with ecological consequences. Current and future research on the drivers of top-heaviness can help elucidate fundamental mechanisms that shape the architecture of ecological communities and govern energy flux within and between communities. Questions emerging from the study of top-heaviness also usefully draw attention to the incompleteness and inconsistency by which ecologists often establish definitional boundaries for communities.

Keywords

Allometric trophic network, biomass, boundary, community, consumer, inverted pyramid, resource, stability, top-heavy, trophic.

Ecology Letters (2018)

INTRODUCTION

One of the earliest aims of ecology has been to identify the rules that govern how biomass is distributed within a community. Standard predictions governing community structure have been heavily influenced by the historical expectation that *c.* 10% of the biomass in any given trophic level should be converted into the biomass of consumers in the next trophic level (Lindeman 1942). In deference to these transfer inefficiencies, standing stock biomass distributions between trophic levels have been assumed to conform to the shape of a pyramid (Elton 1927). In the words of Lindeman (1942): 'The weight of all predators must always be much lower than that of all food animals, and the total weight of the latter much lower than the plant production'. Exceptions to this pyramidal conformation, however, were noted early on (Harvey 1950; Ravera 1969). In the most deviant instances, this structuring assumes the shape of an inverted pyramid, defined here as an instance where consumer biomass exceeds resource biomass at multiple trophic levels (Sandin & Zgliczynski 2015). However, we here wish to focus not only on truly inverted pyramidal situations, but more generally on situations where the consumer–resource biomass relationship is considerably less 'bottom-heavy'. We acknowledge that drawing a distinct line where this occurs is difficult and subjective. We elect to focus here upon situations where the consumer to resource (C/R) biomass ratio in any given trophic level approaches or exceeds unity and call all such systems 'top-heavy' (i.e. more top-heavy than in a Lindeman scenario) (Jonsson 2017). Consequently, we measure and examine the degree of top-heaviness throughout using C/R biomass ratios. For instance, in Pacific coral reef fish communities, ratios of the biomass of predatory fishes to prey fishes can range from < 0.01 (i.e. more bottom-heavy) to well over 1 (i.e. more top-heavy) (Williams *et al.* 2011). Patterns of top-heaviness have also

[1]*University of California Santa Barbara, Ecology, Evolution and Marine Biology & Marine Science Institute, Santa Barbara, CA 93106, USA*
[2]*Colorado State University, Biology, Fort Collins, CO 80523, USA*
[3]*Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721, USA*
[4]*Vibrant Data Inc., 943 Clay Street, San Francisco, CA 94108, USA*
[5]*Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 8750 Biological Grade, La Jolla, CA 92037, USA*

[6]*Hopkins Marine Station and Center for Ocean Solutions, Stanford University, Pacific Grove, CA 93950, USA*
[7]*Marine Spatial Ecology Lab, School of Biological Sciences, Goddard Bldg, The University of Queensland, St Lucia Qld. 4072, Australia*
[8]*University of Guelph, Integrative Biology, Guelph, ON N1G 2W1, Canada*
Correspondence: E-mail: dmccauley@ucsb.edu
[†]*These authors contributed equally to this work.*

Box 1

In this review we present empirical or theoretical evidence for a diversity of endogenous (i.e. drivers from within a community) and exogenous (i.e. drivers external to a focal community) pathways that are hypothesised to contribute to the build-up of inverted biomass pyramids or otherwise top-heavy biomass distributions (a). We summarise here eight such sometimes independent and sometimes overlapping mechanisms that appear to increase the top-heaviness of biomass distributions in tri-trophic food webs consisting of resources (R), consumers (C) and predators (P) situated within a discrete community/habitat (border demarcated by dotted grey square): (1) increased transfer efficiency across trophic boundaries (e.g. >10% biomass transfer) – transfer efficiency can be increased through a variety of mechanisms including increases in the edibility and nutrient content of foods or greater foraging efficiency of consumers; (2) rapid turnover rates – particularly in instances when turnover rates of a given trophic level are higher than the turnover rates of the trophic level above it; (3) moderate levels of habitat structural/morphological complexity can promote resource and prey production and facilitate predator access to different resource/prey pools; (4) the introduction of moderate levels of omnivory allows predators to sidestep trophic middlemen and inefficient feeding pathways; (5) historical subsidisation from consumers or resources that were previously present in a food web can increase the contemporary biomass of predators; (6) increases in the size of higher trophic level organisms relative to the size of organisms in lower trophic levels; (7) the physical or biological vectoring of allochthonous subsidies to predators and consumers; and (8) the active movement of mobile consumers beyond community boundaries to capture allochthonous energy stored in other systems – the resultant effects on top-heaviness are particularly pronounced when this draw is obtained from multiple asynchronously productive resource patches.

Factors that impede the build-up of top-heaviness and maintain more Eltonian patterns of biomass distribution in food webs and trophic pairings (b) include the down-regulation of mechanisms 1–8 as well as: (9) increased rates of intraguild predation/cannibalism; (10) the presence of more costly metabolic physiologies, like endothermy, in dominant predators; (11) long generation times and reduced edibility of resources and prey that slow cross-trophic level transfers of energy; (12) the direct extraction of consumers or top-level predators by external predators (e.g. humans); and (13) interference competition between predators or consumers.

(a) Promote top-heaviness

(b) Inhibit top-heaviness
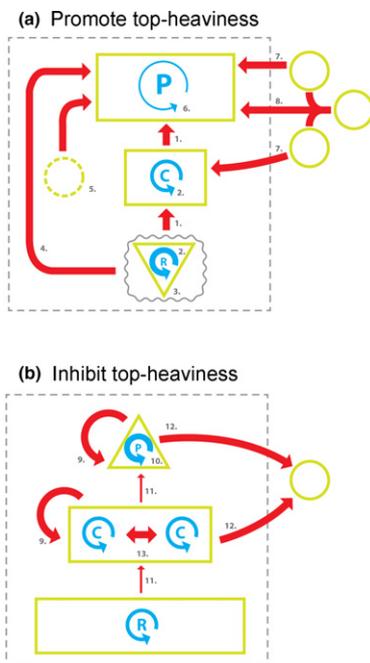
Photo credit: Brian Zgliczynski

been described in the rich literature on size and abundance spectra (Kerr & Dickie 2001; Jennings & Mackinson 2003; Trebilco *et al.* 2013). For example, in an examination of over 100 food webs from terrestrial, marine and estuarine systems, Reuman *et al.* (2008) found widespread evidence of top-heaviness.

Wherever observed, extreme increases in top-heaviness and divergences from the pyramidal structuring have long intrigued and confused ecologists. Superficially, they appear to contradict thermodynamic principles representing instances where more biological matter has been generated from less. Ecological communities, of course, do not operate above thermodynamic laws. The real scientific appeal of these oddly structured systems thus becomes the insight they offer into how increases in energy transfer efficiency can be achieved in living systems and what they reveal about non-obvious pathways by which matter and energy are routed within and between communities. All such discussion of the build-up of

top-heaviness refers to biomass distributions. We examine top-heaviness in both entire food webs and in paired consumer–resource interactions. We treat these cases together because many of the mechanisms that promote top-heaviness at the level of the entire food web are emergent manifestations of the properties that increase top-heaviness in specific trophic pairings. We ask: (1) What are the mechanisms that create top-heaviness? (2) Where do we find top-heavy systems? (3) How stable are these peculiar configurations? (4) How are humans shifting biomass distribution patterns and what are the emergent effects of such shifts? and (5) In what instances can top-heaviness be illusory?

ENDOGENOUS AND EXOGENOUS MECHANISMS FOR GENERATING TOP-HEAVINESS

We recognise two major classes of mechanisms that contribute to the build-up of top-heaviness: (1) endogenous mechanisms involving processes internal to a local ecological community and (2) exogenous mechanisms in which top-heaviness is created via transfers of material and energy across boundaries of time or space into recipient focal communities. Key mechanisms that promote or inhibit the build-up of top-heaviness are summarised in Box 1.

Endogenous mechanisms

One important endogenous pathway for building up top-heaviness involves increasing the efficiency of biomass transfer across trophic levels. It is well known that cross-boundary biomass transfer rates are not fixed at 10% (Turner 1970; Strayer 1991; Gaedke & Straile 1994; Slobodkin 2001). Cross-trophic biomass loss can be caused by myriad internal mechanisms such as inefficiencies in digestion/assimilation, losses during respiration and non-consumptive resource/prey mortality. Mechanisms that minimise these losses play an important role in regulating energy flux and facilitating the build-up of top-heaviness (Jennings et al. 2007).

While there are some contexts in which biomass loss is advantageous (e.g. fruit consumption by seed dispersers), organisms typically limit such losses via adaptations that thwart consumption outright (e.g. camouflage), as well those that reduce the efficiency with which, once captured, their biomass can be usefully metabolised by consumers (e.g. plant chemical defences). Maintaining these defences is costly, but is extremely effective at slowing consumption (e.g. > 90% observed reductions in intake of well-defended resources (Hay et al. 1994) and vertical flux of energy and biomass (deBruyn et al. 2007).

In addition to these intertrophic struggles for the control of energy, an organism's own physiology controls the efficiency by which captured resources are converted into biomass. Evolution has generated a range of pathways to promote these efficiencies. For instance, different metabolic adaptations can increase processing efficiency, reduce energy leakage and increase the diversity of resources that can feed into any given consumer and up a local food web. Symbiotic innovations in the gut microbial community permitted termites, for example, to effectively process lignocellulose, opening up a novel route for a vast amount of energy stored in woody plant tissue to be rapidly routed into

circulation in food webs (Ohkuma 2008). It is generally believed that invertebrate ectotherms process energy more efficiently than vertebrate endotherms, and vertebrate ectotherms fall somewhere in between (Yodzis 1984). This would seem to make top-heaviness more likely in trophic interactions involving ectothermic consumers. The predominance of ectothermic consumers in many top-heavy systems (Table 1, Cebrian et al. 2009) provides preliminary support for this hypothesis.

Rates of endogenous energy transfer and biomass accumulation are also affected by resource nutrition. Higher quality resource species or populations can more effectively be translated into consumer biomass. This is particularly so in nutrient impoverished communities where consumers are regulated by limiting nutrients (Sterner & Hessen 1994; Müller-Navarra et al. 2000). Top-heaviness has been found to be significantly elevated in a wide variety of contexts where consumers have access to more nutritious resource pools (Cebrian et al. 2009).

The behavioural ecology of consumers within any given community can also regulate top-heaviness, particularly as such behaviours relate to foraging. A good example is diet breadth. Omnivores that feed at multiple trophic levels or on a broad array of prey are believed to be able to route energy up food webs more effectively (Shurin et al. 2006; deBruyn et al. 2007). This occurs because they are capable of side-stepping inefficient feeding pathways and can draw in energy directly from alternate resource pools within a community (Utne-Palm et al. 2010). Conversely, intermediate-level consumer species that exhibit a high degree of cannibalism or consumer assemblages that exhibit high rates of intraguild and intratrophic predation can choke rates of vertical energy flux (deBruyn et al. 2007).

Mismatch in turnover rates of resources and consumers is one of the oldest and often advanced internal explanations for building top-heaviness (Odum 1971; O'Neill 1976). Disparity in turnover rates is believed to create the opportunity for producers to rapidly pump biomass up a food web that is captured and stored by more slowly turning over consumers (although see Discussion below concerning inextricable links between turnover and loss rates). The archetypal inverted pyramids have been reported from plankton communities (Dortch & Packard 1989; Cho & Azam 1990; Gasol et al. 1997; Arístegui et al. 2009). In these systems, producers (i.e. phytoplankton) typically have much shorter generation times than consumers (i.e. heterotrophic consumers, zooplankton). Turnover rates themselves are regulated by a suite of interrelated life-history parameters (e.g. body size, metabolic rate, life span).

Body size is often relied upon as a visible proxy for judging imbalances in turnover rates. Differences in the ratio of consumer to resource body size are regularly highlighted as factors that facilitate top-heaviness, particularly in size spectrum research (Jennings et al. 2007; Barnes et al. 2010; Jonsson 2017). Inverted pyramids and extremely top-heavy trophic pyramids have been frequently documented in aquatic contexts, where consumer to resource body size ratios differ significantly (Brose et al. 2006). For example, body size ratios between fish and their zooplankton prey can approach 10^6, and those between fish and phytoplankton may exceed 10^{10} (Cohen et al. 2003).

The physical environment can also regulate vertical energy flow and influence top-heaviness. For example, the density

Table 1 A representative sampling of ecological communities that exhibit extremely top-heavy biomass distributions.

References	System	Locality	C/R pairing	Max C/R	V/I	Met.
Simon *et al.* (2004)	Fresh.	South Island, New Zealand	Trout/aquatic insects	0.9	V	EC
Huryn (1998)	Fresh.	South Island, New Zealand	Trout/aquatic insects	1.0	V	EC
Del Giorgio *et al.* (1999)	Fresh.	20 Québec lakes, Canada	Heterotroph/autotroph	2.0	I	EC
Benke (1976)	Fresh.	Inland pond, USA	Dragonfly larvae/ invertebrate prey	2-3	I	EC
Moustaka-Gouni *et al.* (2006)	Fresh.	Lake Kastoria, Greece	Heterotroph/autotroph	5.1	I	EC
Cyr and Peters (1996)	Fresh.	24 global lakes and reservoirs	Zooplankton/phytoplankton	5.7	I	EC
Romero *et al.* (2016)	Fresh.	Brazil bromeliad phytotelmata	Predatory insect/detritivore	156	I	EC
Mourier *et al.* (2016)	Marine	French Polynesia	Predatory fishes/prey fishes	1.0	V	EC
Herndl (1991)	Marine	Atlantic barrier reef	Bacteria/phytoplankton	1.1	I	EC
Harvey (1950)	Marine	English Channel	Pelagic fish/zooplankton	1.2	V	EC
Buck *et al.* (1996)	Marine	North Atlantic Basin	Heterotroph/autotroph	1.4	I	EC
Williams *et al.* (2011)	Marine	N Mariana Archipelago	Predatory fishes/prey fishes	1.6	V	EC
Cho & Azam (1990)	Marine	North Pacific	Bacteria/phytoplankton	2-3	I	EC
De León *et al.* (2016)	Marine	N Galapagos Islands	Sharks/prey fishes	2.4	V	EC
Carriquiry *et al.* (2013)	Marine	Mexican Caribbean	Predatory fishes/prey fishes	3.9	V	EC
Sandin *et al.* (2008)	Marine	Northern Line Islands	Predatory fishes/prey fishes	4.0	V	EC
Friedlander & DeMartini (2002)	Marine	NW Hawaiian Islands	Predatory fishes/prey fishes	8.0	V	EC
Gasol *et al.* (1997)	Marine	Various, global	Heterotroph/autotroph	15.9	I	EC
Guidetti *et al.* (2014)	Marine	Adriatic Sea	Predatory fishes/prey fishes	23.3	V	EC
Ernst and Buddle (2013)	Terr.	Canadian subarctic tundra	Carnivorous beetles/ prey beetles	2.3	I	EC
Korpimäki *et al.* (1991)*	Terr.	Western Finland	Least weasel/vole	3.7	V	EN
Rodda *et al.* (1997)	Terr.	Guam	Snake/bird	4.0	V	EN
Majer *et al.* (1990)	Terr.	Northern Australia	Ants/arthropod prey	6.3	I	EC

Here consumer to resource biomass ratios (C/R) are used to judge the degree of top-heaviness in these systems. A description of the locality, affiliated system [fresh. (freshwater), marine or terr. (terrestrial)], and taxa involved in the C/R biomass pairing is provided. C/R maxima are reported from studies that provide biomass reporting for > 1 study site. Consumers in these groupings are categorised as all invertebrate (I) or having at least one vertebrate (V) and as having all ectothermic (EC) members of the pair or at least one endothermic (EN) member.
*Biomass values extrapolated from reported density values.

and diversity of physical refuges for prey regulate predation rates, govern competition and shape productivity – all factors that can influence within community trophic flux (Rogers *et al.* 2014). Theory suggests that intermediate levels of habitat complexity may produce the greatest amounts of sustained top-heaviness (Wang *et al.* 2009). This is hypothesised to occur because these intermediate-sized refuges moderate predation, prevent prey extinction and promote prey recruitment (Crowder & Cooper 1982).

Exogenous mechanisms

Top-heaviness can also be created by external dynamics that provide energy to consumers in a focal community from across temporal and spatial boundaries. Intermittent resource pulses provide an apt example of how historically sourced subsidies can promote top-heaviness (Ostfeld & Keesing 2000; Takimoto *et al.* 2008; Yang *et al.* 2008). Mass tree fruiting can unleash large, but short-lived, floods of energy into communities which often result in explosions in consumer biomass, typically after some time lag (King 1983; Wright *et al.* 1999; Curran & Leighton 2000). The iconic case of the snowshoe hare (*Lepus americanus*) and the Canadian lynx (*Lynx canadensis*) provides another example of temporal subsidisation. Here booms in hare biomass cause concomitant, but out of phase, increases in lynx

abundance that intermittently boost system top-heaviness (Elton & Nicholson 1942; Krebs *et al.* 2001).

Another exogenous route for building top-heaviness is by directing allochthonous energy across spatial boundaries directly to top trophic levels in a community (Trebilco *et al.* 2016). Such subsidies can be imported to consumers passively (e.g. nutrients vectoring; Polis & Hurd 1995) or actively (e.g. motile prey enter a new community; Sabo & Power 2002; Mourier *et al.* 2016). Consumers themselves can also pursue new resource pools in other communities (Schindler & Scheuerell 2002). When there is some heterogeneity in the synchronicity of the productivity of these allochthonous source pools, predators can increase in number and inflate top-heaviness (Rooney *et al.* 2006), a phenomenon sometimes termed the 'bird feeder effect' (Eveleigh *et al.* (2007).

Top-heaviness and heterotrophic dominancy in a variety of planktonic or sessile marine invertebrate communities has been explained as a result of the cross-boundary import of resources (Bustamante *et al.* 1995; Duarte *et al.* 1999, 2013). At least part of the extreme top-heaviness observed in less-fished reef fish communities (Stevenson *et al.* 2007; Sandin *et al.* 2008; Guidetti *et al.* 2014; Simpfendorfer & Heupel 2016) appears to be facilitated by consumer vagility. Large and mobile reef predators appear able to travel into neighbouring communities and collect a large proportion of prey

from these external sources (McCauley et al. 2012c; de León et al. 2016). Because mobility often scales with animal body size (McCann et al. 2005; McCauley et al. 2015), communities that contain larger bodied consumers may be more predisposed to becoming top-heavy via this pathway.

Physical habitat attributes also appear to regulate some of these exogenous mechanisms for the formation of top-heaviness. Ecosystem size and shape are two examples. In many contexts, macrohabitats can become increasingly tightly coupled in smaller-sized ecosystems, a factor that may promote top-heaviness. Such dynamics have been observed in small lakes where the heightened adjacency of pelagic and littoral habitats provides pelagic predators, like lake trout, increased access to littoral prey (Tunney et al. 2012). Ecosystem shape can also regulate connectivity between neighbouring habitats and the effectiveness of top consumers in tapping into exogenous resources pools (Dolson et al. 2009). Simple circular lake ecosystems with low morphological complexity are known to exhibit a greater degree of resource coupling and top consumers in these systems are more omnivorous – both factors that should promote top-heaviness. Environmental fluid dynamics can further influence community structure. Seasonal flushing regimes and mixing dynamics have been observed to regulate nutrient movement across aquatic ecosystem boundaries and to control cyclic transitioning between more top-heavy and less top-heavy biomass structuring (Moustaka-Gouni et al. 2006; Boit et al. 2012; Fuks et al. 2012).

THEORETICAL EVIDENCE FOR DIVERSE PATHWAYS TO TOP-HEAVINESS

Here we use two bodies of ecological theory to test possible endogenous and exogenous drivers of top-heaviness. This theory aids also in evaluating the comparative strength and efficiency of different candidate pathways for building top-heaviness. First, we employ modular, refuge-free, non-spatial Lotka–Volterra style models that are typically represented as two-way (consumer–resource) and three-level (predator–consumer–resource) interaction sets (Murdoch et al. 2013). Second, we also employ insight from more realistically complex ecological models that integrate the niche model of food web topology (Williams & Martinez 2000) with the allometric trophic network model, a generalised n-species bioenergetic model of consumer–resource interactions (Williams & Martinez 2004; Williams et al. 2007; Berlow et al. 2009); hereafter referred to collectively as the ATNN (allometric trophic niche network) model. The ATNN framework permits testing to be conducted surrounding the influence of basic consumer attributes such as size and consumer type (e.g. vertebrate vs. invertebrate) on top-heaviness.

Tests of endogenous mechanisms

Consumer–resource models (see Appendix S1 for equations and definitions) illustrate the opportunity for diverse endogenous pathways to create top-heaviness. Three-level predator–consumer–resource models, for example, illustrate that communities can become more top-heavy [proxied here using predator to consumer biomass ratios (P/C)] whenever flux to

the consumer population is high (Fig. 1a). Flux is defined in an analogous manner to previous work (Gilbert et al. 2014) where an increase in flux from one trophic compartment to another is achieved by changes to parameters e (conversion efficiency), a (attack rate), K (resource carrying capacity relative to consumer biomass loss rates [m]) (Wang et al. 2008; Rip & McCann 2011; Gilbert et al. 2014). These results are consistent with other implementations of consumer–resource models that illustrate that top-heavy patterns of biomass distribution are not uncommon and that mechanisms, such as density-dependent mortality, that dissipate energy in food chains can mute this top-heaviness (Jonsson 2017).
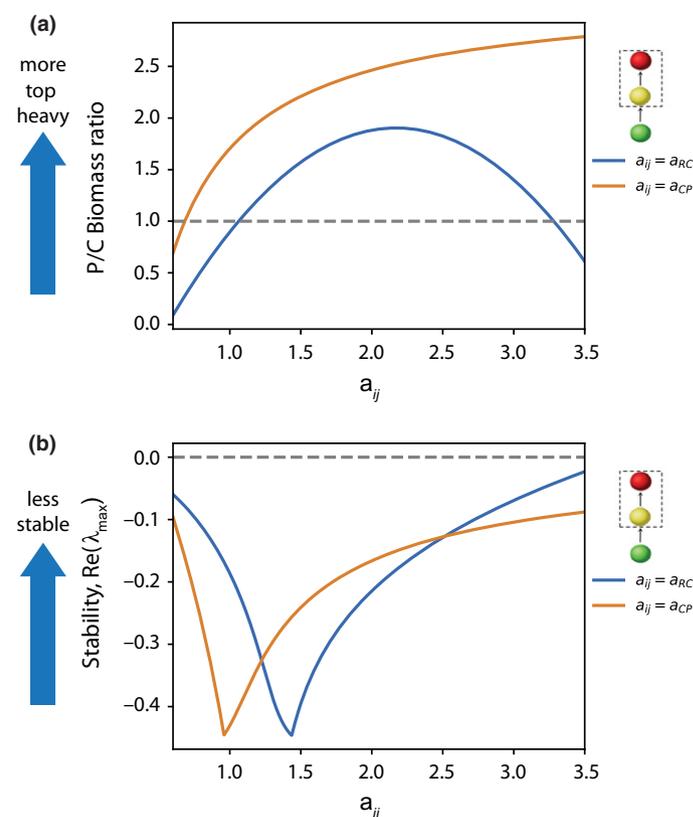
Figure 1 Effects of increasing energy flux across trophic boundaries on system top-heaviness (a) and community stability (b). The build-up of top-heaviness is evaluated in a three-level model (predator, consumer, resource; PCR; see Appendix S1 for model description and parameter values) by examining the predator to consumer (P/C) biomass ratio change as cross-trophic flux rates change. The grey line indicates where P/C biomass ratio = 1. Increasing rates of flux to the top predator (varying the attack rate of the predator on the consumer, a_{CP}) leads to ever increasing top-heaviness. Although increased flux to the consumer (varying the attack rate of the consumer on the resource, a_{CP}) leads to an initial increase in top-heaviness, however, once the flux becomes large enough, the top-heaviness begins to decrease because the consumer's high attack rate on the resource begins to depress the effective productivity of the system. The real part of the maximum eigenvalues [$Re(\lambda_{max})$] plotted in panel (b) are used as a measure of system stability. Systems that increase in top-heaviness as a result of stimulated cross-trophic flux exhibit an initial increase in stability that is caused by the influx of new biomass entering the system. This is eventually followed by a destabilisation phase that results from over-fuelling of predator growth.
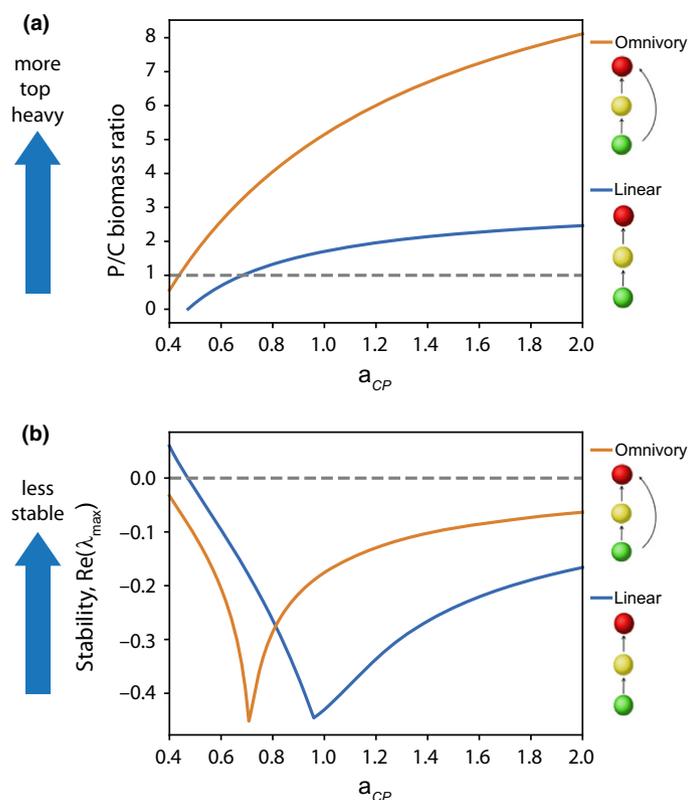
Figure 2 Effects of introducing moderate amounts of omnivory on (a) top-heaviness (measured as predator to consumer [P/C] biomass ratio) and (b) stability in a three-level food chain (i.e. predator feeds on consumer *and* resource) over a range of trophic flux rates (increasing flux to the top predator by increasing the attack rate of the predator on the consumer, a_{CP}, see Fig. 1 and Appendix S1 for model description and parameter values). The introduction of moderate strength omnivory permits a significant increase in overall top-heaviness relative to linear models that lack omnivory. The real part of the maximum eigenvalues [$Re(\lambda_{max})$] plotted in panel (b) are used as a measure of system stability.

Introducing omnivory into these same models further demonstrates that multi-level feeding by predators also promotes top-heaviness (Fig. 2). The observed inflation of top-heaviness is achieved by effectively cutting out some of the inefficiencies associated with obtaining energy exclusively through intermediate consumers that act as energetic 'middlemen'. These effects, however, are only apparent so long as the intensity of omnivory is kept relatively constrained (Holt & Polis 1997; McCann & Hastings 1997; Fig. 2). Strong omnivory within a community can intensify the direct and indirect effects of top predators on intermediate consumers and eventually lead to the extinction of the predator, the consumer or both.

Results from the ATNN model (see Appendix S2 for equations and definitions) suggest that, contrary to some suggestions, top-heaviness that is created via endogenous mechanisms can theoretically be quite common (Table S1). The identity of the consumers in these local webs appears also to matter. ATNN webs in which consumers were modelled as vertebrates were, on average, less top-heavy than invertebrate-only webs (Table S1, Appendix S3), a result that likely arises from the elevated trophic transfer efficiencies of invertebrate consumers (Yodzis 1984). Interestingly, the most top-heavy ATNN webs
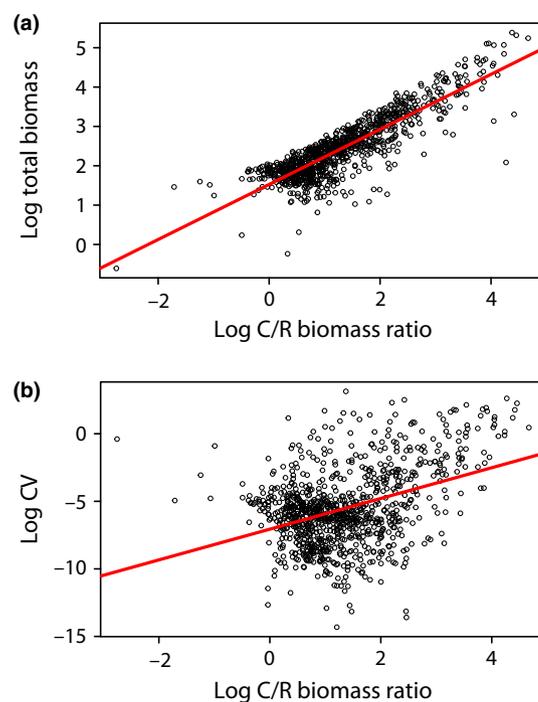
Figure 3 Relationships between top-heaviness (consumer to resource biomass ratio; C/R) and (a) total system biomass or sum of the biomass in all trophic levels ($R^2 = 0.75$, slope = 0.70, $P < 0.0001$) and (b) system stability as measured using coefficients of variation of time-averaged total system biomass or CV ($R^2 = 0.15$, slope = 1.14, $P < 0.0001$) as calculated using allometric trophic network models combined with the niche model ($N = 963$ replicates; see Appendix S2 and S3 for model description and parameter values). All values are log-transformed (logarithm base *e*). Separate analyses in which replicate food webs containing very large body size consumers were removed from the data set and in which alternate measures of top-heaviness were calculated are reported in Figs S1 and S2 respectively (Appendix S3).

were also the systems that contained the greatest amount of whole system biomass – an observation that held true in all scenarios tested (Fig. 3a). This relationship does not appear to be driven exclusively by the contribution of webs containing very large body mass consumers (Fig. S1), but the strength of this observed relationship appears to vary depending on precisely how top-heaviness is defined (Fig. S2; Appendix S3).

In keeping with observations that rates of endogenous trophic flux influence top-heaviness, we predicted that any factors that impede vertical energy flow within a community, such as intraspecific interference, intratrophic interference or intraguild predation, should drive systems to become less top-heavy (deBruyn *et al.* 2007). These predictions were born out in ATNN models where including interference reduced top-heaviness on average by *c.* 30% (Table S1). Similarly, consumer–resource models containing predator interference became less top-heavy under the model parameterisations that we explored (Fig. S3).

Suggestions that top-heaviness may be promoted by mismatch in internal turnover rates are also borne out in the ATNN modelled results. ATNN webs including larger cross-trophic body size differentials were, on average, more top-heavy; size here was used to serve as a surrogate measure of
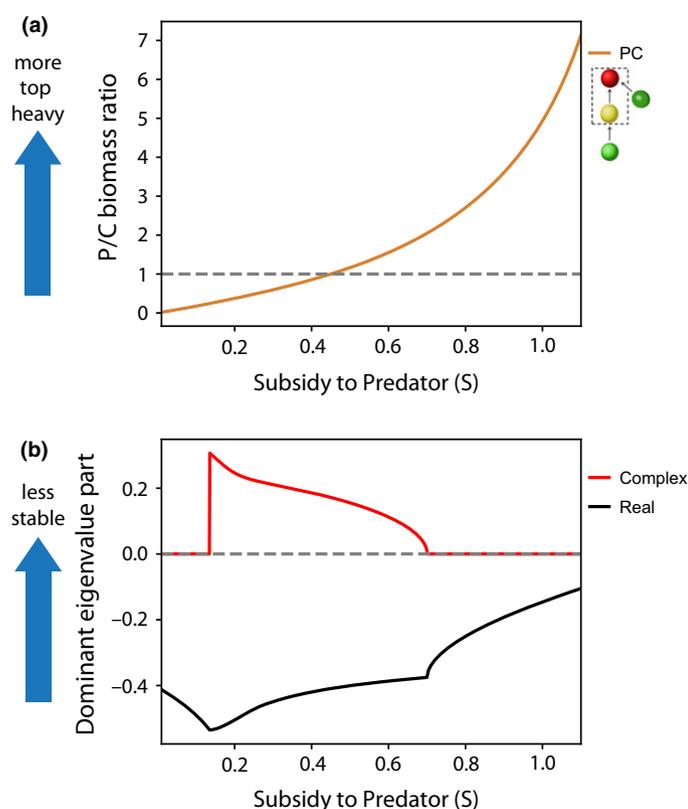
Figure 4 Effects of direct allochthonous subsidisation to predators (S) in a three-level system (predator, consumer, resource) on (a) top-heaviness (measured as P/C biomass ratio) and (b) stability (see Appendix S1 for model description and parameter values). As additional external energy is routed to predators they are able to increase in biomass and the top-heaviness of the system builds, eventually surpassing the demarcated 1 : 1 P/C boundary (grey line). The stability plot (b) depicts both the real and complex portion of the dominant eigenvalue for this subsidised system. As these subsidies begin to enter the system, the complex portion of the eigenvalue is zero and the real component becomes more negative and more stable. However, as subsidisation and top-heaviness increase further, the system becomes destabilised as increased top-down control by predators reduces consumer biomass.

differences in turnover rates (Appendix S3). Outputs from consumer–resource models illustrate that the precise manner by which differences in turnover rates regulate top-heaviness is more multi-faceted than is sometimes acknowledged. Discussions of connections between increased top-heaviness and high turnover rates traditionally emphasise that increased turnover increases upward flux of biomass to consumers, but seldom acknowledge that high turnover also means increased mortality rates of resources and biomass loss from ecological systems. The behaviour of these models indicates that a large amount of energy entering the trophic level, and a small loss rate of consumers becomes the optimal recipe for generating top-heaviness.

Tests of exogenous mechanisms

Consumer–resource theory also demonstrates that top-heaviness can be created by transfers across temporal boundaries. These types of exogenously formed top-heaviness are

achieved via pulsed influxes of resource biomass into the consumer pool, coupled with low consumer loss rate due to longer consumer generation times. The same theory illustrates the efficiency of the various routes through which external spatial subsidies shape biomass distributions. For example, Fig. 4a shows how increasing the rate of allochthonous subsidisation increases the top-heaviness of a three-level food chain (see Appendix S1 for equations). Here, we assume a constant external subsidy rate and that the consumption of this subsidy by the predator has no dynamical impact on the resource behind the subsidy. This decoupling of resource and predator provides the means for the predator within a local community to attain high densities. Others have examined the more realistic case of seasonal fluctuations in spatial subsidies and found similar effects on biomass distributions (Takimoto *et al.* 2002).

Consumer–resource models also illustrate how top-heavy systems can form when mobile consumers themselves tap into spatially external energy pools. This type of exogenous top-heaviness is made apparent in models that allow a consumer to feed off two different spatially segregated but competing resources (see Appendix S1 for model equations). Resources in different habitats are allowed to compete in this scenario because competition can often occur across habitats; for example, spatially segregated fungi and bacteria compete for nutrients travelling through a soil matrix. In this framework, we begin by assuming that the consumer feeds preferentially on the strongest competitor and then we modulate the degree the consumer couples into the alternative resource habitat. Here we do not assume switching, but the qualitative result remains the same if we do. As the consumer increasingly couples to the alternative resource, it tends to increase its biomass and consequently it increases the top-heaviness of these systems (Fig. 5). In fact, in this case the consumer biomass continually increases until one of the resources reaches low densities.

WHERE DOES TOP-HEAVINESS OCCUR?

Top-heavy or inverted pyramid systems have been documented in diverse settings including tundras, coral reefs, kelp forests, phytotelmata, lakes, rivers and marine planktonic communities (Table 1). Examples are common of top-heaviness occurring in trophic pairings that include an autotrophic member, and there is good evidence that certain plant traits can readily promote top-heaviness (Cebrian & Lartigue 2004; Shurin *et al.* 2006; Chapin *et al.* 2012). Examples, however, of top-heaviness are also known in trophic pairings involving predators animals (Table 1).

Top-heaviness appears to be shaped by the dynamics of local ecosystem ecology. In planktonic systems, for example, top-heaviness has been observed to be especially accentuated in oligotrophic contexts (Herndl 1991). The phenomenon has been attributed to mechanisms including the dominance of smaller sized autotrophs (which exacerbate differences in consumer to resource turnover rates) and differential response dynamics of subsidy users in oligotrophic zones (allochthonous subsidies may disproportionately benefit heterotrophs) (Buck *et al.* 1996; Del Giorgio *et al.* 1999; Duarte
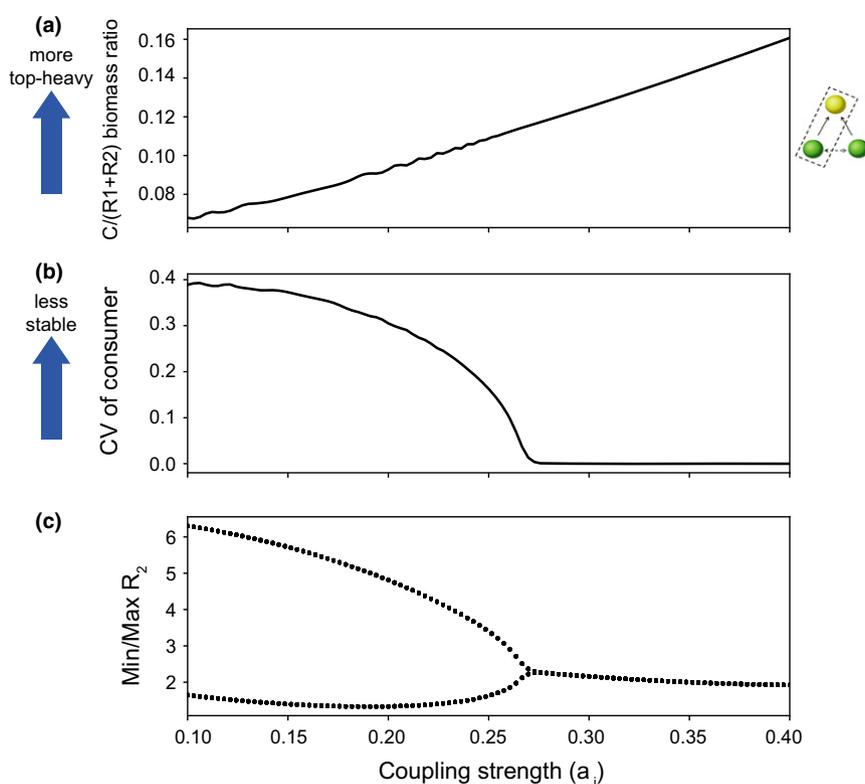
Figure 5 The effects of consumer (C) coupling to an alternate resource (R) in a two-level food chain on (a) top-heaviness (measured as the mean C/(R1 + R2) biomass ratio; see Appendix S1 for model description and parameter values) and (b) stability measured by the coefficient of variation of the consumer (CV). Here a single consumer feeds on two different resources in competition, but it is allowed to couple with increasing intensity (by modulating attack rate) to the competitively sub-dominant resource. As the strength of this coupling increases, the system becomes increasingly top-heavy (a). This initial increase in top-heaviness is associated with an increase in system stability (b). Increased coupling strength dampens out the cycling (c) of the focal resource population (i.e. region with different minimum and maximum), however, this behaviour eventually drives the suppressed resource to extinction.

et al. 2000; Gasol *et al.* 2009; Tamelander *et al.* 2013; Harfoot *et al.* 2014).

Many cases of inverted pyramids or top-heaviness come from aquatic systems – both freshwater and marine (Polis 1999; Cebrian *et al.* 2009; Rip & McCann 2011; Chapin *et al.* 2012; Sandin & Zgliczynski 2015). Predictive models suggest that top-heaviness/inverted pyramids should be much more common in aquatic ecosystems (Harfoot *et al.* 2014). Our parameterisations of ATNN models, which reveal that top-heaviness can be relatively common, are likewise more closely aligned structurally to aquatic systems (Appendix S2). Top-heaviness does, however, occur in terrestrial communities (Table 1; Reuman *et al.* 2008).

A variety of hypotheses have been advanced to explain why top-heaviness is so commonly observed in aquatic ecosystems (Shurin *et al.* 2006; Rip & McCann 2011). These include (1) aquatic producers are often less well-defended than terrestrial primary producers and consequently aquatic herbivores may be 3–4 times more efficient at assimilating their biomass (Cyr & Pace 1993; Polis 1999; Cebrian & Lartigue 2004); (2) autotrophs are larger in terrestrial systems, leading to smaller consumer to autotroph body size ratios and larger differences in turnover rates (e.g. turnover rates of phytoplankton are 1000 times greater than turnover of terrestrial forests and shrublands; Lindeman 1942; del Giorgio & Gasol 1995; Cebrian

1999; Brose *et al.* 2006; Rip & McCann 2011); (3) generalist consumers that can side step trophic bottlenecks may be more common in aquatic settings (Shurin *et al.* 2006); and (4) more open aquatic ecosystems with diffuse habitat boundaries may promote the import of allochthonous subsidies and facilitate extra-community foraging by mobile consumers (McCann *et al.* 2005; McCauley *et al.* 2012c).

THE STABILITY OF TOP-HEAVY ECOSYSTEMS

In structural engineering top-heaviness can be synonymous with instability – buildings constructed as inverted pyramids, for example, would seem prone to collapse. It is worthwhile asking whether the same is true of the architecture of extremely top-heavy communities. Interpretations of the ecological significance of top-heaviness should be influenced by whether such conformations are ephemeral or enduring.

We used the eigenvalues from our consumer–resource models to assay stability. We observed in both two and three trophic level models that increases in system top-heaviness are first associated with a stabilisation phase, but if top-heaviness continues to increase, this rapidly transitions to a destabilisation phase (Fig. 1b). The initial increase in system stability is generated as a result of the influx of consumer biomass. This stabilisation phase always occurs when a consumer is increasing from

zero or near zero densities and is common in these types of models (McCann 2011; Rip & McCann 2011; Gellner *et al.* 2016). Mathematically it occurs when a consumer has just passed through a 'transcritical' bifurcation causing the consumer to go from a stable equilibrium of zero density to a stable equilibrium with a small positive density. Associated with this increasing consumer biomass, arising from movement away from the transcritical bifurcation, the eigenvalues necessarily changes from zero to negative (i.e. system becomes more stable) (Guckenheimer & Holmes 1983). The subsequent destabilisation phase is caused by an over-fuelling of consumer growth, which creates increasing amounts of top-down pressure on prey and eventually oscillatory decays, or cyclic fluctuations in population dynamics that decrease as they approach the equilibrium until another zero eigenvalue occurs and the Hopf bifurcation is crossed (Guckenheimer & Holmes 1983; Rip & McCann 2011; Gellner *et al.* 2016). Note that this destabilisation phase occurs precisely when the eigenvalues become complex (i.e. show signs of oscillatory decay). Here, the addition of energy appears to simply increase oscillatory decay and/or oscillations. It is important, however, to note that the specific stability results shown in Figs 1 and 2 pertain to the parameterisations we explored in these consumer–resource models.

A different relationship is observed in aggregated views of the stability dynamics in ATNN models. Here increasing top-heaviness appears to result in linear increases in system instability (proxied using the coefficient of variation of time-averaged total system biomass), although the strength of this relationship is weak (Figs 3b, S1, S2). The observed differences in the stability dynamics between these low (i.e. consumer–resource) and high dimensional (i.e. ATNN) systems deserve further exploration.

Omnivory also shapes stability dynamics in top-heavy food webs. It has been demonstrated that weak omnivory generally stabilises top-heavy, food chain interactions (Fig. 2b; McCann & Hastings 1997; Gellner & McCann 2012). This result, however, is highly sensitive to the strength of omnivory. Strong omnivory engineers opposite effects in food webs by eventually driving intermediate consumers towards extinction, reducing the overall top-heaviness of system (as above) and decreasing system stability (Holt & Polis 1997).

Our examination of the stability dynamics of consumer–resource models where top-heaviness is created via exogenous pathways involving spatial subsidisation suggests that when predators and allochthonous resources are decoupled, predators are capable of attaining high densities and generating considerable top-heaviness, even as these communities remain relatively stable (Fig. 4). As in other consumer–resource models, this stability can only be sustained up to a point. This switch from a stabilising to destabilising phase occurs concurrent with the switch from a real dominant eigenvalue to a complex dominant eigenvalue, that is, where asymptotic dynamics switch from being dominated by monotonic to oscillatory decay (Fig. 4).

Comparable effects are seen in other models of exogenously created top-heaviness that capture the dynamics of the multi-resource bird feeder effect. We again observe initial increases in top-heaviness and stability, this time because the spatially discrete nature of these different resource patches confers stability to these otherwise 'excitable' systems that already show a propensity for overshoot dynamics (Fig. 5). This stabilisation phase here also ultimately degrades if system top-heaviness continues to increase. This instability occurs because (1) the system becomes unstable in the sense that one of the species is about to go locally extinct, and (2) the non-excitable dynamics (real eigenvalue) rapidly reduce the asynchrony of the two competing resources (Fig. 5). If we remove the asynchronous component of the resource dynamics, then this same model returns a theoretical result consistent with the classical theory discussed above. Thus, systems may exhibit similar levels of top-heaviness, but different long-term stability dynamics depending upon the synchronicity of the external subsidy pools that consumers tap into.

MISMEASURES OF TOP-HEAVINESS AND BOUNDARY DYNAMIC UNCERTAINTIES

Like all ecological phenomena, descriptions of biomass distributions in food webs are subject to measurement error. There is good evidence, for example, that traditional survey methods may inflate abundance estimates of large and mobile consumers, causing systems to appear artificially top-heavy (Soisalo & Cavalcanti 2006; Ward-Paige *et al.* 2010; McCauley *et al.* 2012b; Bradley *et al.* 2017). At the other end of the spectrum, there is also concern about methods used to inventory the biomass of the smallest ecosystem constituents or to assay the metabolic processes that serve as proxies for their biomass. Evaluating reports of top-heaviness in plankton communities becomes especially complicated because of the diverse methods available to estimate plankton abundance and the constant technological updating of these methods (Redalje & Laws 1981; Cho & Azam 1990; Buck *et al.* 1996; Ducklow & Doney 2013). Similar issues arise measuring macroscopically undetectable attached algae in streams (Power *et al.* 2013). While different methods can yield unsettlingly divergent absolute biomass estimates – some argue that the general conclusions about biomass structuring patterns remain robust and consistent (Gasol *et al.* 1997).

By necessity, constructing a portrait of how biomass is partitioned across trophic boundaries and within communities requires making assumptions about ecological boundary dynamics. The practice of delineating the spatial boundaries of ecological communities, however, is rarely straightforward (Post *et al.* 2007; Ricklefs 2008). Consider, for example, the challenges of accurately drawing physical boundaries around systems as fluid as marine pelagic communities. One possible rule of thumb for boundary determination could be defining community boundaries based on the member species with the largest home range. There are many situations, however, where this could be problematic. Would ecologists, for example, studying the dynamics of tide pools strongly influenced by seabird consumers extend the notion of a tide pool hundreds or thousands of kilometres to accord with the vagility of these seabirds (Wootton 1994)? It remains unclear how such issues surrounding boundary determination influence our perceptions of where top-heaviness is most common. Does top-heaviness appear more often, for example, in aquatic systems because ecologists purposefully or inadvertently tend to measure biomass distributions locally and overlook potentially

important patterns of cross-boundary connectivity that might be more apparent on land?

Similar concern applies to temporal boundary dynamics. As discussed, episodic and haphazardly delivered temporal subsidies can play an important role in creating top-heaviness or contributing to the formation of inverted pyramids. Failing to account for these historic contributions of energy and biomass complicates explanations of contemporary top-heaviness. One potentially useful way to accurately include information on how energy and ecological influence move across temporal boundaries to influence community structure is through the use of experiments that monitor biomass structuring patterns over long time periods (Duarte *et al.* 2000).

The process of delineating trophic boundaries can also have high uncertainty. Sometimes this confusion derives from incomplete knowledge of what consumers actually consume and where they feed (Roff *et al.* 2016). Unexpected discoveries are constantly being made about the feeding ecology of consumers both large and small (Davidson *et al.* 2003; McCauley *et al.* 2012c; Heupel *et al.* 2014). Such complications become severe in systems where bacteria are dominant resource consumers. This unique set of organisms takes in organic matter released from community members, consumes organic matter that they themselves release and some microbes and other plankton are even photoheterotrophic and compete with primary producers (Britschgi & Giovannoni 1991; Fuhrman 1992). Plankton researchers have criticised the trophically myopic view of the producer/heterotroph dichotomy (Flynn *et al.* 2012) and those that have employed correction factors for mixotrophy when measuring biomass distributions in plankton communities have observed significant decreases in their assessments of system top-heaviness (Anabalón *et al.* 2014).

There also remains the unresolved matter of where to place pathogens and parasites in food webs and how to integrate them into considerations of processes that regulate top-heaviness. These organisms draw energy from but do not usually wholly consume their hosts. Ecologist rarely do full cost accounting for food webs despite the fact that pathogens/parasite biomass can make up a substantial portion of the total community biomass. For instance, in estuaries, parasite biomass has been shown to exceed the biomass of top predators (Kuris *et al.* 2008). Whether such systems should be considered inverted pyramids or otherwise top-heavy remains an open question. Beyond these bulk effects on community biomass distribution, parasites and pathogens are also capable of regulating rates of consumption between existing predator and prey pairs, creating novel trophic interactions, modulating spatial subsidy pathways and altering overall rates of trophic energy transfer in ways that further shape community structure (Fuhrman 1992; Mouritsen & Poulin 2003; Lafferty *et al.* 2008; Sato *et al.* 2008; Lefèvre *et al.* 2009). Additional study and more consideration are needed to properly place both the biomass and the influence of pathogens and parasitic consumers into discussions about top-heaviness.

ANTHROPOGENIC EFFECTS UPON TOP-HEAVINESS

Loss of top-heaviness

Humans have the potential to profoundly reshape community biomass and size spectra distributions and alter patterns of top-heaviness (Zgliczynski & Sandin 2017). We appear especially capable of reducing top-heaviness because of the disproportionately strong selection we often exert on high trophic-level consumers (Fig. 6, Box 1). Humans often either prefer (e.g. bluefin tuna) or abhor (e.g. wolves) large-bodied top predators and avidly eat or otherwise extirpate them. As the biomass of top predators in a system decreases, people commonly turn their attention to the next most abundant large consumer, that is, fishing/hunting down the food web (Pauly *et al.* 1998; Payne *et al.* 2016; Young *et al.* 2016). This culling of the top predator du jour has precipitated a pattern
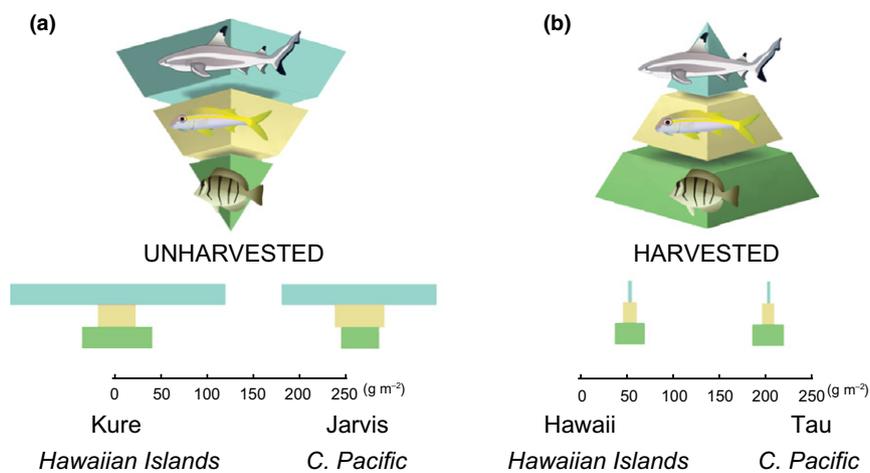
Figure 6 A comparison of biomass distribution patterns for coral reef fish communities (bottom row graphs) in unharvested (a) and harvested (b) contexts provides one illustration of how anthropogenic activity can erode top-heaviness. Biomass distribution plots are depicted for Kure Atoll (unharvested) and Hawaii (harvested) in the Hawaiian Islands, and Jarvis Island (unharvested) and Tau Island (harvested) in the central Pacific. Mean fish biomass values from these four localities are presented in the bottom graphs and were classified into three trophic groupings: predators (i.e. piscivores; blue), secondary consumers (i.e. omnivores, benthic invertivores and planktivores; yellow) and herbivore/detritivores (green). Bar graph values are re-centred relative to biomass scale bar for comparison. Data from Williams *et al.* (2011).

of iterative degradation of community top-heaviness in many ecosystems (Estes *et al.* 2011).

An additional avenue through which humans may reduce the top-heaviness is by disrupting the flow of spatial subsidies or interrupting the synchronicity of temporal subsidies. There are many routes by which this may happen. Introductions of invasive species, for example, can alter linkage networks responsible for providing allochthonous subsidies (McCauley *et al.* 2012a). Climate change may reduce top-heaviness by thermally restricting top predator access to external energy pools that may sustain their biomass (Tunney *et al.* 2012) and by disrupting the temporal synchrony of predator/prey cycles (Winder & Schindler 2004; Durant *et al.* 2005).

Recognition of the prevalence of these assaults upon top-heaviness has led some to hypothesise that inverted pyramids and extremely top-heavy biomass configurations were once the 'native' and historically dominant architectural state of many communities (Jackson 2006; Sandin & Zgliczynski 2015). While certainly not all pre-Anthropocene communities were top-heavy, reviews of historical ecology and examinations of remote and near-pristine ecosystems do lend support to the notion that top-heavy systems were likely more common in many systems before the global expansion of our species (Friedlander & DeMartini 2002; Lotze & Milewski 2004; Jackson 2006; Sandin *et al.* 2008).

Creating more top-heaviness

Humans have, alternatively, quite conspicuously promoted top-heaviness in many contexts. The most common route by which people make food webs more top-heavy is via the introduction of non-native top predators. Particularly dramatic shifts have been achieved in islands and similar settings where dispersal has historically limited the arrival of large consumers. The introduction of arctic foxes to the historically mammal-free Aleutian Islands, for example, markedly increased island top-heaviness (Maron *et al.* 2006). Similarly, non-native trout introduced in New Zealand nearly doubled the biomass density of top-predators in certain streams (Townsend 2003; Simon *et al.* 2004) (Table 1). Other examples of invasive aided top-heaviness abound in terrestrial, freshwater and marine settings.

Climate change may, in certain settings, also promote top-heaviness. Warming, for example, may increase rates of trophic energy flux (Brown *et al.* 2004), although more research is needed to understand how such flux rates may be controlled by differences in the body size and thermal strategy (i.e. ectothermy or endothermy) of consumers and resources. Some, but not all, systems have been empirically shown to become more top-heavy as a result of warming (Yvon-Durocher *et al.* 2011; Shurin *et al.* 2012; Romero *et al.* 2016).

EMERGENT EFFECTS OF SHIFTS IN BIOMASS DISTRIBUTION

What implications do these anthropogenically engendered shifts towards or away from top-heaviness have upon impacted communities and ecosystems? Results from ATNN models suggest that top-heavy systems support more total system biomass (Fig. 3) indicating that such shifts may impact the overall amount of life present within a given habitat at a given time. Our observations of the relationship between top-heaviness and stability indicate that shifts in community architecture may also be associated with major perturbations to the dynamical properties of these systems. Results from our consumer–resource modelling suggest that, in many instances, decreases in top-heaviness may in fact be associated with increased community stability. In this context, however, increased stability may not be wholly desirable, at least from an ecosystem management perspective, as these altered communities may have crossed tipping points and have less capacity to return to pre-disturbance structural states. These observations are at least consistent with empirical reports of transitions to alternative stable states that have been hypothesised to follow from reductions in top-heaviness in contexts such as coral reefs and kelp forests (Folke *et al.* 2004).

An important outcome of human-engineered shifts in top-heaviness are associated alterations in rates of predation or herbivory. These effects are particularly conspicuous in systems where we have artificially increased top-heaviness. In New Zealand streams where trout have been introduced, 100% *in situ* invertebrate production now supports production of this novel predator (Huryn 1998). Community members influenced by the cascading effects of the artificially created top-heaviness in a variety of historically trout-free contexts include native amphibians, macroinvertebrates, zooplankton assemblages, algal communities, birds and snakes (Matthews *et al.* 2002; Townsend 2003; Vredenburg 2004; Epanchin *et al.* 2010). Equally impactful shifts have been observed in myriad other systems where humans have boosted levels of top-heaviness via predator introductions, although some of these effects may be reversible if ecosystem managers are able to successfully purge this artificially created top-heaviness (Buxton *et al.* 2014; Medina *et al.* 2014).

Changing the biomass distribution of food webs can also affect a diverse array of ecosystem processes – from alterations in wildfire frequency to shifts in disease dynamics (Estes *et al.* 2011). Nutrient cycling, for example, is another basal ecosystem process that is very much dependent on community biomass structure. There are numerous instances where changes in top-heaviness have altered core processes of nutrient cycling, including effects on phosphorous (Schindler & Scheuerell 2002), carbon (Cho & Azam 1990; Fuhrman 1992; Cebrian & Lartigue 2004) and nitrogen (Simon *et al.* 2004; Roman *et al.* 2014).

ILLUSION VS. REALITY

It is worthwhile asking an important question: Are all the cases of top-heaviness we have considered ecologically 'real'? Clearly systems discussed previously whose top-heaviness results from sampling error should be considered erroneous (e.g. overestimation of apex predator biomass) and culled from discussions about the dynamics top-heaviness. Communities that become top-heavy as result of endogenous mechanisms (e.g. relative differences in consumer and resource

turnover rates) are likely to be more universally considered rigorous ecological constructs. However, instances in which energy is exogenously sourced to create top-heaviness (e.g. from another time or another ecological space) present more opportunity for healthy debate. If, for instance, we allow ourselves to view the operation of communities at non-traditionally ambitious spatial and temporal scales, many of these systems become less top-heavy – or not top-heavy at all. Top-heavy coral reef communities in which mobile consumers draw energy from neighbouring pelagic communities, for example, begin to look more Eltonian when the dynamics of multiple communities are viewed collectively (McCauley *et al.* 2012c; Bradley *et al.* 2017). The underlying challenge is that by habit or necessity, the modus operandi of many ecologists is to survey the biomass contained within a community in a snapshot fashion – and such practices poorly acknowledge the spatially and temporally remote processes that shape community structure.

Whether or not any given top-heavy system is ecologically real may be more a matter of semantics. Regardless of what determinations are made, a diagnosis of top-heaviness in a given community importantly flags instances where endogenous or exogenous community processes may be complex and deserving of additional study. Instances of top-heaviness also serve to inspire needed debate about the scale at which we build ecological interpretations. The enduring contribution of the study of top-heaviness may ultimately be less about the peculiarities of these unusual ecological structures, and more about the instructive uncertainties that such structures raise concerning ecological boundary dynamics.

CONCLUSIONS

It is evident that there are numerous examples of communities in which the biomass of consumers located in a particular habitat at a particular time rivals or exceeds the biomass of prey or producers in that place at that time. Inverted pyramids and such generally top-heavy systems have been found to occur in a wide variety of ecosystems and to involve a wide variety of taxa. A large number of top-heavy communities have been reported from aquatic contexts and there is support for the notion that the physical and biological properties of aquatic systems make them better suited to facilitate the build-up of community top-heaviness. There are numerous factors that can complicate the process of recognising and properly assaying top-heaviness. Advancements, however, in our methodological capacity to accurately enumerate biomass and elucidate complex feeding relationships, increasing tendencies towards making longer term observation of community structure and our growing awareness of how to critically bound the systems we study are all providing a means to better account for these issues.

The empirical examples that we draw from, as well as the theory that we advance herein, demonstrate that there are a series of diverse pathways through which community top-heaviness can either be endogenously or exogenously created (Box 1). Endogenously generated top-heaviness can be created by increasing energy flow up food webs via variation in attributes internal to a community such as differences in life history (e.g. turnover rates), behaviour (e.g. omnivory) and the

environment (e.g. habitat complexity). Top-heaviness has classically been explained as a result of such endogenous dynamics. It is clear, however, that externally sourced temporal and spatial subsidies can have an equally strong influence on community architecture. Our rapidly evolving capacity to view ecological dynamics at larger spatial scales and longer time spans suggests that exogenous explanations for top-heaviness may be more common than has been historically appreciated.

While it is logically convenient to dichotomise top-heaviness as originating from endogenous and exogenous sourcing, these two bulk pathways overlap and intertwine in important ways. For example, empirical descriptions of top-heaviness in coral reef fish communities reveal that it may arise from increased internal energy flux, as well as subsidisation across spatial and temporal boundaries (Buck *et al.* 1996; Ruttenberg *et al.* 2011; McCauley *et al.* 2012c; Sandin & Zgliczynski 2015).

Consumer–resource and ATNN models provide useful insight into the ecological life span of top-heavy and inverted pyramidal communities. Certain types of top-heavy systems appear to be able to be maintained in a relatively stable fashion. However, both consumer–resource and ATNN models suggest an ultimate tendency towards destabilisation with ever-increasing top-heaviness, although these models differ on the dynamical pathways that lead towards this end. An important avenue for future research will be learning more about the conditions that may permit a system to persist at or near the pre-destabilisation maxima in top-heaviness. The insight from theory that the stability dynamics of a given top-heavy system depends on the ecological pathway through which top-heaviness was generated adds even more value to elucidating the mechanisms, endogenous or exogenous, that foster top-heaviness in focal communities.

We emphasise that the conclusions we report from both the consumer–resource and ATNN models can be sensitive to parameter selection (Hudson & Reuman 2013). Initial exploration of issues of parameter sensitivity in consumer–resource models suggests that certain results reported herein are generalisable (Appendix S1 and S2). While others have introduced stochastic variation into ATNN model parameters (Berlow *et al.* 2009), much remains to be learned in future work about how these model outputs are influenced by parameter value variability. These remaining uncertainties regarding parameter sensitivity are a clear weakness of these theoretical approaches and we caution that they be considered during interpretation of the patterns we present.

Humans are having a major impact on community biomass distributions: We are responsible for both building up and tearing down top-heaviness in myriad settings. The majority of the deconstruction of top-heaviness derives from harvest of consumers at the top of food webs. Anthropogenic construction of top-heaviness often derives from the introduction of novel consumers. These human-engineered changes in the raw architecture of living systems are ecologically significant as they are having severe and far reaching impacts on community stability, nutrient cycling, trophic dynamics and the persistence of biodiversity.

Importantly, this review and the theoretical results we present reveal that a great deal has yet to be learned and settled regarding the dynamics of top-heaviness. There is, for

example, clear need to better reconcile the apparent differences in the stability dynamics of increasingly top-heavy systems observed in the more complex (i.e. ATNN) and less complex (i.e. consumer–resource) models we explored. Empirical evidence should also be sought to evaluate the observation in ATNN models that increasing top-heavy webs tend to increase total community biomass, particularly given how such outcomes would shape how people draw food and income from such communities. Furthermore, additional investigation is needed to empirically validate suggestions that top-heaviness may be more prevalent in systems containing ectothermic and invertebrate consumers and that top-heaviness created via endogenous pathways should be relatively common. Efforts are also clearly needed to better standardise and reduce error in methodologies for assessing the biomass of both small (e.g. plankton) and large (e.g. sharks) consumers. More effort should also be devoted to evaluating whether humans have indeed systematically reduced the amount of top-heaviness once found in nature and to be determining how climate change may shape future patterns of top-heaviness. Finally, more work is needed for developing empirical and theoretical methods that can help readily assay whether top-heaviness, when observed, was generated via endogenous or exogenous pathways.

The simplicity and ease by which we can collect data on biomass partitioning in communities belies the diagnostic insight that these patterns provide into some of the more fundamental elements of ecological assembly and function. The questions raised through the study of top-heavy systems also, importantly, can inspire healthy and needed consideration about how ecologists conceive of spatial and temporal ecological boundaries. Finally, research on top-heaviness has and likely will continue to help us properly broadly view and rank the relative importance of the mechanisms for maximising efficient energy transfer across living systems and assist us in uncovering innovative conduits through which materials and energy can be routed through complex networks.

AUTHORSHIP

DJM collected data and GG, NDM, RJM and KSM performed modelling and analysis of outputs. DJM wrote the first draft of the paper and all authors contributed substantially to revisions.

REFERENCES

Anabalón, V., Arístegui, J., Morales, C.E., Andrade, I., Benavides, M., Correa-Ramírez, M.A. *et al.* (2014). The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa). *Prog. Oceanogr.*, 120, 320–339.

Arístegui, J., Mendonça, A., Vilas, J.C., Espino, M., Polo, I., Montero, M.F. *et al.* (2009). Plankton metabolic balance at two North Atlantic seamounts. *Deep Sea Res. Part II Top. Stud. Oceanogr. The Oceanography, Biogeochemistry and Ecology of Two NE Atlantic Seamounts: OASIS*, 56, 2646–2655.

Barnes, C., Maxwell, D., Reuman, D.C. & Jennings, S. (2010). Global patterns in predator—prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, 91, 222–232.

Benke, A.C. (1976). Dragonfly production and prey turnover. *Ecology*, 57, 915–927.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl Acad. Sci.*, 106, 187–191.

Boit, A., Martinez, N.D., Williams, R.J. & Gaedke, U. (2012). Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecol. Lett.*, 15, 594–602.

Bradley, D., Conklin, E., Papastamatiou, Y.P., McCauley, D.J., Pollock, K., Pollock, A. *et al.* (2017). Resetting predator baselines in coral reef ecosystems. *Sci. Rep.*, 7, srep43131.

Britschgi, T.B. & Giovannoni, S.J. (1991). Phylogenetic analysis of a natural marine bacterioplankton population by rRNA gene cloning and sequencing. *Appl. Environ. Microbiol.*, 57, 1707–1713.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.-F. *et al.* (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

deBruyn, A.M.H., McCann, K.S., Moore, J.C. & Strong, D.R. (2007). An Energetic Framework for Trophic Control. In: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems* (eds Rooney, N., McCann, K.S., Noakes, D.L.G.). Springer, Netherlands, pp. 65–85.

Buck, K., Chavez, F. & Campbell, L. (1996). Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993. *Aquat. Microb. Ecol.*, 10, 283–298.

Bustamante, R.H., Branch, G.M. & Eekhout, S. (1995). Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology*, 76, 2314–2329.

Buxton, R.T., Jones, C., Moller, H. & Towns, D.R. (2014). Drivers of seabird population recovery on New Zealand Islands after predator eradication. *Conserv. Biol.*, 28, 333–344.

Carriquiry, J.D., Barranco-Servin, L.M., Villaescusa, J.A., Camacho-Ibar, V.F., Hector Reyes-Bonilla, H. & & Cupul-Magaña, A.L. (2013). Conservation and sustainability of Mexican caribbean coral reefs and the threats of a human-induced phase-shift, environmental change and sustainability. In: *Environmental Change and Sustainability* (eds. Silvern, S. & Young, S.). InTech Austria, pp. 29–51.

Cebrian, J. (1999). Patterns in the fate of production in plant communities. *Am. Nat.*, 154, 449–468.

Cebrian, J. & Lartigue, J. (2004). Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecol. Monogr.*, 74, 237–259.

Cebrian, J., Shurin, J.B., Borer, E.T., Cardinale, B.J., Ngai, J.T., Smith, M.D. *et al.* (2009). Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE*, 4, e4929.

Chapin, F.S., Matson, P.A. & Vitousek, P.M. (2012). Trophic dynamics. In: *Principles of Terrestrial Ecosystem Ecology* (eds. Chapin, F. S., Matson, P.A. & Mooney, H.A.). Springer, New York, NY, pp. 297–320.

Cho, B.C. & Azam, F. (1990). Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. *Mar. Ecol. Prog. Ser. Oldendorf*, 63, 253–259.

Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003). Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA*, 100, 1781–1786.

Crowder, L.B. & Cooper, W.E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63, 1802–1813.

Curran, L.M. & Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.*, 70, 101–128.

Cyr, H. & Pace, M.L. (1993). Allometric theory: extrapolations from individuals to communities. *Ecology*, 74, 1234–1245.

Cyr, H. & Peters, R.H. (1996). Biomass-size spectra and the prediction of fish biomass in lakes. *Can. Spec. Publ. Fish. Aquat. Sci.*, 53, 994–1006.

Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua, T.H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, 300, 969–972.

de León, P.S., Acuña-Marrero, D., Rastoin, E., Friedlander, A.M., Donovan, M.K. & Sala, E. (2016). Largest global shark biomass found in the northern galápagos islands of Darwin and Wolf. *PeerJ*, 4, e1911.

Del Giorgio, P.A., Cole, J.J., Caraco, N.F. & Peters, R.H. (1999). Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology*, 80, 1422–1431.

Dolson, R., McCann, K., Rooney, N. & Ridgway, M. (2009). Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos*, 118, 1230–1238.

Dortch, Q. & Packard, T.T. (1989). Differences in biomass structure between oligotrophic and eutrophic marine ecosystems. *Deep. Sea Res. Part Oceanogr. Res. Pap.*, 36, 223–240.

Duarte, C.M., Agustí, S., Del Giorgio, P.A. & Cole, J.J. (1999). Regional carbon imbalances in the oceans. *Science*, 284, 1735b.

Duarte, C., Agustí, S., Gasol, J., Vaqué, D. & Vazquez-Dominguez, E. (2000). Effect of nutrient supply on the biomass structure of planktonic communities: an experimental test on a Mediterranean coastal community. *Mar. Ecol. Prog. Ser.*, 206, 87–95.

Duarte, C.M., Regaudie-de-Gioux, A., Arrieta, J.M., Delgado-Huertas, A. & Agustí, S. (2013). The oligotrophic ocean is heterotrophic*. *Annu. Rev. Mar. Sci.*, 5, 551–569.

Ducklow, H.W. & Doney, S.C. (2013). What is the metabolic state of the oligotrophic ocean? a debate. *Annu. Rev. Mar. Sci.*, 5, 525–533.

Durant, J.M., Hjermann, D.Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. *et al.* (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol. Lett.*, 8, 952–958.

Elton, C.S. (1927). *Animal Ecology*. University of Chicago Press, Chicago, IL.

Elton, C. & Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in Canada. *J. Anim. Ecol.*, 11, 215–244.

Epanchin, P.N., Knapp, R.A. & Lawler, S.P. (2010). Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology*, 91, 2406–2415.

Ernst, C.M. & Buddle, C.M. (2013). Seasonal patterns in the structure of epigeic beetle (Coleoptera) assemblages in two subarctic habitats in Nunavut, Canada. *Can. Entomol.*, 145, 171–183.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.

Eveleigh, E.S., McCann, K.S., McCarthy, P.C., Pollock, S.J., Lucarotti, C.J., Morin, B. *et al.* (2007). Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc. Natl Acad. Sci. USA*, 104, 16976–16981.

Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J. *et al.* (2012). Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *J. Plankton Res.*, 35, 3–11, fbs062.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. *et al.* (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.*, 35, 557–581.

Friedlander, A.M. & DeMartini, E.E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol. Prog. Ser.*, 230, 253–264.

Fuhrman, J. (1992). Bacterioplankton roles in cycling of organic matter: the microbial food web. In: *Primary Productivity and Biogeochemical Cycles in the Sea* (eds. Falkowski, P.G. & Woodhead, A.D.). Plenum Press, New York, NY, pp. 361–383.

Fuks, D., Ivančić, I., Najdek, M., Lučić, D., Njire, J., Godrijan, J. *et al.* (2012). Changes in the planktonic community structure related to trophic conditions: the case study of the northern Adriatic Sea. *J. Mar. Syst.*, 96–97, 95–102.

Gaedke, U. & Straile, D. (1994). Seasonal changes of trophic transfer efficiencies in a plankton food web derived from biomass size distributions and network analysis. *Ecol. Model.*, 75–76, 435–445.

Gasol, J.M., Del Giorgio, P.A. & Duarte, C.M. (1997). Biomass distribution in marine planktonic communities. *Limnol. Oceanogr.*, 42, 1353–1363.

Gasol, J.M., Vazquez-Dominguez, E., Vaque, D., Agusti, S. & Duarte, C.M. (2009). Bacterial activity and diffusive nutrient supply in the oligotrophic Central Atlantic Ocean. *Aquat. Microb. Ecol.*, 56, 1–12.

Gellner, G. & McCann, K. (2012). Reconciling the omnivory-stability debate. *Am. Nat.*, 179, 22–37.

Gellner, G., McCann, K.S. & Hastings, A. (2016). The duality of stability: towards a stochastic theory of species interactions. *Theor. Ecol.*, 9, 477–485.

Gilbert, B., Tunney, T.D., McCann, K.S., DeLong, J.P., Vasseur, D.A., Savage, V. *et al.* (2014). A bioenergetic framework for the temperature dependence of trophic interactions. *Ecol. Lett.*, 17, 902–914.

del Giorgio, P.A. & Gasol, J.M. (1995). Biomass distribution in freshwater plankton communities. *Am. Nat.*, 146, 135–152.

Guckenheimer, J. & Holmes, P.J. (1983). *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*. Springer-Verlag, New York.

Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E. *et al.* (2014). Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. *PLoS ONE*, 9, e91841.

Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V. *et al.* (2014). Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biol.*, 12, e1001841.

Harvey, H.W. (1950). On the production of living matter in the sea off Plymouth. *J. Mar. Biol. Assoc. U. K.*, 29, 97–137.

Hay, M.E., Kappel, Q.E. & Fenical, W. (1994). Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. *Ecology*, 75, 1714–1726.

Herndl, G.J. (1991). Microbial biomass dynamics along a trophic gradient at the Atlantic barrier reef off Belize (Central America). *Mar. Ecol.*, 12, 41–51.

Heupel, M.R., Knip, D.M., Simpfendorfer, C.A. & Dulvy, N.K. (2014). Sizing up the ecological role of sharks as predators. *Mar. Ecol. Prog. Ser.*, 495, 291–298.

Holt, R.D. & Polis, G.A. (1997). A theoretical framework for intraguild predation. *Am. Nat.*, 149, 745–764.

Hudson, L.N. & Reuman, D.C. (2013). A cure for the plague of parameters: constraining models of complex population dynamics with allometries. *Proc. R. Soc. B*, 280, 20131901.

Huryn, A.D. (1998). Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, 115, 173–183.

Jackson, J.B.C. (2006). When ecological pyramids were upside down. In *Whales, Whaling, and Ocean Ecosystems*. (ed. Estes, J.A.). University of California Press, Berkeley, CA, pp. 27–37.

Jennings, S. & Mackinson, S. (2003). Abundance–body mass relationships in size-structured food webs. *Ecol. Lett.*, 6, 971–974.

Jennings, S., Oliveira, J.A.A.D. & Warr, K.J. (2007). Measurement of body size and abundance in tests of macroecological and food web theory. *J. Anim. Ecol.*, 76, 72–82.

Jonsson, T. (2017). Conditions for Eltonian pyramids in Lotka-Volterra food chains. *Sci. Rep.*, 7, 10912.

Kerr, S.R. & Dickie, L.M. (2001). *The biomass spectrum: A predator-prey theory of aquatic production*. Columbia University Press, New York, NY.

King, C.M. (1983). The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *J. Anim. Ecol.*, 52, 141.

Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. (1991). Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? Oecologia, 88, 552–561.

Krebs, C.J., Boonstra, R., Boutin, S. & Sinclair, A.R.E. (2001). What Drives the 10-year Cycle of Snowshoe Hares? The ten-year cycle of snowshoe hares – one of the most striking features of the boreal forest – is a product of the interaction between predation and food supplies, as large-scale experiments in the Yukon have demonstrated. *Bioscience*, 51, 25–35.

Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A. et al. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454, 515–518.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P. et al. (2008). Parasites in food webs: the ultimate missing links. *Ecol. Lett.*, 11, 533–546.

Lefèvre, T., Lebarbenchon, C., Gauthier-Clerc, M., Missé, D., Poulin, R. & Thomas, F. (2009). The ecological significance of manipulative parasites. *Trends Ecol. Evol.*, 24, 41–48.

Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–417.

Lotze, H.K. & Milewski, I. (2004). Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecol. Appl.*, 14, 1428–1447.

Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C. & Buckelew, S.L. (2006). An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecol. Monogr.*, 76, 3–24.

Majer, J.D. (1990). The abundance and diversity of arboreal ants in northern Australia. *Biotropica*, 22, 191–199.

Matthews, K.R., Knapp, R.A. & Pope, K.L. (2002). Garter snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and nonnative trout introductions? *J. Herpetol.*, 36, 16–22.

McCann, K.S. (2011). *Food Webs*. Princeton University Press, Princeton, NJ.

McCann, K. & Hastings, A. (1997). Re–evaluating the omnivory–stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.*, 264, 1249–1254.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8, 513–523.

McCauley, D.J., DeSalles, P.A., Young, H.S., Dunbar, R.B., Dirzo, R., Mills, M.M. et al. (2012a). From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. *Sci. Rep.*, 2, 409.

McCauley, D.J., McLean, K.A., Bauer, J., Young, H.S. & Micheli, F. (2012b). Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecol. Appl.*, 22, 385–392.

McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X. & Micheli, F. (2012c). Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol. Appl.*, 22, 1711–1717.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. & Warner, R.R. (2015). Marine defaunation: animal loss in the global ocean. *Science*, 347, 1255641.

McCauley, M., Gellner, G., D. Martinez, D.M., Williams, W., A. Sandin, A.S. & Micheli, M. (2017). Data and code from: On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities. Figshare, doi:10.6084/m9.figshare.c.3946945.

Medina, F.M., Bonnaud, E., Vidal, E. & Nogales, M. (2014). Underlying impacts of invasive cats on islands: not only a question of predation. *Biodivers. Conserv.*, 23, 327–342.

Mourier, J., Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M.L. et al. (2016). Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. *Curr. Biol.*, 26, 2011–2016.

Mouritsen, K.N. & Poulin, R. (2003). Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. *Int. J. Parasitol.*, 33, 1043–1050.

Moustaka-Gouni, M., Vardaka, E., Michaloudi, E., Kormas, K.A., Tryfon, E., Mihalatou, H. et al. (2006). Plankton food web structure in a eutrophic polymictic lake with a history in toxic cyanobacterial blooms. *Limnol. Oceanogr.*, 51, 715–727.

Müller-Navarra, D.C., Brett, M.T., Liston, A.M. & Goldman, C.R. (2000). A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature*, 403, 74–77.

Murdoch, W.W., Briggs, C.J. & Nisbet, R.M. (2013). *Consumer-resource dynamics (MPB-36)*. Princeton University Press, Princeton, NJ.

Odum, E.P. (1971). *Fundamentals of ecology*. Saunders, Philadelphia, PA, USA.

Ohkuma, M. (2008). Symbioses of flagellates and prokaryotes in the gut of lower termites. *Trends Microbiol.*, 16, 345–352.

O'Neill, R.V. (1976). Ecosystem persistence and heterotrophic regulation. *Ecology*, 57, 1244.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.*, 15, 232–237.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing down marine food webs. *Science*, 279, 860–863.

Payne, J.L., Bush, A.M., Heim, N.A., Knope, M.L. & McCauley, D.J. (2016). Ecological selectivity of the emerging mass extinction in the oceans. *Science*, 353, 1284–1286.

Polis, G.A. (1999). Why are parts of the world green? multiple factors control productivity and the distribution of biomass. *Oikos*, 86, 3–15.

Polis, G.A. & Hurd, S.D. (1995). Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proc. Natl Acad. Sci.*, 92, 4382–4386.

Post, D.M., Doyle, M.W., Sabo, J.L. & Finlay, J.C. (2007). The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. *Geomorphology, 36th Binghamton Geomorphology Symposium Geomorphology and Ecosystems*, 89, 111–126.

Power, M.E., Holomuzki, J.R. & Lowe, R.L. (2013). Food webs in Mediterranean rivers. *Hydrobiologia*, 719, 119–136.

Ravera, O. (1969). Seasonal variation of the biomass and biocoenotic structure of plankton of the Bay of Ispra (Lago Maggiore). *Verh. Int. Ver. Theor. Angew. Limnol.*, 17, 237–254.

Redalje, D.G. & Laws, E.A. (1981). A new method for estimating phytoplankton growth rates and carbon biomass. *Mar. Biol.*, 62, 73–79.

Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008). Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecol. Lett.*, 11, 1216–1228.

Ricklefs, R.E. (2008). Disintegration of the ecological community. *Am. Nat.*, 172, 741–750.

Rip, J.M.K. & McCann, K.S. (2011). Cross-ecosystem differences in stability and the principle of energy flux. *Ecol. Lett.*, 14, 733–740.

Rodda, G.H., Fritts, T.H. & Chiszar, D. (1997). The disappearance of Guam's wildlife. *BioScience*, 47, 565–574.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.-M., Krueck, N.C., Aurellado, E. et al. (2016). The ecological role of sharks on coral reefs. *Trends Ecol. Evol.*, 31, 395–407.

Rogers, A., Blanchard, J.L. & Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr. Biol.*, 24, 1000–1005.

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J. et al. (2014). Whales as marine ecosystem engineers. *Front. Ecol. Environ.* 12, 377–385

Romero, G.Q., Piccoli, G.C., de Omena, P.M. & Gonçalves-Souza, T. (2016). Food web structure shaped by habitat size and climate across a latitudinal gradient. *Ecology*, 97, 2705–2715.

Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265–269.

Ruttenberg, B.I., Hamilton, S.L., Walsh, S.M., Donovan, M.K., Friedlander, A., DeMartini, E. *et al.* (2011). Predator-induced demographic shifts in coral reef fish assemblages. *PLoS ONE*, 6, e21062.

Sabo, J.L. & Power, M.E. (2002). River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*, 83, 1860–1869.

Sandin, S.A. & Zgliczynski, B.J. (2015). Inverted trophic pyramids. In *Ecology of Fishes on Coral Reefs*. (ed. Mora, C.). Cambridge University Press, Cambridge, UK, pp. 247–251.

Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M. *et al.* (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*, 3, e1548.

Sato, T., Arizono, M., Sone, R. & Harada, Y. (2008). Parasite-mediated allochthonous input: do hairworms enhance subsidized predation of stream salmonids on crickets? *Can. J. Zool.*, 86, 231–235.

Schindler, D.E. & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98, 177–189.

Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2006). All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B Biol. Sci.*, 273, 1–9.

Shurin, J.B., Clasen, J.L., Greig, H.S., Kratina, P. & Thompson, P.L. (2012). Warming shifts top-down and bottom-up control of pond food web structure and function. *Philos. Trans. R. Soc. B Biol. Sci.*, 367, 3008–3017.

Simon, K.S., Townsend, C.R., Biggs, B.J.F., Bowden, W.B. & Frew, R.D. (2004). Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. *Ecosystems*, 7, 777–792.

Simpfendorfer, C.A. & Heupel, M.R. (2016). Ecology: the upside-down world of coral reef predators. *Curr. Biol.*, 26, R708–R710.

Slobodkin, L.B. (2001). The good, the bad and the reified. *Evol. Ecol. Res.*, 3, 1–13.

Soisalo, M.K. & Cavalcanti, S.M.C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biol. Conserv.*, 129, 487–496.

Sterner, R.W. & Hessen, D.O. (1994). Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.*, 25, 1–29.

Stevenson, C., Katz, L.S., Micheli, F., Block, B., Heiman, K.W., Perle, C. *et al.* (2007). High apex predator biomass on remote Pacific islands. *Coral Reefs*, 26, 47–51.

Strayer, D.L. (1991). Perspectives on the size structure of Lacustrine zoobenthos, its causes, and its consequences. *J. North Am. Benthol. Soc.*, 10, 210–221.

Takimoto, G., Iwata, T. & Murakami, M. (2002). Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. *Ecol. Res.*, 17, 433–439.

Takimoto, G., Spiller, D.A. & Post, D.M. (2008). Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology*, 89, 3001–3007.

Tamelander, T., Reigstad, M., Olli, K., Slagstad, D. & Wassmann, P. (2013). New production regulates export stoichiometry in the ocean. *PLoS ONE*, 8, e54027.

Townsend, C.R. (2003). Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conserv. Biol.*, 17, 38–47.

Trebilco, R., Baum, J.K., Salomon, A.K. & Dulvy, N.K. (2013). Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol. Evol.*, 28, 423–431.

Trebilco, R., Dulvy, N.K., Anderson, S.C. & Salomon, A.K. (2016). The paradox of inverted biomass pyramids in kelp forest fish communities. *Proc. R. Soc. B*, 283, 20160816.

Tunney, T.D., McCann, K.S., Lester, N.P. & Shuter, B.J. (2012). Food web expansion and contraction in response to changing environmental conditions. *Nat. Commun.*, 3, 1105.

Turner, F.B. (1970). The ecological efficiency of consumer populations. *Ecology*, 51, 741–742.

Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A. *et al.* (2010). Trophic structure and community stability in an overfished ecosystem. *Science*, 329, 333–336.

Vredenburg, V.T. (2004). Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proc. Natl Acad. Sci. USA*, 101, 7646–7650.

Wang, H., Kuang, Y. & Loladze, I. (2008). Dynamics of a mechanistically derived stoichiometric producer-grazer model. *J. Biol. Dyn.*, 2, 286–296.

Wang, H., Morrison, W., Singh, A. & Weiss, H. (Howie). (2009). Modeling inverted biomass pyramids and refuges in ecosystems. *Ecol. Model.*, 220, 1376–1382.

Ward-Paige, C., Mills Flemming, J. & Lotze, H.K. (2010). Overestimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. *PLoS ONE*, 5, e11722.

Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nat. Lond.*, 404, 180–183.

Williams, R.J. & Martinez, N.D. (2004). Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.*, 163, 458–468.

Williams, R.J., Brose, U. & Martinez, N.D. (2007). Homage to Yodzis and Innes 1992: scaling up feeding-based population dynamics to complex ecological networks. *Energ. Ecosyst. Dyn. Struct. Ecol. Syst.*, 49, 37–51.

Williams, I.D., Richards, B.L., Sandin, S.A., Baum, J.K., Schroeder, R.E., Nadon, M.O. *et al.* (2011). Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western pacific. *J. Mar. Biol.*, http://dx.doi.org/10.1155/2011/826234.

Winder, M. & Schindler, D.E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, 85, 2100–2106.

Wootton, J.T. (1994). Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology*, 75, 151–165.

Wright, S.J., Carrasco, C., Calderón, O. & Paton, S. (1999). The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, 80, 1632–1647.

Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008). What can we learn from resource pulses? *Ecology*, 89, 621–634.

Yodzis, P. (1984). Energy flow and the vertical structure of real ecosystems. *Oecologia*, 65, 86–88.

Young, H.S., McCauley, D.J., Galetti, M. & Dirzo, R. (2016). Patterns, causes, and consequences of anthropocene defaunation. *Annu. Rev. Ecol. Evol. Syst.*, 47, 333–358.

Yvon-Durocher, G., Montoya, J.M., Trimmer, M. & Woodward, G. (2011). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Glob. Change Biol.*, 17, 1681–1694.

Zgliczynski, B.J. & Sandin, S.A. (2017). Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecol. Indic.*, 73, 411–421.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.