Distributional (In)Congruence of Biodiversity–Ecosystem Functioning

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Abstract

The majority of research on biodiversity–ecosystem functioning in laboratories has concentrated on a few traits, but there is increasing evidence from the field that functional diversity controls ecosystem functioning more often than does species number. Given the importance of traits as predictors of niche complementarity and community structures, we (1) examine how the diversity *sensu lato* of forest trees, freshwater fishes and soil invertebrates might support ecosystem functioning and (2) discuss the relevance of productive biota for monophyletic assemblages (taxocenes).

In terrestrial ecosystems, correlating traits to abiotic factors is complicated by the appropriate choice of body-size distributions. Angiosperm and gymnosperm trees, for example, show metabolic incongruences in their respiration rates despite their pronounced macroecological scaling. Scaling heterotrophic organisms within their monophyletic assemblages seems more difficult than scaling autotrophs: in contrast to the generally observed decline of mass-specific metabolic rates with body mass within metazoans, soil organisms such as protozoans show opposite mass-specific trends.

At the community level, the resource demand of metazoans shapes multitrophic interactions. Hence, population densities and their food web relationships reflect functional diversity, but the influence of biodiversity on stability and ecosystem functioning remains less clear. We focused on fishes in 18 riverine food webs, where the ratio of primary versus secondary extinctions (hereafter, 'extinction partitioning') summarizes the responses of fish communities to primary species loss (deletions) and its consequences. Based on extinction partitioning, our high-diversity food webs were just as (or even more) vulnerable to extinctions as low-diversity food webs.

Our analysis allows us to assess consequences of the relocation or removal of fish species and to help with decision-making in sustainable river management. The study highlights that the topology of food webs (and not simply taxonomic diversity) plays a greater role in stabilizing the food web and enhancing ecological services than is currently acknowledged.

ABBREVIATIONS

B biomass
B–EF biodiversity–ecosystem functioning
C carbon content
C connectance of a food web or network
eNPP ecosystem's Net Primary Productivity
FD functional diversity
L trophic links
m mass at individual level
$\bar{M}$ mass average at population level (site-specific)
M species-specific estimate of body-mass average
MIH More Individuals Hypothesis
N numerical abundance at population level
N nitrogen content
P phosphorus content
PD fraction of primary deletions (1 − #SD)
R metabolic rate at individual level
R_{SD} robustness against SD
S number of species within one monophyletic taxocene (taxonomic diversity)
SD fraction of secondary deletions (1 − #PD)

All substances, in so far as they can be perceived in space at the same time, exist in a state of complete reciprocity of action.
Immanuel Kant *(1781) Kritik der reinen Vernunft:* Dritte Analogie.

1. INTRODUCTION

1.1. Vexing drivers and responses

Despite scientific rationalism, too many generalizations and recent extrapolations on the so-called sixth Great Extinction Event are widely supported and spread by modern media (criticism on NGO's statements and current concerns already by Mann, 1991). On the one hand, the growing human impact on Earth is beyond discussion and many scientists even assigned the term Anthropocene to the present epoch (Crutzen, 2002; Estes et al., 2011). On the other hand, forecasting global changes is hampered by the

lack of consensus on interactions among the causes (e.g. Sala et al., 2000), the existence of overstating implications (e.g. 'taxa committed to extinction' by Thomas et al. (2004a) are soon claimed as lost in many press releases) and contradictory conclusions (e.g. Samanta et al., 2010 vs. Xu et al., 2011). Too often, in the public opinion, biodiversity seems therefore to sound vague despite of full awareness of resource exploitation and habitat loss. Hence, a dangerous consequence that must be avoided is a possibly growing cynicism and complacency about the current changes at planetary scale as a whole, although the interest with which policy-decision makers and stakeholders look to models is higher than ever.

Given that biodiversity on Earth is only superficially explored, functional groupings used up to date have arisen from a pragmatic approach to categorize biota into ecologically meaningful aggregates (Brussaard, 2012; Kerkhoff et al., 2005; Loreau et al., 2001). For example, body size, among other (frequently related) traits, is ultimately important in determining interaction strengths between consumers and resources. Moreover, organisms of different sizes can have very different effects on ecosystem functioning (EF), both within and among species (Perkins et al., 2010; Reiss et al., 2010, 2011). Size measurements can be carried out at either the individual or the species level, might be used comparatively across species, and have the power to become more directly correlated with properties that influence the performance of organisms and communities (Hodgson et al., 1999; Ledger et al., 2012; McGill et al., 2006).

Life is a matter of scale: faunal dispersal over broad spatial scales favours plasticity (Sultan and Spencer, 2002), in contrast to vascular plants, for which adaptation is limited by seed dispersal mechanisms (Hagen et al., 2012; Olesen et al., 2010). Differently sized plants with variable leaf N and P contents may affect ongoing ecological processes, either actively, due to their direct influence on decomposition efficiency, or passively, through biomass production (Bradford et al., 2002; Fortunel et al., 2009; Garnier et al., 2004; Reich et al., 2010). Further, plants change the amount and composition of root exudates depending on life form (Du Rietz, 1931; Raunkiaer, 1934; Walter, 1964) and nutrient status (Johnson, 2010; Ladygina and Hedlund, 2010; Lipton et al., 1987; Lynch and Ho, 2005; Richardson et al., 2009; Yoneyama et al., 2007).

Still, most researchers have not addressed the role of size as an effect trait at the species level, but have instead preferred to address the response trait as biomass at community level, as for many aboveground ecosystems with

different productivity (e.g. Hartnett and Wilson, 1999; Klironomos et al., 2000; Wardle, 2002; Watkinson and Freckleton, 1997). Given the correlation between response and effect traits, that is, the 'response–effect hypothesis' (Lavorel and Garnier, 2002), the complexity and (mutual) importance of such direct and indirect interactions among biodiversity, EF and the environment is challenging (Bradford et al., 2002; Lavorel et al., 2009; Zobel, 1997). A resulting niche complementarity is in fact the product of not only species interactions but also a direct consequence of combinations of traits (Flombaum and Sala, 2012). Hence, many of these phenomena are interwoven and are commonly merged together into 'services', like nutrient availability, soil structure, water regulation, biological pest control and resilience (Millennium Ecosystem Assessment, 2005).

Effects of dominant species at the ecosystem level (whether a certain community composition is necessary to form and support a given ecosystem) and the EF are two 'linchpins' which matter at several levels (Perrings et al., 1992, 2011). Due to closely interrelated mechanisms, B–EF relationships have been described at many operational levels in an attempt to forecast effects of global change: although determinants of structural variability across different operational levels are not fully understood yet, changes in organismal, demographic and abundance responses might be predicted by nutrient availability or disturbance (Caswell and Cohen, 1991; Elser and Urabe, 1999; Lavorel et al., 1997; Sterner and Elser, 2002; Suding et al., 2003; Tilman, 1988).

1.2. Contrasting dichotomies

EF depends on 'dynamic relationships within species, among species and between species and their abiotic environment, as well as the physical and chemical interactions within the environment' (Millennium Ecosystem Assessment, 2005; UNEP/Convention on Biodiversity, 2004; Wall, 2008). Quantifying EF in terms of biomass, productivity and size structure within and among different ecosystems is important in ecology as it can provide clues about the underlying processes that shape communities. But how close to reality are the correlations between EF and biodiversity? And why are so many research papers and their related questions scale-specific? An excellent starting point would be Waide et al. (1999), who performed an authoritative and extensive meta-analysis of the correlations between biomass and/or production (both excellent

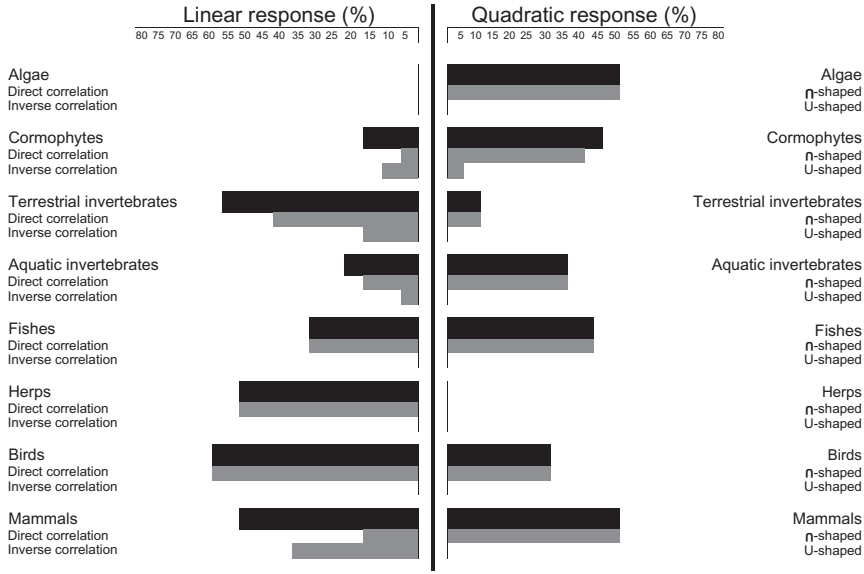


Figure 1 Meta-analysis of the biomass/production and biodiversity relationships published between 1967 and 1996, modified from Waide et al. (1999). For each of these groups of organisms, the amount of biomass–biodiversity studies was set equal to 100%: Trends in biomass as predicted by biodiversity (here, B–EF relationships) can be either linear or quadratic, including unimodal and U-shaped distributions, and can be lumped into different subunits (in grey). The horizontal sum of the black units is always $\leq$100%, because the difference is the percentage of non-significant trends. The vertical sum of the grey subunits is equal to the black unit just above them.

proxies to quantify EF) and biodiversity published between 1967 and 1996, summarized in Fig. 1.

The relationships between biodiversity and primary productivity show the extent to which, under different scales, most controlling processes differ as well, because biodiversity is not merely a simple function of primary productivity, but it may feed back onto it (Adler et al., 2011; Fridley, 2001; Hooper et al., 2005; Loreau et al., 2001). In reality, experimental communities in the field (e.g. Dukes et al., 2005; Menge and Field, 2007) and in micro- or mesocosms (e.g. Benton and Beckerman, 2005; Hunting et al., 2012; Reiss et al., 2011) represent one assemblage of randomly chosen species from a virtually available species pool (Huston, 1997; Naeem, 2008).

According to Lepš (2001), this can be a problem with the design of experiments, as the responses to change determining the success of an experimental community must be viewed with caution, due to either species that

avoid competitive exclusion under low productivity, or species adapted to productive environments given the limited number of species able to compete in high-nutrient environments. Regardless of the species pool and experimental design, if vascular plants (cormophytes) share a significant response, they tend to have a bell-shaped (unimodal) biomass–biodiversity relationship (cf. Adler et al., 2011; Fig. 1). In contrast, for algae, both biomass/productivity proxies seem to have no linear response with increasing biodiversity, and for herps, there is only evidence of direct linear correlations with increasing diversity of amphibians and reptiles (Fig. 1).

Fishes are a powerful example for contrasting biomass–biodiversity correlations: along a biodiversity gradient, does function respond linearly or not? Considering that fishes are commonly overexploited (FAO, 2000) despite their intrinsic capacity to respond to environmental changes, fish assemblages must be representative in their abiotic and biotic properties as well as their faunal composition for a range of sites. The proxies for aquatic and terrestrial invertebrates are even more contrasting, with direct correlates with soil biodiversity less than three times more frequent than inverse correlates (Fig. 1). If so, contrasting biomass–biodiversity relationships within and between taxonomic groups might have clear implications for the ecosystem.

During the same period of the extensive review by Waide and others, Hector et al. (1999, 2002) published BIODEPTH, resulting in a flood of B–EF studies showing robust linear trends on one side and strongly debated statistical arguments on the validity of the experimental design on the other (e.g. Cottingham et al., 2001; Huston et al., 2000). Few experimental studies have since measured biodiversity and biomass production: in those cases, discontinuous relations between biodiversity and productivity, rather far from linearity, were shown (Boit et al., 2012; Roscher et al., 2008).

There is compelling evidence that process rates associated with animals that influence ecosystem services vary with body size: small organisms vary more rapidly in population density and behave differently from larger organisms (Fenchel and Finlay, 1983; Huston and Wolverton, 2011; Sterner and Elser, 2002), such as having a very different metabolic capacity per unit biomass if an assemblage is comprised of many small versus a few large individuals (Perkins et al., 2010). At individual and population levels, plants exhibit contrasting responses to the animal framework of Table 1: plants are mostly growing slowly in unfertile ecosystems (i.e. low eNPP), although they may live longer. For animals, tradeoffs in physical, biochemical and ecological constraints related to parental energy

Table 1 Predictions of ecologically and evolutionarily relevant properties for low and high net primary production scenarios across organizational levels as defined by Huston and Wolverton (2011); table modified (Michael Huston, personal communication) and redrawn with permission from ESA

	Low eNPP	**High eNPP**
Culture, socioeconomics	Small stature, short	Large stature, tall
	Low per capita income	High per capita income
	Malnutrition, vitamin deficiencies	Good health, nutrition
	Homes small, crowded	Homes large, spacious
	Low educational attainment	High educational levels
	Small social groups, cooperation	Hierarchy social stratification
Community	Facilitation, mutualism common	Competition, aggression common
	Small species predominate	Large species dominant
	High species evenness	Low species evenness
	High species richness	Low species richness
Species	'K' traits predominate	'*r*' and 'K' traits present
	Sensitive to mortality	Robust to mortality
	Locally rare	Locally common
	Small average size	Large average size
Population	Low emigration rate	High emigration rate
	Low biomass density	High biomass density
	Low population density	High population density
	Low rate of increase	High rate of increase
Individual	Poor health, strength	Good health, strength
	Low longevity	High longevity
	Few or small offspring	Many or large offspring
	Low adult size	High adult size
	Low growth rate	High growth rate
	Low birth mass	High birth mass

Ubiquitous biogeochemical effects of nutrients and proteins on organisms support at ecosystem level an elemental-affected net primary production (eNPP).

investment have been hypothesized to be responsible for many observed body growth patterns and behavioural traits (e.g. Blomberg et al., 2003; Bongers, 1999; Calder, 1984; Carbone et al., 2011; Guénard et al., 2011; Hendriks and Mulder, 2008, 2012; Peters, 1983; Suding et al., 2003). Many of these faunal attributes are mentioned in Table 1, such as offspring number, dispersal rate, maximum lifespan and territory, and vary predictably with the organism's body size with respect to the species' phylogenetic position (Guénard et al., 2011).

Body size remains a fundamental determinant of an organism's ecology, including territory and niche (Jenkins et al., 2007; Werner and Gilliam, 1984), and is one of the most-studied aspects of animal ecology (Blackburn and Gaston, 1994; Isaac and Carbone, 2010). Therefore, we can hypothesize that 'body size' might at least constrain the dispersal rate, population density and 'foraging' of smaller organisms in a different way from those of larger organisms (e.g. Castle et al., 2011; Finlay, 1998, 2002; Foissner, 2006, 2008; Hagen et al., 2012; Mulder and Elser, 2009). And if so, consistent relationships between bio(geo)chemistry and multitrophic interactions will open exciting ways to assess EF (Friberg et al., 2011).

1.3. Aims of our study

While framing our questions on B–EF relationships is relatively straightforward, testing them is not. Biodiversity collectively refers to all aspects of biotic diversity (Naeem et al., 1999) and its effects are believed to differ among ecosystem types (Hooper et al., 2005; Schmid et al., 2009). To avoid possible confusion, biodiversity will be used here for 'biodiversity as a whole', *S* (species diversity) for taxonomic diversity and FD for functional diversity. As Ghilarov addressed (2000: p. 410), any meaning of biodiversity for EF is strictly dependent on the definitions of ecosystem types and EF; like Ghilarov—and Lindeman (1942) before him—we adhere here to a functional definition of the ecosystem, separated from the surrounding 'environment'. For this purposes, we chose monophyletic ecological assemblages ('taxocenes' *sensu* Hutchinson, 1978) as units to investigate numerical abundance and species diversity relationships (Kaspari, 2001). Productivity and species diversity are influenced by resource limitation and nutrient supply (Allen et al., 2005; Brown et al., 2004; Hubbell, 2001; Huston and Wolverton, 2009; Mulder et al., 2005a; Sterner and Elser, 2002). Hence, the total number of coexisting individual monophyletic assemblages is hypothesized to reflect the ability to harvest and divide energy within a single taxocene (Kaspari, 2001).

Previous attempts to compare different monophyletic assemblages with each other show an unrecorded parallel among insect, bird and plant species (Thomas et al., 2004b). In an attempt to foster a new mechanistic debate, which is important for understanding EF (Chapin et al., 2000), we selected three characteristic taxocenes from the plant and animal kingdoms as well: vascular plants (seagrasses and forest trees), terrestrial invertebrates (soil nematodes and social insects) and freshwater fishes. These three taxocenes are representative of two terrestrial systems, the 'green world' (Polis, 1999) and the 'brown world' (Allison, 2006), and one aquatic system, the 'blue world' (Fig. 2). We also focus on two harsh soils systems, the Atacama Desert with its hypolithic communities of underneath living phototrophs and the Antarctic Dry Valleys with their extremely low biodiversity (Wall, 2008), and two temperate, human-disturbed biota, the rivers of Ohio (Burton et al., 2012), and agroecosystems across the Netherlands (Mulder et al., 2011a–c).

We believe that our study has broad implications with respect to developing more effective management of our biotic resources and consequently we shall:

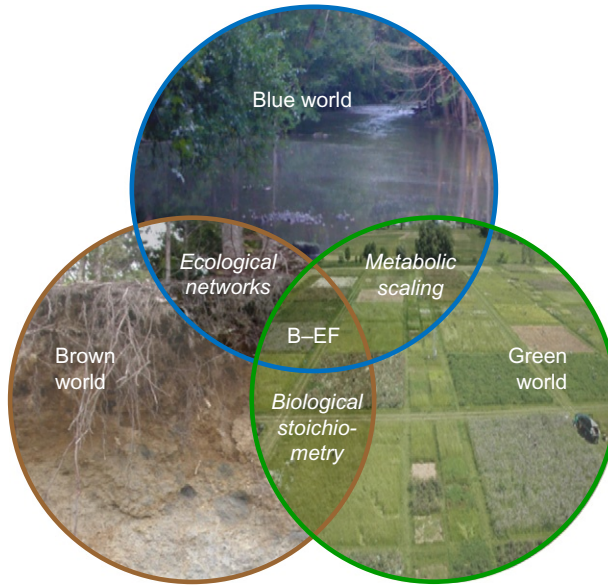


Figure 2 Operational classification of the blue world (water compartment), the brown world (belowground) and the green world (aboveground). The overlapping parts address the kind of B–EF responses measured in this study for three independent taxocenes (freshwater fishes, soil invertebrates and vascular plants). Photo credits: Scott D. Dyer, Shigeta Mori and Winfried Voigt, respectively.

1. analyze biodiversity–productivity relationships in the framework of EF to provide empirical evidence for allometric scaling in reference to ecological stoichiometry,
2. relate the environmental abiotics to presence, mass and abundance of organisms within taxocenes, to assess the importance of species traits that can be seen as stoichiometrically similar and
3. investigate the extent to which aquatic and terrestrial communities composed of species that are stoichiometrically similar may differ from those where species have wide differences in their elemental composition.

2. SCALING B–EF

2.1. Implications of scaling

The scaling of the rates of organismal functions with body size in communities or ecosystems is effectively addressed by allometry, a central—although still somewhat controversial—feature of ecosystems. Allometric scaling has been successfully used, among others, in macroecology (e.g. Arim et al., 2011; Brown et al., 2004; Jacob et al., 2011; Nakazawa et al., 2011; Savage et al., 2004; Storch et al., 2007; West and Brown, 2004), ecological stoichiometry (Mulder and Elser, 2009), the assessment of human-induced biomass exploitation by fishing (Jennings and Blanchard, 2004; Jennings et al., 1999), the impact of global warming on freshwater communities (Dossena et al., 2012; Yvon-Durocher et al., 2010, 2011a) and even for the characterization of fossil food webs (Dunne et al., 2008).

The ecological implications of scaling are great. Figure A1 shows that allometric diversity–yield relationships between species mass and species density (mass–abundance) can be translated into ecological processes transcending discrete boundaries. The metabolic rate, in particular, can be easily estimated by allometric scaling (Enquist et al., 1999; Ernest et al., 2003; Mulder et al., 2005b), with the metabolic respiration rate *per capita*, R, as function of the individual organismal body mass m:

$$R \propto m^{3/4} \quad [1]$$

A notable example of such research beyond biogeographical boundaries comes from a continental transect across Asia, where the field investigation of tree species of different ages (from saplings up to giant trees) is possibly the best physiological example of macroecological scaling (Fig. 3, recalculated from Mori et al., 2010) in which respiration and fresh weight were determined for

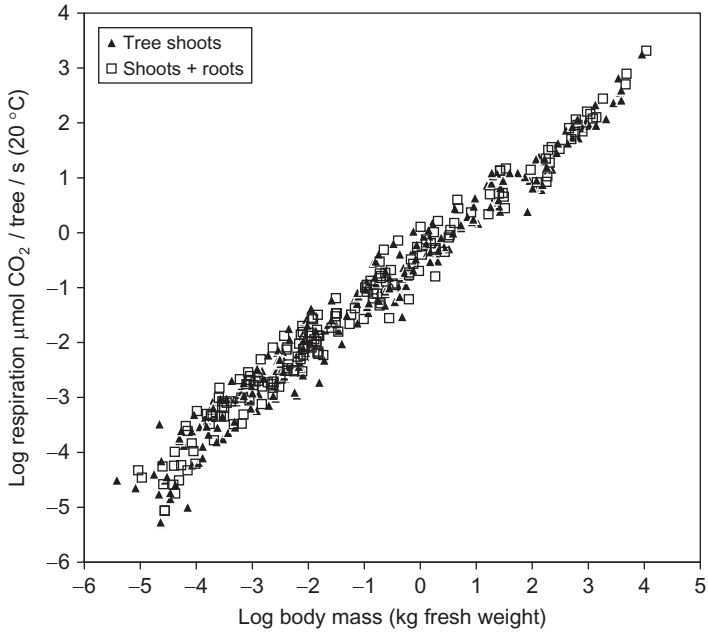


Figure 3 Power laws at autecological scale: plant allometry is perfect for physiological forecasting from saplings up to giant trees. Original data by S. Mori on 320 angiosperms and 120 gymnosperms: all the respiration measurements were made at 20 °C and separate scaling analyses for the aboveground part and the whole-tree mass are shown in Fig. 4. Methods, locations and data are further described in Mori et al. (2010). These authors show that a robust non-isometric scaling of respiration versus fresh weight occurs across all pooled data along one continental transect across Asia, in contrast to previously reported shifts of angiosperms versus gymnosperms and saplings versus adult trees reported in Reich et al. (2006) and Makarieva et al. (2008). The latter debate has been addressed among others by Hedin (2006) and Enquist et al. (2007).

440 trees. The respiration and photosynthesis of plants are opposite and reversible chemical reactions: plant respiration is closely related to translocation of photosynthate, uptake of soil nutrients, N-assimilation, protein turnover, resulting in biosynthesis of new biomass (Amthor, 2000), although considerable discussion on the actual implications of respiration is ongoing (Thornley, 2011 and references therein). Plant size is also known to scale inversely with foliar nutrient (N and P) contents (e.g. Elser et al., 2010). The complexity of these physiological processes makes the scaling of production and metabolism of (photo)autotrophs an important and rapidly growing area in the field of global change biology, especially because of the temperature dependence of the metabolic rates involved (Yvon-Durocher et al., 2010, 2012).

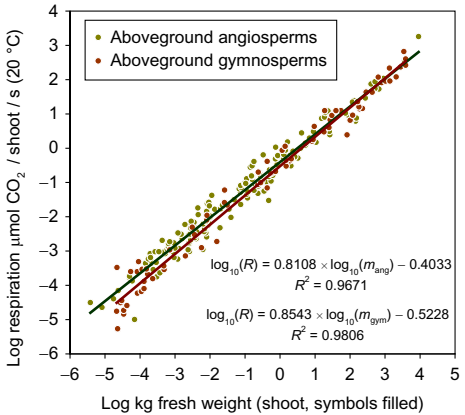
2.2. Green world allometry

A mechanistic explanation which merges allometry with ecological stoichiometry was hypothesized by Reich (2000): given that shaded species restricted to the understory might allocate nitrogen differentially, the saplings of tall trees can possibly allocate less nitrogen to photochemical compounds—and proportionally more nitrogen to compounds directly involved in CO_2 fixation—than the saplings of shorter species. Different light responses and nitrogen allocations are well-known for many plants, such as the *Solidago altissima* forb investigated by Hirose and Werger (1987), lending empirical support to this hypothesis.

A further comparison of the trend embedded in Fig. 3 at a finer scale reveals that although the predicted respiration rates (μmol CO_2/tree/s) for small adults are rather comparable, the differences between gymnosperm and angiosperm saplings and between their respective adults are remarkable (Fig. 4). This occurs for both the aboveground masses and for the whole trees and enables the investigation of the magnitude of carbon uptake and loss through CO_2 exchange (Fig. 4). Mori et al. (2010) selected trees of various heights and ages spanning from the smallest to the largest tree species in each forest to cover the full width of individual respiration rates.

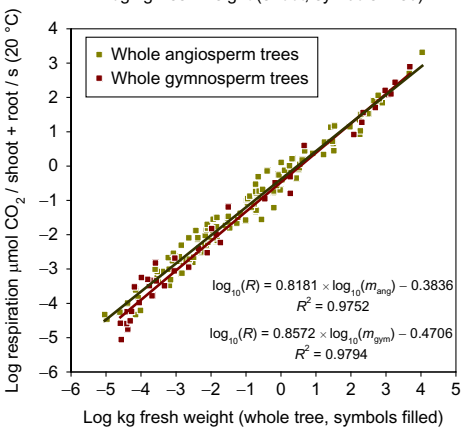
It must be noted that in any forest community, the depressed trees with a small amount of leaves are not always the smallest tree species. Therefore, some of the smallest trees have much of their adventitious branches adapted to the environments in a forest canopy gap, and relatively high specific respiration rates per individual mass in contrast to dominant tree species. Smaller trees determine the understory and play therefore an important role in maintaining the sustainability of natural forests.

The observed differences between angiosperm and gymnosperm trees were unexpected. Ernest et al. (2003) compared the plants with metazoan taxocenes and found that the metabolic scalings for either 'all plants' or 'all organisms' (i.e. 387 plants and 360 metazoans pooled together) were ¾ (absolute) and −¼ (mass-specific). Metazoan mass-specific metabolic rates with body mass can change (Glazier, 2005, 2010; Lovegrove, 2000; White, 2010), among others due to different thermal responses across life stages (Forster et al., 2011), whereas the protozoan metabolic rates can even be completely unrelated to their body mass (Makarieva et al., 2008). Protozoan metabolism deviates from allometric scaling rules: protist groups are widely scattered all over the eukaryotic tree of life (Adl et al., 2005), differ fundamentally in morphology



Above ground

Fresh weight (shoot kg)	Gymnosperm (µmol CO_2)	Angiosperm (µmol CO_2)	Respiration rate (adimensional)
0.0001	0.00011	0.00023	0.51
0.001	0.0008	0.0015	0.56
0.01	0.006	0.009	0.62
0.1	0.04	0.06	0.69
1	0.3	0.4	0.76
10	2.1	2.6	0.84
100	15.3	16.5	0.93
1000	109.7	106.9	1.03
10,000	784.15	691.67	1.13



Above and below ground

Fresh weight (whole-tree kg)	Gymnosperm (µmol CO_2)	Angiosperm (µmol CO_2)	Respiration rate (adimensional)
0.0001	0.00013	0.00022	0.57
0.001	0.0009	0.0015	0.62
0.01	0.007	0.010	0.68
0.1	0.05	0.06	0.75
1	0.3	0.4	0.82
10	2.4	2.7	0.90
100	17.5	17.9	0.98
1000	126.2	117.7	1.07
10,000	908.24	774.11	1.17

Figure 4 Plant physiological efficiencies for gymnosperm and angiosperm trees as predicted by the scaling analyses for the aboveground part (upper panel) and the whole-tree weight (lower panel). In the headers from left to right, the fresh weight of the plant (kg shoots), the tree respiration at 20 °C in µmol CO_2 forecasted for gymnosperms and angiosperms, and the physiological efficiency rate between gymnosperm and angiosperm trees of the same weight. The aboveground part of angiosperm saplings is about two times as efficient in the respiration rate as the shoot of gymnosperms of the same weight. For taller trees (> 100 kg fresh shoot weight), the switch in the aboveground respiration for (adult) gymnosperms versus angiosperms is expected to occur around 600 kg fresh shoot weight. For the whole tree, angiosperm saplings remain much more efficient in the respiration rate than gymnosperm saplings or small adults. Physiological efficiency switches for whole-tree respiration are expected to occur between 100 and 1000 kg. Raw data from Shigeta Mori.

and can show contrasting relationships between metabolic rates and body mass (Makarieva et al., 2008; Reiss et al., 2010).

According to the data of Makarieva et al. (2008), the metabolic rate of free-living amoebae scales with their body mass to the $-1/6$ power, opposite to non-amoeboid parasites (i.e. human endopathogenic protozoans) whose metabolic rate scales with body mass to the $1/6$ power. One feature is that we might speculate that non-amoeboid parasites are adapted to constant, high temperatures and downregulate gene expression or even lose genes as organelles, that is, mitochondria, are commonly lost by such parasites (Cavalier-Smith, 1993; Walker et al., 2011). Thus, we may need to take the external conditions, that is, the host, into consideration to evaluate metabolic rates or generally treat obligate parasites separately. Another feature is that in the case of free-living protist groups, this might indicate that locomotion in viscous water is less energy demanding for amoebae which move forward attached to surfaces and do not swim actively like ciliates and flagellated organisms. Amoebae were already regarded by Fenchel and Finlay (1983) to be metabolically different from other protozoans. In summary, currently available data do not enable the recognition of global allometric trends between and within all taxocenes occurring in the green, brown or blue worlds.

2.3. Allometry and management

These allometric approaches to B–EF relationships have been applied increasingly in the real-world setting of assessing human impacts on fisheries and understanding the causes and consequences of the current global collapses in fish stocks. On a local scale, the taxocene that describes the fish assemblage provides not only critical ecosystem processes but also goods and services of huge economic value to humans. The historical correlations between density-dependent stocks, mesh size, fishing efforts and resulting overexploitation are clearly evident (e.g. Cardinale and Svedang, 2004; Jackson et al., 2001; Walters and Maguire, 1996) and have consequently contributed to make allometry an accepted tool in fisheries and marine sciences (Jennings, 2005; Shin et al., 2005; White et al., 2008; Section 4.5).

Despite the abundance of papers unravelling aspects of the blue world, fewer examples are known for the green and the brown world. Although a comparable correlation between canopy density and forest productivity also seems to be a representative example of B–EF congruences, the data by Mori et al. (2010) also show B–EF incongruences between the metabolic scaling of angiosperms and gymnosperms (Fig. 4). Lumping the variability of

individual metabolism in a community (e.g. roughly comparing angiosperms with gymnosperms or evergreen trees with deciduous trees) sums over the limits of forecasting (Fig. 3).

Our findings might have implications for different aspects of forest management: in *conservation* management, significant carbon stocks are protected in living biomass, whereas in *sequestration* management, carbon is retained in ecosystems by (increasing) reforestation. The decomposition process of converting the organic carbon in the (surface or root) litter to CO_2, making nitrogen available for plants without rhizobia, is influenced by the chemical nature of carbon compounds (cellulose vs. lignin), by the kind of mycorrhizal symbiosis, by root exudates and by the microbial pools (bacteria vs. fungi) that support plant life and therefore ultimately underpin terrestrial EF (Beerling and Woodward, 2001; Gams, 1992; Lynch and Whipps, 1990; Moore et al., 2004).

Although the capability of plants to sequester carbon and emit CO_2 to the atmosphere varies across species (Bala et al., 2007), allometry has been used scarcely to forecast or manage global changes (Fahey et al., 2010). Size-related allometry provides dynamic tools for wild and domestic population management, such as in the framework of restoration ecology, reducing carbon footprints and implementing activities to minimize deforestation effects. Despite many countries focusing on conservation (e.g. planted trees must belong to native species) or thinning wood, a sustainable agroforestry management should avoid the current large-scale recommendation of gymnosperm trees (such as in United Kingdom, see www.direct.gov.uk/thebigtreeplant, and in the United States, see http://apps.fs.fed.us/fido) because the different capabilities of gymnosperm and angiosperm adults to emit CO_2. Such considerations will surely demand more attention during the planning of afforestation projects in the near future, especially given the increasing socioeconomic momentum behind developing low-carbon-based economies.

3. CONSTRAINING B–EF

3.1. Allometry rules the world

There is a need to investigate B–EF to gain understanding of the biological and ecological factors underpinning sensitivities and traits of species in the context of environmental stressors. In the previous sections, we show the extent to what EF may become recognizable with macroecological approaches such as allometric scaling. Allometry is a suitable method to assess

the emergent characteristics of large data sets of organisms (Jonsson et al., 2005; Marquet et al., 2005). According to Brown et al. (2004) and Marquet et al. (2004), the fundamental rules of chemistry, physics and biology provide the means to link individual organisms and their populations to ecosystems and their ecological processes. However, although 'it is clear that scaling relationships hold best when examining patterns across a wide spectrum of body sizes' (Tilman et al. (2004): p. 1798), Brown and Gillooly (2003) show that separate taxocenes derived from small data sets exhibit biomass and mass–abundance scaling relationships that can be opposite from the scaling relationships for all data sets together (Cohen et al., 2003). These divergent relationships raise the question about predictability of species sensitivity to stoichiometrically driven processes, even within comparable size classes. For instance, certain taxa sharing comparable sizes may occupy the most extreme trophic positions not only in a food web but even within a loop, as in the case of viruses as top predators (despite their viral host specificity) and bacteria as basal producers (e.g. Thingstad, 2000). Therefore, it seems difficult to always extrapolate (opposite) results to a wider context, although similarities in the response of phyla and biota become more evident as soon as studies are addressed across scales.

Some, but not all, organisms can be easily identified at species level and a comparable methodology does not *per se* imply equivalent taxonomic resolution: microbial taxa, which drive so many ecosystem processes, remain a particular challenge in this respect (Mulder et al., 2005a,b, 2009; Purdy et al., 2010; Reuman et al., 2009). Regardless of their Latin binomial, all taxa within one community can be modelled using either the unbinned body mass (size) versus numerical abundance scaling or the binned biomass-size spectrum. Successful examples on large-scale investigations come from the blue world (Clarke and Johnston, 1999; Cohen et al., 2003; Killen et al., 2010; Pope et al., 1994, 2006), focusing on traits for behavioural adaptation (like in the case of suspension feeders: Goldbogen et al., 2012; Jeschke et al., 2004; Jørgensen, 1966). Investigations on whales in particular show extreme trophic positions in pelagic ecosystems, because the huge baleens are not only *able* to feed on very small prey (Goldbogen et al., 2012; Jacob et al., 2011), in contrast to toothed whales and teleosts, but are *specialized* to feed on patchy resources. Moreover, trophic levels do not imply a discrete body size (Borgmann, 1987), for although sharing the same trophic level across a wide size distribution, phytoplankton belonging to smaller size classes may achieve faster nitrogen uptake rates than phytoplankton belonging to large size classes (Hein et al., 1995).

This is in contrast to the nitrogen uptake by zooplankton, whose smaller individuals are forced to feed on algae only and whose larger individuals can feed on both phytoplankton and zooplankton (Boit et al., 2012; Fry and Quiñones, 1994; Ptacnik et al., 2010). Body size is thus a fundamental trait for both autotrophs and heterotrophs, as a taxon occupies in a size-based model a much more defined position than it does in a trophic level model' (Cohen, 1994; Cousins, 1980).

Body size can also greatly influence ecological interactions among terrestrial organisms, although perhaps less obviously so than in the blue world, with important consequences at the community and ecosystem level (Yvon-Durocher et al., 2011b). The metabolic scaling of a given organism (Calder, 1984; Damuth, 1981, 1991; Peters, 1983) is one of the best examples of B–EF because functional scaling is species-independent (i.e. unrelated to taxonomic diversity). Across species and within one or more taxocenes, many physiological models may hold. Figure 5 shows that pollinating insects (here, some extremely diverse bees, wasps, butterflies and moths) can cover the entire allometric range of reported measurements. The metabolic rate (R) of *all* insects (data recomputed from the publicly available data of Chown et al., 2007) scales with insect mass to the 0.87 ($\pm$0.02 SE) power, but different metabolic scaling exponents are recognizable within finer taxonomic groupings. Scaling with mass to the 0.78 ($\pm$0.06) and the 0.72 ($\pm$0.03) power, respectively, hymenopterans and coleopterans are the groupings closest to the scaling exponent for the metabolic rate for all insects. In the upper part of the scatter-plot of Fig. 5, the metabolic rates of lepidopterans and orthopterans scale to the 0.67 ($\pm$0.06) and the 0.60 ($\pm$0.09) power, respectively (much lower than the isopterans, which scale isometrically with mass to the 1.04 ($\pm$0.18) power). Some dipterans, hemipterans and coleopterans (two genera of Curculionidae) have the lowest metabolic rate among all insects. Given the ubiquity of insects in freshwater ecosystems, their different allometric scaling must have implications for the blue world as well and should be addressed in the future.

3.2. How local biodiversity determines individual abundances at taxocene level

The number of species is believed to be particularly critical for B–EF in environments with low biodiversity, where there is less scope for redundancy to be manifested (i.e. 1–10 species; Wall, 2007). For protozoa and microorganisms,

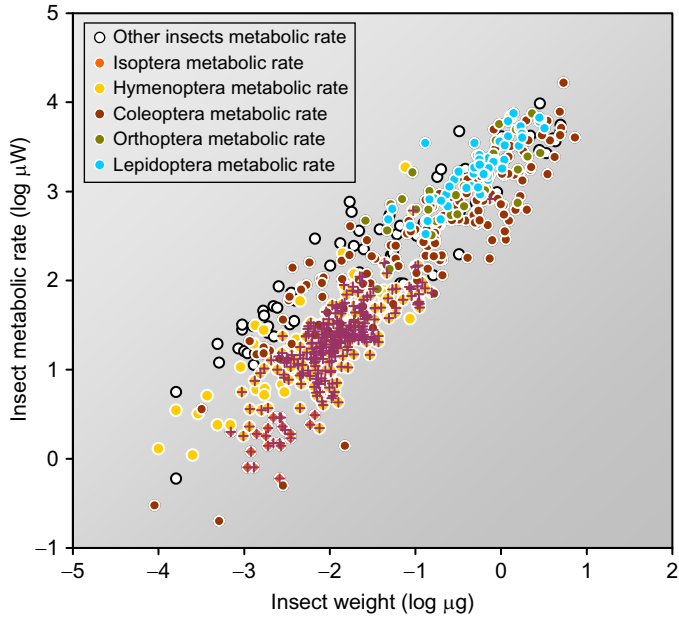


Figure 5 Power laws at synecological scale: allometry is suitable for functional forecasting of brown food web invertebrates such as insects. All eusocial insects like size-polymorphic colony ants (Hymenoptera) and termites (Isoptera) are additionally marked by one cross. Raw data from Chown et al. (2007, their Supplementary Material); these authors converted different metabolic rates from scientific literature to microwatts assuming $Q_{10} = 2.0$ at 25 °C. Values for the scaling exponents vary among groups and fall approximately between $^2/_3$ and 1.

rare species are likely to compose the majority of species within a habitat (Dawson and Hagen, 2009; Finlay, 1998). Less abundant microorganisms might have pronounced bottom-up effects, as shown for several bacterial species under lab conditions (Höppener-Ogawa et al., 2009). This holds for soil invertebrates as well: in the McMurdo Dry Valleys of Antarctica, there may be three to five (or even fewer) nematode species (Moorhead et al., 2002; Treonis et al., 1999, 2000). However, the numerical abundances of nematodes in pristine Antarctica can be comparable to those of temperate agroecosystems (Fig. 6), in apparent contradiction to the More Individuals Hypothesis (MIH), as originally defined by Srivastava and Lawton (1998), who related the higher biodiversity of productive locations *to the ability of such sites to support large populations of each species*. However, although the most

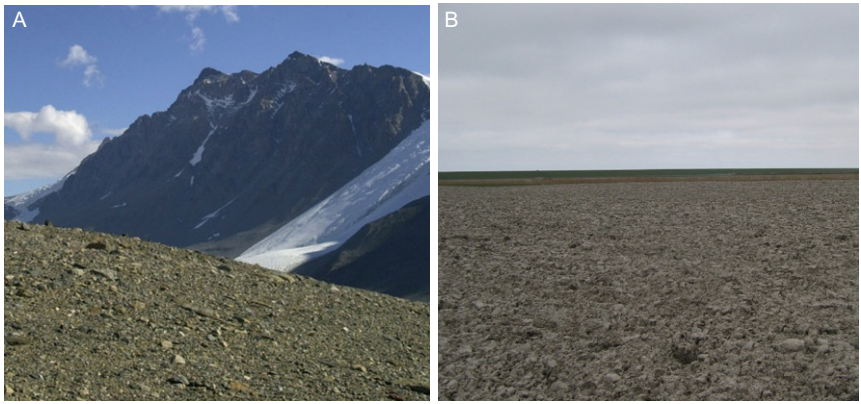


Figure 6 What do the extreme desert of the Taylor Valley in Antarctica and one recovered sea clay in the Netherlands have in common? One soil sample might contain an almost equal abundance of soil nematodes, but with greatly contrasting numbers of species. Photo credits: Diana H. Wall/Emily Stone (A) and Christian Mulder (B).

productive sites of that study (physically isolated water-filled microhabitats such as tree holes; see further Hagen et al., 2012) contained more species (Srivastava and Lawton, 1998), this was not a matter of more individuals, as the increase in species richness with productivity occurred only when the energy amount was reduced.

Assuming that the opposite holds as well (the fewer the species, the lower the total abundance), smaller populations under low productivity are likely to be prone to extinction. In that case, the polar deserts are a unique exception, because they do not only support fewer species, but exhibit large populations with far more individuals (Wall, 2007, 2008). The low human-induced disturbance in most deserts makes such environments attractive to assess the ecosystem responses to climate and therefore, other drylands received more attention as well. Recently, Maestre et al. (2012) clearly show that sustainability and multifunctionality (defined, among others, as the ecosystems' ability to maintain productivity, to support carbon storage and to buildup nutrient pools) are positively related to species richness. Deserts like those investigated by Maestre et al. (2012) and the Antarctic Dry Valleys are most valuable to test the MIH because drylands are less affected by sampling effects and patchiness, in contrast to fragmented landscapes such as the moss carpets of Gonzalez et al. (1998). Deserts can therefore reveal the key function (if any) of biodiversity *sensu lato* under environmental stress.

To test the MIH model of Srivastava and Lawton (1998), we analyzed the nematofauna from 200 agroecosystems with different habitat fertility (Mulder and Vonk, 2011), that is, productivity proxies: in contrast to the first study, where the authors used debris, we used primary nutrients to characterize productivity. Being the Shannon-Wiener index function of the (number of) species and given that higher values indicate even species distribution, Fig. A2 shows a hump-shaped relationship for both the exponential Shannon index and the taxonomic diversity of nematodes. Soil fertility (i.e. resource supply) and nematode species richness seem there to be interdependent (a classical B–EF example), indirectly supporting the historical paradigm that productivity drives species richness in contrast to the contemporary view that species richness drives productivity (Cardinale et al., 2009; Gross and Cardinale, 2007). However, such a set of variables might have a predictive power that dynamically changes in space (e.g. Hurlbert and Jetz, 2010; Huston, 1994, 1997; Loreau and Hector, 2001), possibly due to sampling bias or species competition, and in time (e.g. Kaspari (2005) for temperature and Yee and Juliano (2007) for phenology).

Spatial scaling predicts a positive decelerating relationship between abundance and species richness in a way comparable to the MIH: in the sampling hypothesis, for a given species pool, a tropical plot should *per se* contain more species than a low-productivity boreal plot. Kaspari et al. (2003) tested this by randomly sampling simulated m^2 plots with 1, 2, . . . n individuals from the measured species pool for a site and compared that curve with those observed. Where species richness versus total abundance relationships is predictable, it is at such a large aggregation that abundance reflects immigration and/or extinction processes, an intriguing topic when considering that over 100 ant species can be found in 100 m^2 of forest (Kaspari et al., 2001).

To test the extent to which EF increases with biodiversity, we plotted several communities of invertebrates, from ants in pristine rainforests and temperate forests up to nematodes and non-flying arthropods in deserts in the southern hemisphere. All numerical abundances in Fig. 7 were converted to densities per m^2. Assuming the N of the entire population within one taxocene represents a proxy for local resource availability, the taxonomic diversity *within one taxocene* (e.g. the number of arthropod species) scales directly with the abundance of all individuals (e.g. all the arthropods of a given location as in Mulder et al., 2005a). All significant species–density relationships of Table 2 follow power laws with exponents smaller than ½ (i.e. the total species diversity within one taxocene increases monotonically with abundance N), whereas density–species relationships

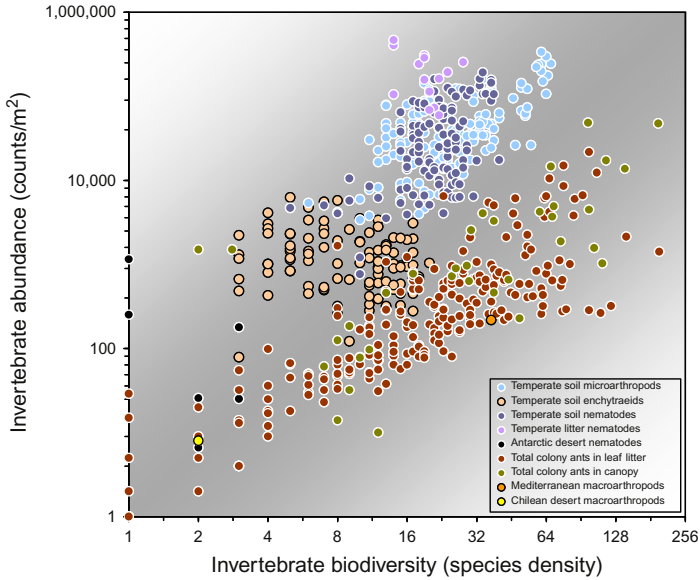


Figure 7 Direct B–EF correlations between species density (biodiversity) and total abundance of individuals are expected to be widespread in comparable plots. Ants data downloadable from Weiser et al. (2011); polar nematofauna from the Taylor Valley, Antarctica, as in Courtright et al. (2001: their Table III) and Barrett et al. (2006: their Table IV); temperate nematofauna downloadable from Mulder and Elser (2009) and Mulder and Vonk (2011). Macroarthropods from the coastal zone of the Atacama Desert, Chile, were described in González et al. (2011); temperate soil microarthropods—mites and collembolans—described in Mulder et al. (2005a); Dutch data on soil enchytraeids from grasslands, heathlands and forests are novel; data on the litter nematofauna from pine forests in the Netherlands and on the litter macroarthropods from a Mediterranean beech forest in Italy are unpublished (C. Mulder and G. Mancinelli, respectively). Please note the two logarithmic scales, being different bases (2 and 10) used.

follow power laws with exponents larger than 1 (i.e. the total abundance within one taxocene increases with species diversity S, cf. Fig. 7).

All macroarthropods in Fig. 7 had $R^2 = 0.66$ ($P < 0.00001$), rejecting the null hypothesis of no correlation between density N and diversity S. With different combinations, including or excluding soil and litter invertebrates, respectively, the results for the taxocenes are given in Table 2, along with the regression lines of density as function of biodiversity and vice versa. Assuming that resource availability within a sampling area is homogeneous, different distributions become recognizable, irrespective of environmental conditions: smaller animals belonging to the micro- and the mesofauna

Table 2 Scaling at different aggregation levels of the total density *N* as function of biodiversity *S* and vice versa for the invertebrates shown in Fig. 7

ID	Faunal taxocenes	Environment types	Plots	*N* scales to *S*	*S* scales to *N*	Pearson's *r*	Variance explained (%)
A	Microfauna	Soil and litter	142	2.24 ± 0.17	0.25 ± 0.02	0.742^{***}	55.1
A1	Free-living soil nematodes	Soil	120	1.70 ± 0.26	0.16 ± 0.02	0.521^{***}	27.1
A2	Moss-inhabiting nematodes	Litter	22	3.15 ± 0.34	0.26 ± 0.03	0.901^{***}	81.2
B	Mesofauna	Soil	246	1.98 ± 0.12	0.27 ± 0.02	0.733^{***}	53.7
B1	Mites and other microarthropods	Soil	146	1.24 ± 0.13	0.32 ± 0.03	0.635^{***}	40.3
B2	Enchytraeids	Soil	100	-0.21 ± 0.16	-0.09 ± 0.06	-0.136	<2
C	Macrofauna	Litter and canopy	259	1.42 ± 0.06	0.46 ± 0.02	0.809^{***}	65.5
C1	Litter macroarthropods	Litter	225	1.40 ± 0.06	0.49 ± 0.02	0.831^{***}	69.2
C2	Canopy macroarthropods	Canopy	34	1.26 ± 0.24	0.37 ± 0.07	0.680^{***}	46.3
	Partial aggregation						
A + B2	Enchytraeids + nematodes	Soil and litter	242	2.18 ± 0.14	0.23 ± 0.01	0.704^{***}	49.6
A1 + B	Soil micro + mesofauna	Soil	366	2.04 ± 0.10	0.25 ± 0.01	0.721^{***}	52.0
B1 + C	Micro + Macroarthropods	Soil, litter and canopy	405	1.66 ± 0.13	0.17 ± 0.01	0.529^{***}	28.0
	Complete aggregation						
A + B + C	All taxocenes together	Soil, litter and canopy	647	1.48 ± 0.11	0.15 ± 0.01	0.472^{***}	22.3

N and *S* values were $\log_{10}$-transformed to measure strength and direction of their linear dependence by the Pearson's correlation coefficient and the standard error. Such base-10 log–log linear regressions can be easily transformed in power laws. Besides enchytraeids ($P = 0.179$, implying a random, non-linear relationship), all these linear relationships were significant: ***($P < 0.00001$). Note the steepness increase in abundance–biodiversity relationships from the larger-sized macroarthropods (here: colony ants under pristine conditions) down to the microarthropods (mites and collembolans) and nematodes.

(like nematodes, enchytraeids, mites and collembolans) clearly have a much higher average density per species than is true for larger macroarthropods (ants, beetles, etc.). Although taxocenes showed significant positive correlations between biodiversity and total abundance, enchytraeids showed no significant trend (Table 2).

3.3. The extent to which scaling changes between taxocenes

The way in which the correlation between density N and number of species S changed between taxocenes may largely be interpreted as secondary tradeoffs (demographic responses to abiotic or biotic factors *sensu* Suding et al., 2003). In 2006, Meehan classified the occurring taxa in his brown world study into two broad guilds: 'Grazers', including soil nematodes, oribatid mites, collembolans and enchytraeids, and 'Carnivores', including spiders, ants, chilopods and non-oribatid mites (these in apparent contrast to freshwater literature, where grazers typically mean consumers of algae and carnivores do not *per se* imply only piscivorous fishes). Notwithstanding the difference of more than five orders of magnitude in the total faunal density N (Fig. 7), for differently sized invertebrates the slopes of the density–biodiversity regression lines were 1.42, 1.98 and 2.24 for litter and soil macrofauna, mesofauna and microfauna, respectively (Table 2).

The exclusion of litter macroinvertebrates from our log(N) on log(S) analysis makes the slope of the regression line steeper than lumping all invertebrates together. This was expected, given that invertebrates using different resources (i.e. different fractions of energy supply, as in the case of litter vs. canopy arthropods), collectively deplete energy more effectively (Kaspari and Weiser, 2012). Hence, scaling to higher levels of aggregation may track the ecosystem's productivity (eNPP) more accurately (Kaspari and Weiser, 2012). Scaling varied markedly between taxocenes, from the numerical abundance of Neotropical canopy ants (highest eNPP), which scale to the $^{5}/_{4}$ power of (high) species diversity, up to the abundance of Antarctic nematodes (lowest eNPP), which scale to almost the $^{7}/_{2}$ power to their (low) species diversity (Table 2).

Conversely, the log(S) on log(N) functions show a sharper increase in steepness, varying from 0.25 to 0.27, and finally 0.46 for macrofauna, mesofauna and microfauna, respectively. The coefficients of variation (CVs = 100 × SD/degree average) for diversity S, as predicted by density N, were higher than for density N as predicted by diversity

S (32.7% vs. 9.4%, respectively). Again, the power scaling differs from the species diversity of litter nematodes, which scales to the ¼ power to their numerical abundance, up to the species diversity of litter arthropods, which scales to the ½ power to their numerical abundance (Table 2). This reflects an antagonism between belowground 'Grazers' and 'Carnivores', as the biodiversity of the entire 'Grazer' group scales to the ¼ power of the total group and the biodiversity of the entire 'Carnivores' group scales to ~½ power of the total group (Section 3.2).

Our results reflected those from other macroecological studies. Marquet et al. (2005) found linearity of log-transformed total number of species *S* versus log-transformed mass average $\bar{M}$: for South American mammals, their log(*S*) on log($\bar{M}$) slope was close to $-¾$. If we assume an isometric mass–abundance scaling (a log(*M*) on log(*N*) regression slope equal to -1, implying a constant biomass across populations), then $N \propto \bar{M}^{-1}$ (Cohen et al., 2003; Mulder et al., 2005b; Woodward et al., 2005a). In Table 2, however, all soil invertebrates belonging to micro- and mesofauna (nematodes, enchytraeids, mites and collembolans) share $S = N^{0.25}$. If we merge these two equations together, we get for our soil invertebrates

$$S = N^{0.25} = \bar{M}^{0.25-1} = \bar{M}^{-0.75} \quad [2]$$

as expected from general metabolic scaling and macroecological theory (Marquet et al., 2005; Storch et al., 2007; Wardle, 2006) and as empirically supported by randomly chosen assemblages of soil nematodes (Mulder and Vonk, 2011).

There are a few exceptions to this law (Eq. 2) in soil food webs, one of which is the enchytraeids, which occupy only one trophic level (this taxocene comprises strictly peripheral consumers of microbial resources). In high productivity grasslands, soil microbivores like enchytraeids seem to be the most sensitive to density-dependent regulation according to classical theory (Lack, 1954), but the relationship between the species diversity and density of enchytraeids is the only non-significant correlation in Fig. 7. Already in 1982, Standen recognized a certain tendency for sites with few enchytraeid species to have high abundances (Standen, 1982), while sites with many enchytraeid species rarely achieve high abundances (see also Standen, 1980). The possibility that this ecologically important size-scaled taxocene is also stoichiometrically different from others (like soil nematodes) merits further investigation in the future.

4. PREDICTING B–EF

4.1. B–EF and functional redundancy in the blue world: Theoretical background

Generalist feeding strategies and omnivory are well-known in the food web literature (e.g. Gilljam et al., 2011; Woodward et al., 2010a). Therefore, a quantification of the degree of redundancy within food webs, either as interspecific or intraspecific (if at different life stages) differences in trophic position and diet, is crucial for B–EF modelling. In contrast to empirical studies, where complexity provides according to Polis (1998) 'an interwoven matrix that holds . . . a community together', few studies have really addressed the role of the redundancy within a predator–prey matrix (Reiss et al., 2009). The assignment to a specific guild (trait) is important because it determines the amount (and vertical direction) of possible links. For the classification of freshwater fish species, we followed Goldstein and Simon (1999) and Goldstein and Meador (2004). Fish species are good indicators of freshwater ecosystems health (e.g. Simon, 1999) and cover many feeding types (Attrill and Depledge, 1997). We assigned fishes to five main feeding guilds: planktivore, detritivore, invertivore, herbivore and carnivore *sensu stricto* (Table 3).

Assuming that no species is isolated and that all species are part of one network with more subunits, then possible trophic links depict consumer–resource interactions within the fish assemblages (Table 4 shows empirically validated trophic links as recorded in current literature). After Winemiller (1989), Martinez (1992) and Dunne et al. (2002, 2004), interaction richness is defined as the trophic links L per species S, also referred to as link density, and by connectance C. If both interspecific and intraspecific effects are considered, C is defined as

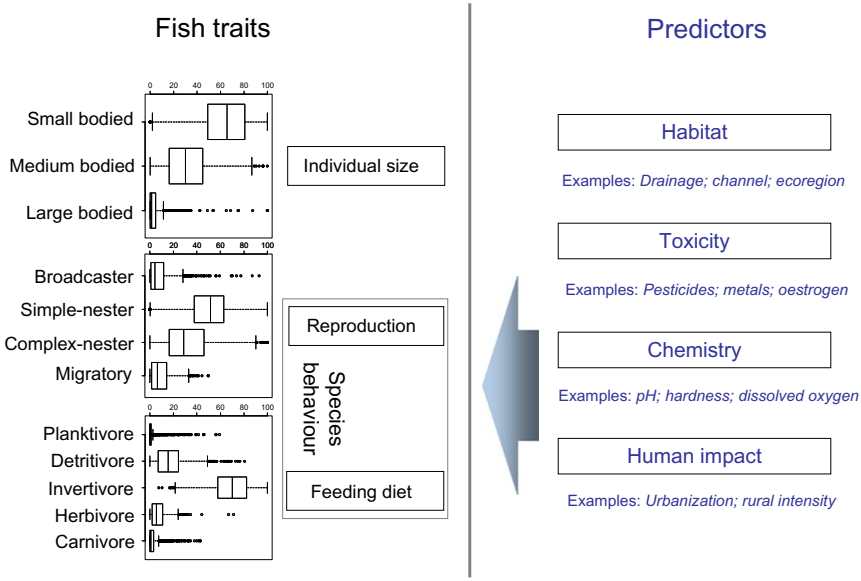
$$C=\frac{L}{S^2} \qquad [3]$$

and if intraspecific effects are not considered, that is, the realized fraction of all pair-wise interactions, besides cannibalism, as

$$C=\frac{L}{[S\times(S-1)]} \qquad [4]$$

C as defined in Eq. (3) is used more frequently, and termed 'directed connectance' (Beckerman et al., 2006; Ebenman and Jonsson, 2005; Martinez,

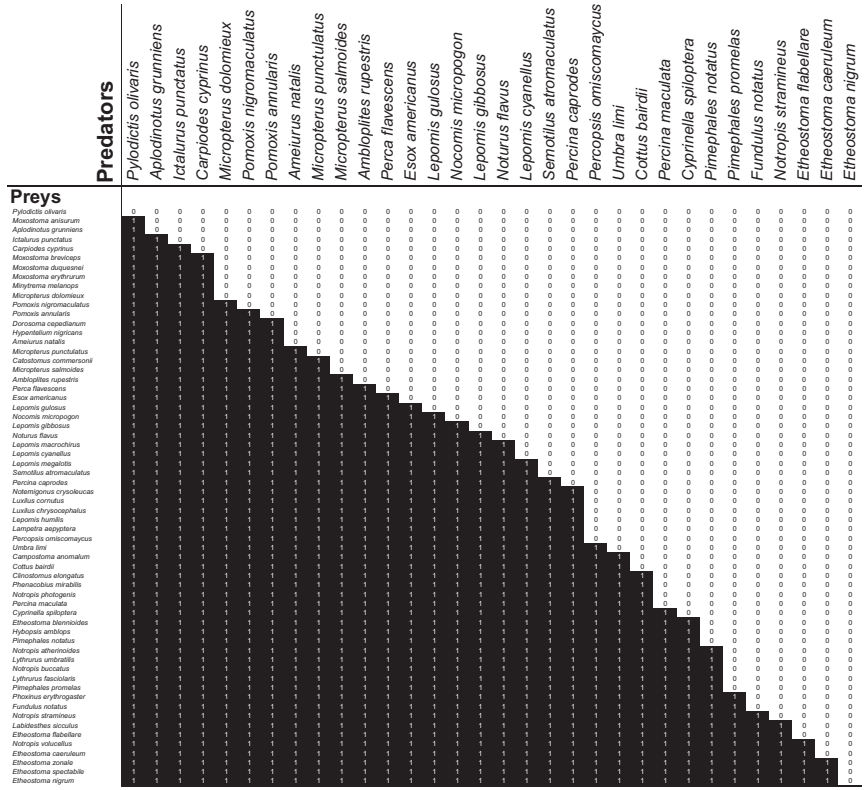
Table 3 Lessons from stress ecology. Abiotic predictors are known to affect the occurrence of fish species (e.g. Hawkins, 2006; Hendrixson et al., 2007; Posthuma and De Zwart, 2006), albeit fish traits are influenced as well, as expected by the relevant properties across taxonomical and organizational levels from Table 1 (Huston and Wolverton, 2011; but see Sterner and Elser, 2002). The fish traits at population level are based on species assignment according to Goldstein and Meador (2004); traits at individual level are based on empirical data across the State of Ohio



1991). The 'link density' is also known as linkage density (Pimm et al., 1991; Winemiller 1989, but see the original definition in Briand, 1985).

To avoid confounding C of different food webs by differences in sampling methods, we focused in the next section on a consistent methodology (Havens, 1992; Martinez, 1993; Romanuk et al., 2009). Rather than computing the link density as the number of realized trophic interactions per locally occurring species, we chose an adapted taxocene-specific web connectance (hereafter, C_t as in Fig. A3), where the proportion of all trophic links between fish species (i.e. who eats whom but not who eats what) that are realized in one fish assemblage as derived from the matrix in Table 4. C_t reflects either a dominance of generalists (high C_t values:

Table 4 Predator–prey matrix showing the dominant freshwater fish species occurring in 18 rivers of Ohio, horizontally and vertically ranked according their average fresh weight. Rows as resources, columns as consumers, black cells the realized trophic links the largest consumer (predator) is plotted upper left of the table, the smallest consumer (*Etheostoma nigrum* feeds on eggs of other fishes) is plotted bottom right. More details in Table A1



omnivory and piscivory dominate) or a skew towards specialists (low C_t values: high sensitivity to environmental stress and low resilience).

The definition of species categories in a food web determines the interactions (these two issues are mutually dependent for Cousins, 1996: p. 244) and static food webs use aggregate attributes like connectance to predict other aggregate attributes, such as the proportion of omnivores (Loreau, 2010: p. 56). However, based on our empirical knowledge of both

species-related traits and size-related guilds within the Pisces monophyletic taxocene, the C_t proportion of all links is suggested to reflect the dominance of piscivory without requiring a more systematic data structure. Hence, being unrelated to other compartments or taxonomical groups, C_t values indirectly represent the mutual fish behaviour *within one taxocene* (Fig. A3), analogous to intraguild predation, which is a common feature of many food webs, especially in the blue world (Woodward et al., 2010b).

4.2. Inland water biodiversity: Effects of landscape complexity on B–EF

4.2.1 Streams and ecoregions

Fishes are mobile and useful to assess large-scale (and long-term) effects because many species cover a wide area during their lifespan. The taxonomy of fish is well defined, reflecting their importance as a food resource. Three American Midwestern ecoregions presenting a comparable number of sampling sites were selected for a pilot study on Ohio fish assemblages: Eastern Corn Belt Plains, Erie Drift Plain and Western Allegheny Plateau (Fig. A4). These North-American regional communities were used to quantify and compare the variation in fish body mass and the *properties* of individuals, populations and assemblages across ecoregions.

An ecoregion is defined here as a unit of land that is homogenous with respect to multiple landscape characteristics such as geology, soil characteristics, natural vegetation and climate (after Wagner et al., 2007). The underlying assumption behind the use of ecoregions and watersheds is that classification of surface waters will reduce natural within-class variation of biological and ecological data (Gerritsen et al., 2000). Streams within ecoregions generally respond in a broadly similar manner to comparable management practices (Lyons, 1989), although heterogeneity in physical habitat and water quality conditions may confound the measurement of their biotic responses (cf. Feld et al., 2011; Friberg et al., 2011; Hawkins, 2006; Larrañaga et al., 2010; Toepfer et al., 1998).

4.2.2 Computational methods

Fish species and their assemblages (numerical abundance, body size and interactions) are hypothesis to reflect environmental conditions (e.g. Feld et al., 2011; Layer et al., 2010, 2011). Our analyses of the freshwater fish assemblages were performed at different levels: firstly, via the construction

of networks for sites sampled in a comparable way and secondly via the calculation of size spectra and power laws to describe network topology.

At the first level, we used the US-EPA raw counts and body mass of individual fishes in the State of Ohio (www.epa.gov). After data mining, we had 2656 fish taxocenes sampled in different ways. Electrofishing (often in conjunction with seines or nets) was the principal sampling methods for fish individuals in wadeable and boatable streams (Flotemersch, 2001): in wadeable streams, block nets are placed downstream and upstream of the sampling pool, in contrast to boatable streams, where boat-based electrofishing is done throughout.

At the second level, an allometric assessment of the fish size distribution was performed. We conducted analyses for the 2656 locations on possible deviations from linearity of the upper tail of the binned biomass-size spectra: reflecting the use of different sampling methods, the 534 boatable streams exhibited three times lower standard deviations than the 2132 wadeable streams (0.0787 SD vs. 0.2440 SD, respectively). Based on the allometric uncertainties in biomass estimates as derived from the size spectra for all the locations (summarized in Fig. A5), we chose a subset of 302 locations unaffected by either habitat heterogeneity, sampling bias or survey differences, aiming for a consistent sampling methodology (in our case, boatable streams).

Some of these fish assemblages will be discussed in the next sections. In particular, we investigated whether the food web structure within one taxocene might be relatively vulnerable to different static deletion sequences to diagnose the magnitude of changes in biodiversity, for example, through potential fish extinctions caused by ecological impacts in rivers, and allowing for a more effective environmental management. We shall use three different deletion scenarios:

1. the 'connectivity descending' scenario (we will erode from the top of the food web where the most connected nodes are, thus well-connected hubs will get removed as first, so it is likely that we remove a top predator and only that node is gone and neighbouring nodes get isolated),
2. the 'connectivity ascending' scenario (we will erode from the basis of the food web where the less connected nodes are, thus we will get inevitably a high probability of removing a resource which will starve its consumers and the web will collapse with several secondary extinctions) and
3. the 'random' scenario (intermediate simulation, removing nodes randomly from the top, the middle and the bottom of the food web).

4.2.3 Can a web be robust?

Most studies in the last decades have focused on the values of biodiversity. When considering wide ranges in body size, species richness cannot have one value *per se*, even if consistent resolution is used (Leaper and Raffaelli, 1999). These authors showed that different taxonomic resolutions affect allometric scaling and they advocated the use of evenly resolved taxa (for instance, all nodes at either species level, genus level or as life stages). The horizontal axis of Fig. 8 shows a clear increase in the fish species diversity (CV = 36%, from 13 species up to 40 species) and the scatter suggests a (weak) inverse correlation between the species diversity of the ecological networks S and connectance C_t (Pearson's product–moment correlation coefficient of -0.41, $P = 0.090$), in partial agreement with theory (Havens, 1992; May, 1972; Winemiller, 1989). Connectance typically shows greater variability for low-diversity aquatic webs, but $^2/_3$ of our aquatic webs fall into a narrow range between $L/S^2 = 0.2$ and 0.3. For comparison, only $^1/_5$ of the soil food webs addressed in Section 6.1 fall into the same 0.2–0.3 range ($^4/_5$ share $L/S^2 < 0.2$). These results are notable because such differences in connectance values imply that fishes attack up to three times more often other individuals within their own taxocene than soil nematodes do.

A second feature that the food webs have in common is that although the linkage density shows a strong direct correlation with biodiversity both in the blue and brown worlds (Pearson's r = correlation coefficient of 0.90, $P < 0.00001$ for the 18 freshwater food webs of Fig. 8 and Pearson's $r = 0.63$, $P = 0.0016$ for the 22 soil food webs in Mulder and Elser, 2009), the most significant relationships between primary versus secondary extinctions and food web attributes are provided by number of nodes and connectance (Fig. 9). Although strong correlations between S and L/S as well as S and L/S^2 are acknowledged and may seem trivial here, the ecological implications are great. The correlation between S and L/S is more than a statistical artefact, because it indirectly shows the degree to which the possibility to encounter an(other) omnivore species in the food web *increases* with a larger species pool. Hence, it also implies that the average linkage density for a food web *must increase* with the total of investigated species.

According to Williams and Martinez (2004), with no information on link-strengths, the short-weighted trophic level is the most accurate approximation for quantifying trophic levels within (real) food webs that include omnivory, cannibalism and mutual predation. In freshwater ecosystems, like those investigated here (Table 4), fishes consume resources from many

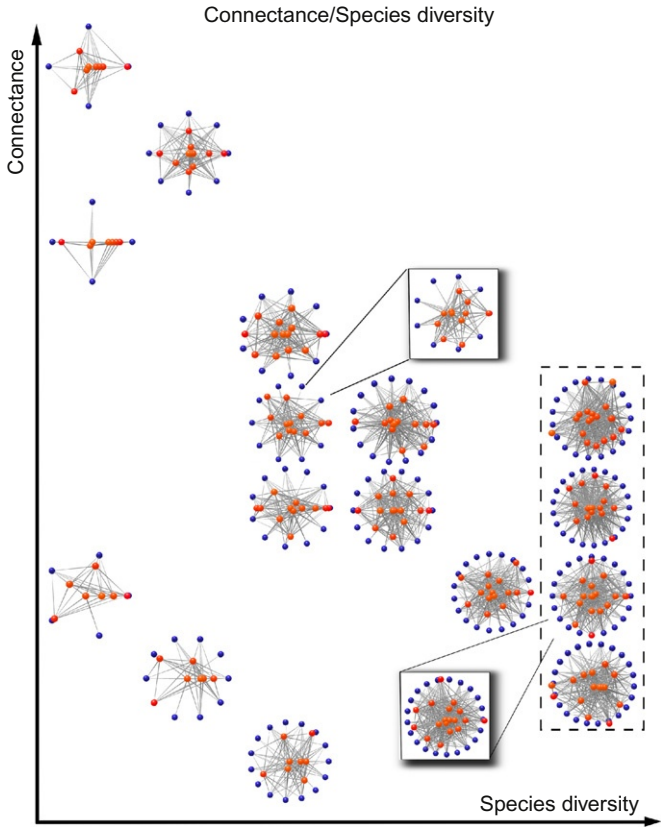


Figure 8 Connectance in relationship to fish species diversity of 18 river food webs visualized with Network3D (Yoon et al., 2004). Two food webs are depicted as overlays (solid boxes) because they fall into the same range in the connectance–diversity space (cf. Table 5). The variability and maximum value of connectance are highest in low-diversity webs, while high-diversity food webs (dashed frame) show a more consistent connectance pattern according to the constant connectance hypothesis (please see the text). The columns of this matrix show that food webs with similar (or even statistically undistinguishable) biodiversity can have different linkage patterns.

trophic levels from hatching to death, including other fishes that were feeding on them during early life stages (Froese and Pauly, 2005; Gilljam et al., 2011; Layer et al., 2010; Montoya et al., 2006; O'Gorman and Emmerson, 2010; Woodward et al., 2010a). This structural complexity is reflected by certain food web properties such as the mean of the short-weighted trophic level, the characteristic path length and the probability that two nodes linked to the same resource are clustered (Dunne, 2009).

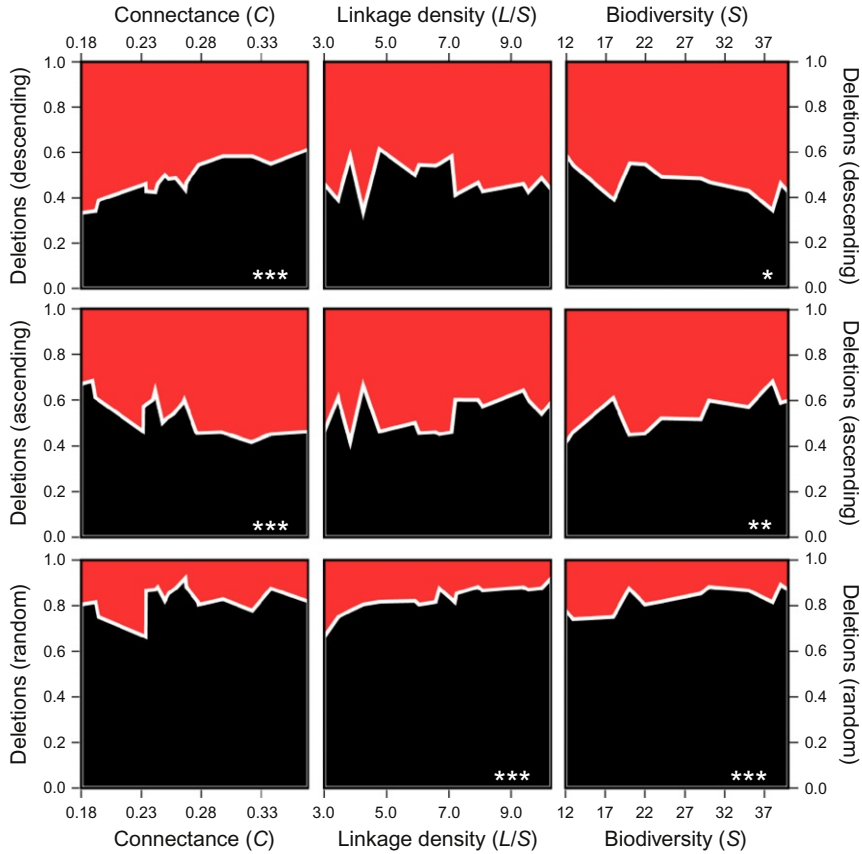


Figure 9 Extinction partitioning for the 18 river food webs according to the 'connectivity descending' (upper three plots), the 'connectivity ascending' (middle three plots) and 'random' (bottom three plots) scenarios along connectance (left part), linkage density (central part) and biodiversity (right part) gradient. The black part is the fraction of species lost by primary deletions and the red part is the fraction of species lost by secondary deletions (all trends as moving averages). The mean primary deletion fraction in the 'descending', 'ascending' and 'random' scenarios is 0.48, 0.56 and 0.83, respectively, and the mean secondary deletion fraction until breakdown of the web is 0.52, 0.44 and 0.17, respectively. If statistically significant, significance is as follows: $^{*}P = 0.035$, $^{**}P = 0.003$ and $^{***}P < 0.001$. Along our linkage density gradient, the fraction of secondary deletions in the descending scenario is very similar to the fraction of primary deletions in the ascending scenario. See text for details.

One common measure of a food web's vulnerability to extinctions is the fraction of primary and secondary deletions until final collapse of the web. For our fish assemblages (Table 5), the two fractions #PD and #SD are roughly similar in the 'connectivity descending' scenario. In contrast, the other scenarios ('connectivity ascending' and 'random') show considerably higher fractions of primary deletions and less secondary extinctions than 'connectivity descending' does. In Fig. 9, we show the extinction partitioning for the 18 food webs according to the 'connectivity descending', 'connectivity ascending' and 'random' scenarios. Food webs are most sensitive to the 'connectivity descending' scenario because their well-connected hubs get removed as first, so secondary deletions occur rapidly, as neighbouring nodes get isolated (Fig. 9, upper left plot). Most connected hubs are at the top in our food web structures. In the 'connectivity descending' scenario, the threshold for web collapse is below 50% of primary deletions, that is, primary species loss. On the other hand, in the 'connectivity ascending' scenario, we removed the less connected (basal) node. As they are resources to others (Table 4), it is inevitable that as soon all of them have gone extinct, any web will collapse quickly, with secondary extinctions becoming prevalent (Fig. 9, middle left plot). Considering the average fraction of basal nodes in the 18 food webs, the value of 51% (Table 5) is close to the average of 54% for the threshold for web collapse in the 'connectivity ascending' scenario. Therefore, the web must collapse quickly close to this point because all basal nodes were already removed. This is the explanation why these descending and ascending scenarios have similar thresholds, but behave differently in reaching them (Fig. 9).

The random scenario differs from the previous scenarios because species were removed from the middle, bottom and top of the web regardless of their connectivity. Therefore, the web is not eroded systematically (either removing all hubs, as in the upper part of Fig. 9, or all basal nodes, as in the middle part of Fig. 9), but merely by chance. Hence, the probability for each species occupying either a hub or a basal node to persist is, on average, higher in the random scenario (Fig. 9, bottom plots). Random changes in the resulting connectivity might generate large extinction events (Solé et al., 1999: p. 159), but not in the freshwater assemblages investigated here.

The average biodiversity of our food webs is 27 fish species: food webs with a lower than average biodiversity have a higher than average connectance, and vice versa (Table 5). Low-connected and more diverse webs

Table 5 Food web properties and vulnerability to simulated species deletion of 18 fish assemblages (location in Fig. A4) ranked according to their initial biodiversity. Summary of properties (red) and vulnerability to three deletion sequences: connectivity descending (green), connectivity ascending (yellow) and random (blue, 1000 simulations). *S*, Number of species; L/S^2, connectance; *L*/*S*, linkage density; Top, fraction of piscivorous species; Inter, fraction of intermediate species; Basal, fraction of zooplanktivorous species; Omni, fraction of species eating on more trophic levels; GenSD, standard deviation of mean consumer generality; VulSD, standard deviation of mean consumer vulnerability; ConnSD, standard deviation of connectivity for a consumer; SWTL, mean short-weighted trophic level; Char, characteristic path length; Clu, mean cluster coefficient; # PD, fraction of primary deletions (= species deleted/initial species diversity); # SD, fraction of secondary deletions; R_{SD}, robustness against secondary deletions computed as $R_{SD} = PD_1/S$ with PD_1 as number of primary deletions that caused the first secondary deletion(s). If R_{SD} equals # PD, all the secondary deletions occurred at the last primary deletion with web collapse.

	Food web properties													Descending			Ascending			Random		
River name	*S*	L/S^2	*L*/*S*	Top	Inter	Basal	Omni	GenSD	VulSD	ConnSD	SWTL	Char	Clu	# PD	# SD	R_{SD}	# PD	# SD	R_{SD}	# PD	# SD	R_{SD}
1 Cuyahoga River	12	0.32	3.83	0.08	0.50	0.42	0.50	1.05	0.66	0.39	1.73	1.30	0.36	0.58	0.42	0.17	0.42	0.58	0.42	0.78	0.22	0.66
2 Sandusky River	13	0.23	3.00	0.08	0.46	0.46	0.46	1.31	0.75	0.59	1.71	1.50	0.31	0.46	0.54	0.08	0.46	0.54	0.46	0.66	0.34	0.37
3 Mahoning River	13	0.37	4.77	0.08	0.54	0.38	0.54	1.01	0.54	0.27	1.76	1.21	0.43	0.62	0.38	0.46	0.46	0.54	0.46	0.82	0.18	0.60
4 Buck Creek	18	0.19	3.44	0.06	0.33	0.61	0.33	1.58	0.65	0.70	1.45	1.59	0.31	0.39	0.61	0.06	0.61	0.39	0.61	0.75	0.25	0.38
5 West Mahoning River	20	0.34	6.70	0.05	0.50	0.45	0.50	1.08	0.54	0.36	1.67	1.29	0.43	0.55	0.45	0.20	0.45	0.55	0.45	0.87	0.13	0.77
6 Duck Creek	22	0.27	6.05	0.05	0.50	0.45	0.50	1.23	0.59	0.49	1.72	1.42	0.38	0.55	0.45	0.09	0.45	0.55	0.45	0.80	0.20	0.44
7 Paint Creek East	24	0.18	4.25	0.04	0.29	0.67	0.29	1.69	0.61	0.76	1.38	1.63	0.33	0.33	0.67	0.04	0.67	0.33	0.67	0.81	0.20	0.50
8 Hocking River	24	0.25	5.92	0.04	0.46	0.50	0.46	1.31	0.62	0.56	1.64	1.49	0.39	0.50	0.50	0.04	0.50	0.50	0.50	0.82	0.18	0.48
9 Blanchard River	24	0.27	6.58	0.04	0.50	0.46	0.50	1.23	0.58	0.50	1.72	1.43	0.39	0.54	0.46	0.04	0.46	0.54	0.46	0.82	0.18	0.39
10 West Mahoning River	24	0.30	7.08	0.04	0.54	0.42	0.54	1.12	0.62	0.46	1.79	1.39	0.40	0.58	0.42	0.04	0.46	0.54	0.42	0.83	0.17	0.49
11 Hocking River	29	0.25	7.24	0.03	0.45	0.52	0.45	1.27	0.64	0.56	1.61	1.48	0.38	0.48	0.52	0.07	0.52	0.48	0.52	0.85	0.15	0.65
12 Scioto Brush Creek	30	0.26	7.93	0.03	0.43	0.53	0.47	1.35	0.49	0.53	1.59	1.46	0.42	0.47	0.53	0.17	0.60	0.40	0.60	0.88	0.12	0.76
13 Big Darby Creek	35	0.23	8.09	0.03	0.40	0.57	0.40	1.42	0.57	0.61	1.52	1.52	0.39	0.43	0.57	0.03	0.57	0.43	0.57	0.87	0.13	0.46
14 Paint Creek West	38	0.19	7.18	0.03	0.37	0.61	0.32	1.60	0.61	0.73	0.62	1.61	0.36	0.34	0.66	0.03	0.68	0.32	0.66	0.82	0.18	0.26
15 Little Miami River	39	0.24	9.38	0.03	0.44	0.54	0.44	1.35	0.58	0.59	1.58	1.51	0.41	0.46	0.54	0.05	0.64	0.36	0.54	0.88	0.12	0.59
16 Little Miami River	39	0.26	9.97	0.03	0.46	0.51	0.49	1.29	0.59	0.55	1.67	1.48	0.41	0.49	0.51	0.03	0.54	0.46	0.54	0.88	0.12	0.42
17 Walhonding River	39	0.26	10.28	0.03	0.41	0.56	0.41	1.34	0.48	0.54	1.52	1.46	0.43	0.44	0.56	0.13	0.59	0.41	0.56	0.92	0.08	0.78
18 Little Miami River	40	0.24	9.55	0.03	0.43	0.55	0.40	1.37	0.57	0.59	0.68	1.51	0.40	0.43	0.58	0.03	0.60	0.40	0.58	0.87	0.13	0.26
Average	27	0.26	6.74	0.04	0.44	0.51	0.44	1.31	0.59	0.54	1.52	1.46	0.39	0.48	0.52	0.10	0.54	0.46	0.53	0.83	0.17	0.51

behaved differently from highly connected and less diverse webs (Fig. 9). In the 'connectivity descending' scenario, food webs with high connectance were more robust (higher fraction of primary deletions until collapse) because the probability to remove a 'resource node' for other nodes was low: it was far more likely that a top predator was removed. Webs with higher connectance have a higher probability that there are still enough links left so no species becomes isolated, limiting species loss to the primary deletion in each event. In contrast, in a 'connectivity ascending' scenario, the food web is eroded from its base, starving predators of prey. So, low connectance webs are more robust in this scenario because the resource node has fewer predators that will also disappear when the resource node is gone. In contrast, those webs with higher connectance collapse faster because more secondary extinctions occur when one of the resource nodes is removed.

The kind of deletion sequence clearly affects the vulnerability of the network to species loss (Dunne et al., 2002; Fig. 9). To further evaluate the importance of diversity and connectance on the vulnerability to species deletions, we compared two creeks with intermediate biodiversity (Scioto Brush Creek: $S=30$, Eastern Paint Creek: $S=24$), but different connectance (Scioto Brush Creek: $C=0.26$, Eastern Paint Creek: $C=0.18$) in the 'connectivity descending' scenario (Table 5). Figure A6 shows how rapidly the total deletions equal S and the entire fish network disappears. The shape of the blue curves reflects an increasing number of secondary extinctions and the number of trophic links per fish species descends approximately linearly (Fig. A6B and D), with highly connected species being the most vulnerable. The 'threshold period' until secondary extinctions occur is 17% higher in Scioto Brush Creek than in Eastern Paint Creek (Fig. A6A and C). Despite substantial biological improvement in the environmental health of the Scioto Brush Creek (Burton et al., 2012; OHIO-EPA, 2008), simulated secondary deletions with connectivity descending happen quickly after only 20% of total species removed on average, and all species are gone with on average about 47% of primary deletions. Eastern Paint Creek's web appears even more vulnerable, with the first secondary extinction occurring at 17% of total species loss and the food web collapses at only 33% of primary species loss. Low linkage density implies that the removal of a highly connected node (here, one fish species) results in a loss of fewer links than for webs with higher linkage density (but lower connectance), limiting species loss to primary deletion (Figs. 8 and 9).

4.3. Inland water biodiversity: Vulnerability of B–EF across ecoregions

Another, less frequently discussed aspect of food web vulnerability to species loss is the robustness R_{SD} against secondary deletions, as measured by the fraction of primary deletions that occurred in the web without triggering a secondary extinction. The higher the R_{SD}, the later the secondary extinctions occur as a consequence of a primary one. Secondary species extinctions mostly occur because a primary extinction creates an unfeasible interaction between the predator and the lost prey (Table 4). The different topologies of the webs (cf. Fig. 8) translated into greatly varying vulnerabilities to secondary extinctions in the three species deletion scenarios of Table 5 (Fig. 9). Secondary deletions occur much earlier in the 'connectivity descending' (R_{SD}: mean = 0.10) than in the 'connectivity ascending' scenario (R_{SD}: mean = 0.53). This again implies that, although the total number of primary and secondary extinctions is similar in these two scenarios, the extinction process to final web collapse is very different. Most webs in the 'connectivity descending' start disintegrating early and continuously with one or a few secondary extinctions following each primary one. In contrast, most webs in the 'connectivity ascending' scenario only suffer primary extinctions for a long time, but then break down suddenly with a high number of secondary extinctions. The extinction processes in the 'random' scenario fall between the two extremes (i.e. high and low vulnerability to secondary extinctions for the descending and ascending scenarios) and are more similar to the 'connectivity ascending' scenario (R_{SD}: mean = 0.51). The standard deviations for the 1000 random scenarios are low for the primary deletions (~10% of the mean) and high for the secondary deletions (~50% of the mean).

The differences between the three deletion scenarios demonstrate that web attributes as well as the order of species deletions have a considerable impact on the (species) vulnerability to extinction events: that is, it is not just biodiversity of nodes but also of the interactions within a food web that will affect B–EF trajectories of species loss. On the other hand, even sites from a polluted watershed such as the Hocking River (Burton et al., 2012) seem to have intermediate connectances (Table 5), implying that sensitive fish species that may have previously stabilized the web have already been lost. Although higher connectance led to higher robustness against secondary extinctions in earlier studies (Dunne and Williams, 2009; Dunne et al., 2002), our results only show such an effect ($R_{SD} > 0.1$) for two low-diversity webs (Cuyahoga and Mahoning rivers) and three webs of intermediate to high species richness (West branch of the Mahoning

River, Scioto Brush Creek and Walhonding River). An explanation of this effect for the low-diversity webs may be that they have higher connectance (scales with S^2), but also lower linkage density (scales with S) than other webs (Table 5). For intermediate to high-diversity webs, higher connectance may convey high robustness in some cases, but our results also demonstrate the very opposite, namely that highly vulnerable webs exist despite of high connectance and high linkage density (i.e. Big Darby Creek, Blanchard River, Duck Creek, Hocking River, Paint Creek and all three locations at the Little Miami River shown in Fig. 10).

Food webs (at least those in Fig. 9) are clearly more sensitive to deletion sequences with 'connectivity descending' than to those with 'connectivity ascending'. Node connectivity plays a critical role for the vulnerability of the food web regardless of species diversity and is largely independent of connectance. Our results indicate that high-diversity webs are just as (or even more than) vulnerable to static extinctions as low-diversity webs, a non-intuitive result which may have important implications for ecosystem management. Since higher trophic levels are strongly interlinked with feeding relationships, in contrast to the producer and herbivorous community, this pattern implies that the loss of well-connected intermediate and top

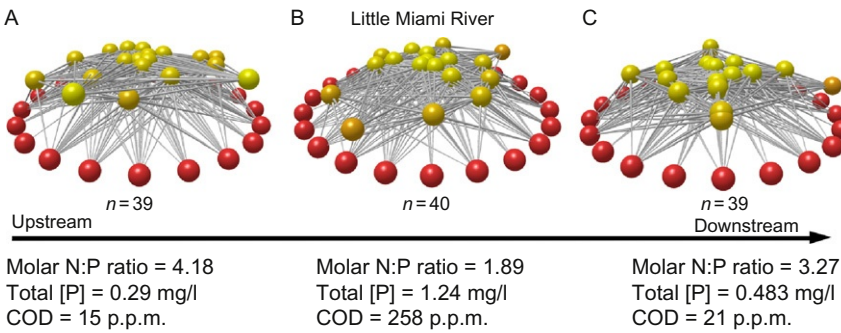


Figure 10 Comparison of species diversity (n = number of fish species) between three locations along the Little Miami River, Ohio, United States (Fig. A4). Although biodiversity is maintained, structural changes in food webs reflect subtle changes in water chemistry, being the central assemblage—collected in a slowly streaming and particulate-rich creek with most organic compounds and high P concentration—the most vulnerable despite of its high connectance and high linkage density (Table 5). The mean of all the coefficients of variation (CVs) for each environmental parameter described by Dyer et al. (1998) for this watershed equals 33%. Below the arrow indicating stream direction, the molar N:P ratio, the total phosphorus concentration and the chemical oxygen demand (COD) in water are provided for each location.

predators is critical to the persistence of species. It could also increase the risk of extinction cascades in ecosystems undergoing environmental and/or anthropogenic change, as is the case in many freshwaters on a global scale (Friberg et al., 2011; Woodward et al., 2012). Such a conclusion has been partly corroborated by previous studies on both model food webs (De Visser et al., 2011; Srinivasan et al., 2007) and empirical food webs (Estes et al., 2011; O'Gorman et al., 2008). Given that the Ohio fish data set comprises, besides predators and consumers, herbivore species only as prey (Table 4), our statistics might have severe implications for extinction risk in a broader context. In fact, even in consumer-free ecosystems, like those modelled by Solé and Montoya (2006), species richness can drop and taxocenes will collapse as soon colonization is no longer sufficient to compensate for habitat fragmentation and habitat destruction.

Apart from connectivity, other species properties such as body size (De Visser et al., 2011), relative abundances (Lyons and Schwartz, 2001) and interaction strength (Allesina and Pascual, 2009) also play a decisive role for a food web's vulnerability to extinction events, especially in dynamic species deletion simulations (Layer et al., 2010; Pimm, 1980; Quince et al., 2005) and long-term empirical studies (Stachowicz et al., 2008). This long-standing, complex issue of the diversity–stability relationship is still controversial (Banašek-Richter et al., 2009; Montoya et al., 2006; Rossberg et al., 2011) and many of its implications for B–EF relationships remain open (as reviewed by Cardinale et al., 2006; Hooper et al., 2005). When species diversity is maintained despite (increased) nutrient loading, biodiversity may act as a kind of buffer against environmental disturbance (Cardinale, 2011) and if this evidence holds for metazoans as well, management or restoration of native fish species becomes desirable (Feld et al., 2011). We provided here an overview that helps to quickly yet coarsely assess the risk of species loss without time-consuming sampling or modelling.

4.4. Population fluctuations at standardized taxonomical resolution: A virtual case study

In both aquatic and terrestrial ecosystems, Srinivasan et al. (2007) and De Visser et al. (2011) showed high sensitivity of (relatively pristine) food webs to the loss of large, dominant or even common species. Moreover, such rare species can inflate allometric relationships, depending on their occurrence and distribution within size classes and areas with different spatial resolution (Valcu et al., 2012; http://cran.r-project.org/package=rangeMapper).

Since size spectra do not distinguish between species, they are easily measured and more robust to inclusion/exclusion of rare species than is the case for species-based community measures of allometric scaling, such as the trivariate food webs that have gained increasing prominence in recent years (Woodward et al., 2010b).

Mass–abundance scatter-plots have the advantage that they can more consistently combine information and, in contrast to size spectra, can be plotted as functions of either endogenous traits (body mass, mostly weight, or body size, mostly length) or exogenous traits (typically numerical abundance). Brown and Gillooly (2003) argued that only traits like endogenous body mass can be used to predict numerical abundance. Unfortunately, the inversion of the M and N axes in some papers published after Brown and Gillolly's plea contributed to a recent generation of terms which slows down the research itself, as the resulting overlap in terminology may confound many readers. Still, the predictive power of exogenous traits such as N for M and/or B is often surprisingly high. If size-dependent physiology of individuals within one taxocene is extended to entire communities, the allometric scaling of the latter should converge on a biomass-constant isometric line (among others, Cohen et al., 2003; Hildrew, 2009; Mulder et al., 2005b; Rossberg et al., 2008; White et al., 2007; Woodward et al., 2005a).

Previous analyses demonstrated that $\log(N)$, $\log(M)$ and $\log(B)$ are strongly correlated, as theoretically expected (Brown and Gillooly, 2003; Damuth, 1981; Mohr, 1940) and empirically shown (Cohen and Carpenter, 2005; Cohen et al., 2003; Mulder et al., 2008; Reuman et al., 2008). When the classical log–log mass–abundance linear regression model

$$\log(N) = a_1 \times \log(M) + b_1 \quad [5]$$

is merged into the log-transformed biomass (originally weight times abundance)

$$\log(B) = \log(M) + \log(N) \quad [6]$$

we can rewrite Eq. (6) as

$$\log(B) = \log(M) + a_1 \times \log(M) + b_1 = (1 + a_1) \times \log(M) + b_1 \quad [7]$$

which is now in the form of a typical biomass-size spectrum

$$\log(B) = a_2 \times \log(M) + b_2 \quad [8]$$

although the two intercepts b_1 and b_2 are not comparable to each other, in contrast to both slopes which are correlated and are supposed to differ by one unit from each other (Jennings and Mackinson, 2003; Mulder et al., 2008; Schneider et al., 2012).

The linear allometric model of Eq. (8) was fitted to the locations in Ohio separately (confidence interval 99%), and the lumped log(*B*) for all sampled fishes was plotted at the middle of the respective size class along the binned log(*M*) gradient. Binned and lumped log(*B*) with zero observations were excluded, because log(0) is undefined. Size bins can influence the resulting power functions: our fish size spectra tend to show a fluctuating increase in biomass with body size up to a peak near the largest mass-bins comparable to those of Duplisea and Drgas (1999) in the blue world and to those of Mulder et al. (2008, 2009) in the brown world. The huge influence of larger (predatory and omnivorous) fishes is reflected by the regressions that fit the dome before the site-specific modal size bin: the linear regressions fitted to size spectra of the (boat-sampled) fish networks have positive slopes ranging from 0.72 ± 0.074 SE (min) up to 1.24 ± 0.216 SE (max) and the (from Eqs. 5–7 derived) mass–abundance linear regression slopes are rather shallow (their power laws fluctuate between $-¼$ and $+¼$, with an average very close to 0). Mass–abundance positive slopes are known as possible within a taxocene (e.g. Ulrich et al., 2005).

For fish assemblages with ¼ power scaling, if population density had a body mass scaling exponent of 0.25, a 10-fold increase in weight would increase the fish population by $10^{0.25}$, equal to a 1.78-fold increase in density. Conversely, if population density had a body mass scaling exponent of -0.25, a 10-fold increase in weight would decrease the population as a function of $10^{-0.25}$, which is equal to a 0.56-fold decrease in density of the smaller individuals. To illustrate these opposite trends for further interpretation of freshwater biodiversity, some brief examples may be useful. Let us imagine a very simple freshwater food web consisting of only four fish species, namely Emerald Shiner (*Notropis atherinoides*), Yellow Perch (*Perca flavescens*), Walleye (*Stizostedion vitreum*) and Muskellunge (*Esox masquinongy*). Let their respective wet weights be 4, 40, 400 and 4000 g on a site-specific average. After log-transformation, their log(*M*) will become 0.6, 1.6, 2.6 and 3.6. Given that with abscissa log(*M*) and with ordinate log(*N*) populations fall approximately along a straight line with a negative slope (e.g. Brown and Gillooly, 2003; Cohen et al., 2003; Damuth, 1981, 1987, 1991; Hildrew, 2009; Mulder et al., 2005b; Woodward et al., 2005a), we

assume for simplicity that the population densities of these four fish species are equal to 100, 10, 1 and 0.1 individuals, respectively. After log-transformation, their log(N) will become 2, 1, 0 and −1. Their specific log(B) equals $\log(M)+\log(N)=0.6+2=1.6+1=2.6+0=3.6-1=2.6$. Hence, these four fish populations will keep a biomass of $10^{2.6}\approx 400$ g and, if plotted on log–log axes, the theoretically resulting linear regression slope should be isometric. In the case of a −¼ power scaling, keeping the aforementioned weights and a comparable number of fishes, the population densities of these species could be 60, 40, 30 and 10, and in the case of a ¼ power scaling, the respective densities should be 10, 30, 40 and 60. In the first case, the resulting specific fish biomass is negatively correlated with the increase in fish body mass, whereas in the second case the opposite occurs. In the case of the 534 boat-sampled sites (Fig. A5), 57.7% showed the negative mass–abundance scaling, albeit on average only $-1/8$, but 42.3% showed a positive scaling for the bin approach.

4.5. Superimposed disruption of fish biodiversity on cascading interactions

Cascade effects on other species and trophic levels, for instance due to either invasive or extinct species, can potentially be quantified by allometric analyses and characterization of multitrophic interactions. Sterner and Elser (2002) and Hall (2009) formalized the complexity of elemental constraints and thresholds from stoichiometrically explicit perspectives, reviewing several studies from microbiology to aquatic ecology, emphasizing how important the modulation of chemical imbalances between trophic levels can be for understanding B–EF relationships.

In our study, we modelled the site-specific changes in total biomass (Fig. 11, upper panel) and average weight (Fig. 11, lower panel) along gradients of fish diversity (number of species, left plots) and molar N:P ratio (right plots). The marked decrease in fish size with biodiversity (presumably a consequence of decreasing energy at higher trophic levels) provides a measure for assessing the sensitivity of these species-poor networks (less than 10 species) to predation, even though their environmental conditions (here, the molar N:P ratio) can be considered optimal (Fig. 11D). The average mass of individual fishes does not show a linear correlation with the molar N:P ratio of the water column, in contrast with previous studies where body size (both as fish length and as fish weight) increased with the molar N:P ratio of cyprinids (Sterner and George, 2000) but in line with more recent research, which shows marked stoichiometric imbalances between the environmental availability and tissue content of consumers in freshwaters (Lauridsen et al., 2012).

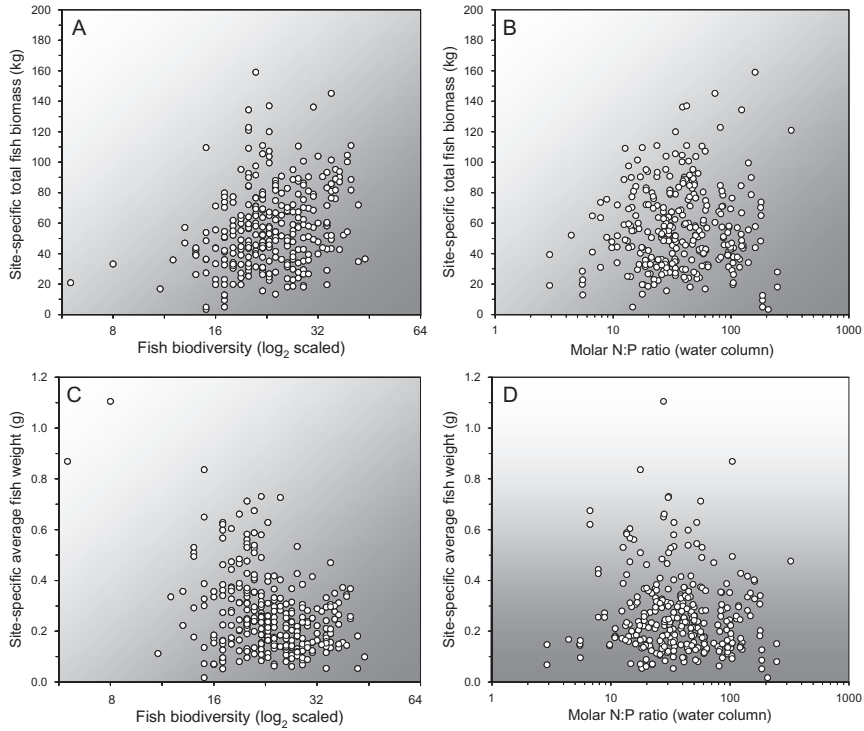


Figure 11 Site-specific fish biomass (A, B) and average fish weight (C, D) related to fish biodiversity (A, C) and water column N:P ratio (B, D) for freshwater fishes from boat-sampled Ohio rivers (Fig. A5). Although American freshwater ecosystems are well-known for their remarkably high N:P ratios (Cotner et al., 2010), the clump in the fish biomass distribution reflects a certain (positive) bias in the amount of Ohio rivers with 'lower' N:P ratios, a log-normal distribution that is known to occur in large datasets (Kattge et al., 2011). According to Pfisterer and Schmid (2002), the species-poor experimental systems achieved under unperturbed conditions show a lower biomass production than the species-rich experimental systems. The left panel clearly resembles their grassland model, where in this case species-poor fish communities not only reduced biomass production under unperturbed conditions (A), but also achieved the highest individual body-size averages (C). The darkness of the grey effect suggests increasing environmental perturbation as derived from abiotic data.

Since regularities might be expected in biodiversity and/or biomass distributions, to what extent can a possible introduction of specifically sized organisms be necessary to preserve ecosystems, for instance counteracting negative effects of overfishing or habitat destruction? As early as 1955, MacArthur pointed out that abundance of species can vary greatly, and that if one species has an abnormal abundance, a community may be unstable if the abundances of other species become inflated (MacArthur, 1955). In Section 4.2.3, we have shown 'cascade effects' on occurring species after

simulated removal of fish species in 18 rivers (primary and secondary deletions).

Simulated deletion sequences provide a clear picture of food webs responses to the possible removal of specific taxa (either consumers or resources). In the field, small-scale manipulation experiments (enclosure/exclosure of larger predators) often reveal that relatively few resources are strongly depleted (Woodward and Hildrew, 2002; Woodward et al., 2005b), although whole-lake manipulation experiments can provide a different perspective. Large-scale manipulation experiments include recruitment of Rainbow Trout (*Oncorhynchus mykiss*), that altered the planktivory regime and the water quality (Elser et al., 1995), the addition of Northern Pike (*Esox lucius*), which led to crashes in cyprinid minnow populations (Carpenter et al., 2011; Elser et al., 1998, 2000), and the replacement of planktivorous minnows with a comparable mass of piscivorous bass (Ives et al., 1999), with consequent long-term changes in the zooplankton biomasses (Ives et al., 1999; Jonsson et al., 2005). One example for controlled alteration of abiotic factors are whole-lake N:P treatments to prevent nitrogen limitation with consequences at different trophic levels, as planktivore biomass was inversely related to piscivore biomass (Carpenter et al., 2001) and changes in the fish-driven phosphorus cycle (Carpenter et al., 1992). Given that low linkage density implies that the removal or replacement of a highly connected species results in a loss of fewer links than for webs with higher linkage density, the traits of endangered (or recruited) fish species must be taken into greatest account.

5. CONCEPTUAL UNIFICATION

5.1. Articulating B–EF in terrestrial ecosystems

Different functional responses and effects within and across adjacent trophic levels (x and $x+1$) can be articulated within a conceptual framework to predict EF under future scenarios (Lavorel et al., 2009). To analyze B–EF relationships, the application of such a framework requires that each compartment (box) is specified for individual species in terms of functional diversity (FD) and/or trait attributes and can be applied to most ecosystems stepwise. We will use nutrient cycling and trophic interactions as examples and will define the functional effect trait(s) contributing to the ecosystem function at the trophic level most related to the function itself (x in Fig. 12) and, if relevant, at the adjacent ($x+1$) trophic level.

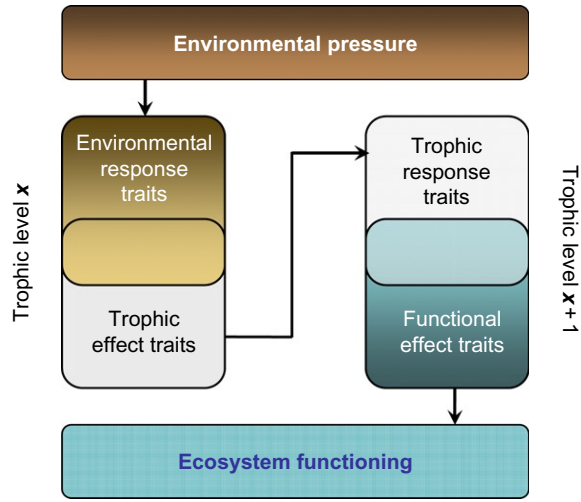


Figure 12 Framework articulating functional responses and effects within and across two adjacent trophic levels to forecast ecosystem functioning. The analysis of the effects of functional diversity on ecosystem functioning will then integrate the quantitative effects of diversity for the environmental response traits, the trophic effect traits, the trophic response traits and the functional effect traits. This can be done by partitioning the variance of the ecosystem functioning according to these trait types (Díaz et al., 2007). According to us, such a framework can be applied to run specific scenarios of environmental change in a predictive approach.

Step 1. Given that the environmental response traits are often taxon-specific, if more than one functional effect trait is involved within the considered (sub)food web, then association patterns between different traits need to be taken into account. The outcome is a trade-off among positive and negative effects at adjacent trophic levels.

Step 2. Trophic effect traits and trophic response traits and associated processes must be identified. In the case of ecological stoichiometry, for example, the chemical quality of soil systems (C:N:P and $[H^+]$ either as pH or pOH) enhances the numerical abundance (and hence the biomass) of soil mesofauna much more than the soil microfauna (Mulder and Elser, 2009). Moreover, soil mesofauna incorporates most fungivores and microfauna incorporates most bacterivores (Mulder et al., 2005a; Wu et al., 2011) and bacteria and fungi respond to chemical resources in different ways according to their ability to break down carbon- versus nitrogen-rich compounds (De Vries et al., 2006; Hunt and Wall, 2002; Krivtsov et al., 2011; Wardle, 2002; Wardle et al., 2004).

Step 3. This step identifies the response traits for each of the trophic levels (starting from the lowest, *x* in Fig. 12) to the environmental predictor of

interest. In the case of total soil phosphorus, a lower C:P ratio directly favours larger arthropods (Mulder and Elser, 2009) and the proliferation of bacteria with an *r*-like strategy (Makino et al., 2003). Given that most microarthropods are predators or fungivores (Mulder et al., 2005a; Wardle, 2002), a shift in the fungi-to-bacteria ratio is expected in soil systems (De Vries et al., 2006; Mulder et al., 2009).

Step 4. Having established the relationships between functional effect traits for a given environmental condition (or a predictor), the responses of different trophic levels to pressure and multiple functional relationships involved in a selected ecosystem service, the final analyses will allow the translation of effects at individual or species level into actual ecological processes at community (or even biome) level.

5.2. Articulating B–EF in aquatic ecosystems

The framework of Fig. 12 may be applied not only to a given ecosystem process influenced by a range of contrasting conditions (and a comparative analysis conducted in order to identify generic vs. contingent relationships), but it can also identify (in)congruences in B–EF. Therefore, it is also potentially suitable to assess the ecological risks of environmental pressure.

Eutrophication, for example, is a widespread kind of environmental pressure which affects key ecosystem services. Global increase in use of urea in both agriculture and manufacturing has resulted in increased run-off to sensitive coastal systems and is important in the nitrogenous nutrition of some harmful algal bloom species (Glibert et al., 2006). Reduction in water quality directly influences important coastal ecosystems like seagrass meadows (Waycott et al., 2009), which trap sediments and nutrients and have a large net primary productivity (Orth et al., 2006). Seagrass meadows are also sensitive to changes in turbidity and nutrient enrichment and provide ecosystem services such as supporting commercial fisheries through habitat provisioning and globally significant sequestration of carbon (Duarte et al., 2005). Besides indirect effects of eutrophication due to reduction of light penetration in the water column (changes in turbidity) and enhance coverage by epiphytes (biological disturbance), direct effects include shifts in nutrient ratios of seagrass leaves (Antón et al., 2011) which influence grazing patterns and cause selective abrasion and even removal of the plants. Leaves of persistent species such as *Thalassia hemprichii* have a lower C:N ratio than leaves of the ephemeral *Halodule uninervis* or the intermediate *Cymodocea rotundata* (Fig. 13). Seagrasses with higher C:N ratios have higher palatability for sea urchins *in situ* (tropical seagrasses, Vonk et al., 2008) or for

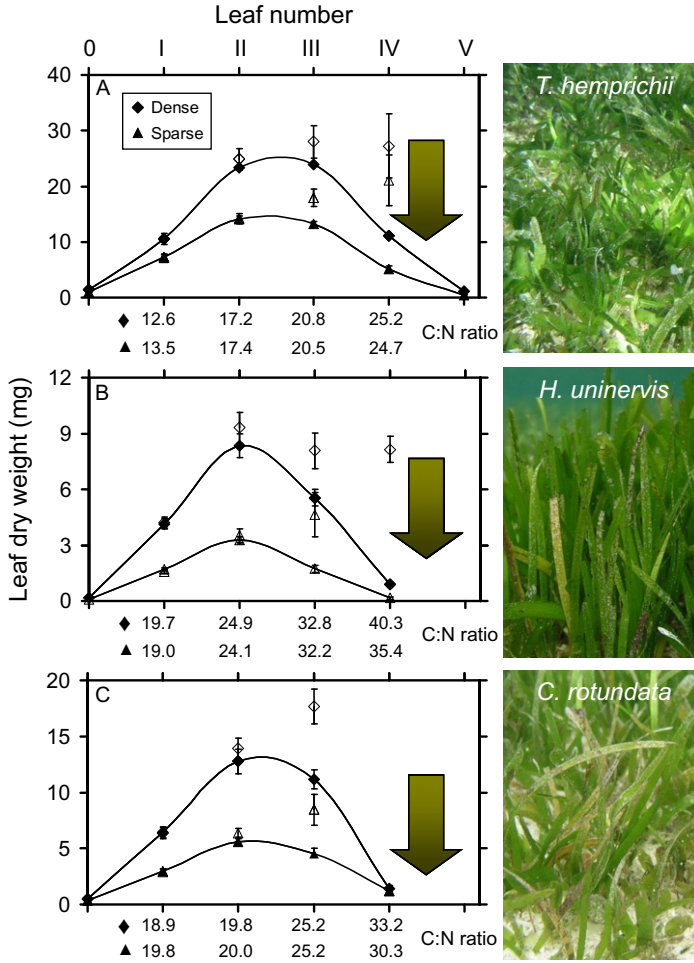


Figure 13 Example of *trophic effect* and *trophic response* traits (*sensu* Fig. 12) from the green world: grazing pressure (vertical arrow) and elemental quality in three species from seagrass meadows of the Spermonde Archipelago (Indonesia). Mean leaf weight development ± SE of seagrasses in dense (◆) and sparse (▲) canopies (Vonk and Stapel, 2008) with comparable PO_4^{3-} concentrations (in water columns: 0.24 and 0.23 μM and in pore water: 0.39 and 0.40 μM, respectively). From top to bottom: (A) *Thalassia hemprichii*, (B) *Halodule uninervis* and (C) *Cymodocea rotundata* (photo credits: Jan Arie Vonk). All three seagrass species continuously produce leaf tissues at a fixed basal meristem (Short and Duarte, 2001); the Roman number refers to the leaf layout during destructive counting (I is the youngest leaf, V the oldest leaf collected). The closed symbols and lines represent the natural mixture of leaves and open symbols represent intact leaves only. Leaf molar C:N ratios for dense and sparse canopies provided below each plot; all samples ($n = 9$) of 10–20 shoots per species, depending on size. Despite increased palatability, *T. hemprichii* (A) appears to be the most resistant to grazing pressure.

isopods in mesocosm (temperate seagrasses, Tomas et al., 2011). Contrasting trophic effect and trophic response traits not only affect the composition of seagrass meadows, but also enhance the nitrogen pool, with both the N concentration in aboveground seagrass biomass as the dominance of species with lower C:N ratio higher in grazed treatments (Vonk et al., 2008). Similarly, C:N of detrital resources in freshwaters, which is a key determinant of decomposition rates (Hladyz et al., 2009), is also a function of both the surrounding riparian vegetation and the nutrient status of the waterbody itself (Hladyz et al., 2011).

6. SYSTEM-DRIVEN B–EF

6.1. Elemental changes within one taxocene: Less is more

Abiotics (pH and C:N:P) play a key role in determining the abundance of diversity of the soil nematofauna and nutrients in particular enhance the productivity (here, their total biomass) of free-living nematodes (Fig. 14) as well as the unevenness of the soil nematofauna (Fig. A2). In P-enriched, intensively managed soils (low N:P molar ratios), nematode total biomasses are much greater than in sites with a (relatively) higher N:P molar ratio. In other words, a lack of soil P in agroecosystems kills off the predatory nematodes or strongly diminishes the abundance of all nematodes (Mulder and Vonk, 2011), and there is increasing evidence of similar patterns even in extreme environments (Barrett et al., 2007).

Although comparable patterns have been detected among taxocenes (Mulder and Elser, 2009, more details in Section 6.2), Fig. 14 shows that the distribution of the free-living nematode biomass may overlap constrained bottom-up responses to microbial producers. Under higher grazing pressure (low soil N:P), either the microbial activity is diminished or the density of bacterial cells is low. In contrast, under lower grazing pressure (high soil N:P), microbial activity can become stimulated and the density of bacterial cells is high (Mulder et al., 2009; Reuman et al., 2009). If so, given that most free-living nematodes are bacterial feeders, Fig. 14 resembles the classical 'energy enrichment paradox', which shows here at both tails of the nematode distribution the exacerbated incongruences between the bacterial autotrophs and the bacterivore nematodes under either low or high N (cf. Hall, 2009 and references therein). Nematode patterns seem comparable to those predicted by the 'hump-backed model' (Grime, 1973, 1979), which used an arbitrary scale from 0 to 1 (Grime, 1977). Biomass may in fact increase with respect to the limiting

STxET	pH (H_2O)		Molar ratios C:N		N:P		C:P		*N* (# / kg soil)		$\overline{M}$ (µg dry wgt)		*B* (µg / kg soil)	
HI×MG	5.51	(0.06)	17.23	(0.41)	13.31	(0.56)	233.3	(14.2)	79,718	(7274)	0.046	(0.003)	3626	(391)
FC×MG	6.40	(0.08)	13.86	(0.38)	8.97	(0.32)	123.7	(5.0)	58,740	(4121)	0.044	(0.003)	2606	(248)
FC×AF	7.76	(0.03)	15.81	(0.60)	4.17	(0.56)	64.9	(8.1)	11,657	(1312)	0.035	(0.002)	391	(40)
LU×AF	6.76	(0.05)	18.61	(0.26)	3.26	(0.09)	60.5	(1.3)	21,299	(3461)	0.058	(0.004)	1220	(208)
PO×MG	5.95	(0.05)	18.76	(0.37)	7.41	(0.28)	138.3	(5.6)	41,620	(1925)	0.059	(0.002)	2391	(133)
PO×AF	5.85	(0.06)	20.73	(1.16)	7.71	(0.96)	172.3	(27.3)	36,258	(3210)	0.052	(0.004)	1868	(275)
PO×SW	3.98	(0.08)	31.71	(2.27)	32.10	(2.96)	998.9	(105.0)	17,609	(1704)	0.027	(0.002)	486	(66)

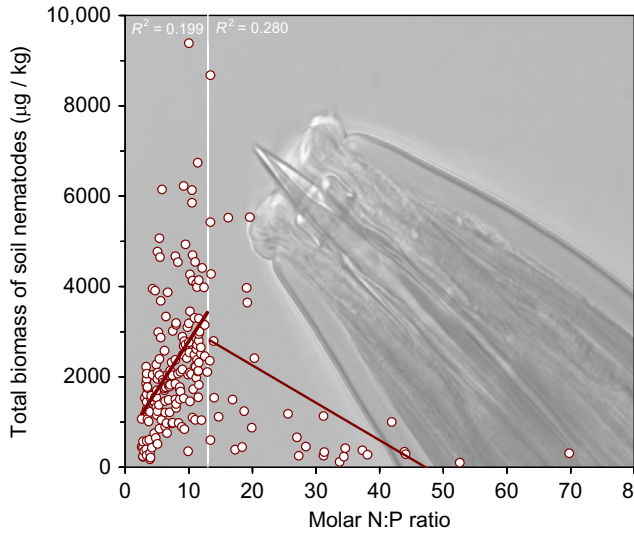


Figure 14 Occurrence of *environmental response* traits in the brown world: synergetic processes of land history and abiotics are reflected in the soil nematodes (upper panel: nematode density (*N*), mean weight ($\bar{M}$), biomass (*B*) and (SE) in brackets). From left to right (upper photos) and from top to bottom (synoptic table), managed grasslands on peat (HI × MG), managed grasslands on clay (FC × MG), arable fields on clay (FC × AF), arable fields on Loess (LU × AF), arable fields on sand (PO × AF), managed grasslands on sand (PO × MG) and shrublands on sand (PO × SW). Lower molar N:P ratios seem to enhance the productivity (biomass) of nematodes (lower panel), but also the unevenness within the nematofauna (Fig. A2). *Raw data from Mulder and Vonk (2011).*

nutrient (here, phosphorus) via a saturating, non-linear function, whereas diversity may increase, decrease or exhibit a hump shape (Sterner and Elser, 2002 and Sterner, 2004, respectively). Our threshold of 13 is supported by the two regression trends for high and low fertility (Fig. 14) and is similar to the atomic N:P ratio by Cleveland and Liptzin (2007) for soils and roughly comparable with the historical atomic N:P ratio of

16 by Redfield (1958) for the blue world. The left and right regression lines of Fig. 14 show, in fact, a direct correlation between the total biomass of soil nematodes and the soil N:P ratio until 13 (higher eNPP sites, see Table 1) and an inverse correlation between biomass and N:P afterwards (lower eNPP sites).

We found no consistent relationships between the average mass $\bar{M}$ and the average predator–prey body-mass ratios across ecosystem types and soil types (Mulder et al., 2011a). Widely distributed horizontal distributions of $\bar{M}$ across environmental C:N:P transects (as those in Fig. 15) might revitalize the discussion on the use of $\bar{M}$ as the best independent sole predictor for mass–abundance scaling (compare Cohen et al., 2003; Hildrew, 2009; Mulder et al., 2005b; Woodward et al., 2005a with Brown and Gillooly, 2003; Reuman et al., 2009). Indeed, it is the numerical abundance that changes the most, not the mean mass, as expected from a well-known direct correlation between population density and resource availability (e.g. Kaspari, 2004; Meehan, 2006; Wardle, 2002) and Kaspari (2004) focuses on the variable N instead of $\bar{M}$. Under relatively stable environmental conditions, this implies that EF might be driven more by the total numerical abundances N of organisms than by their body-mass average $\bar{M}$ or by the resulting total biomass ($N \times \bar{M}$ as in Fig. 14). Our productivity gradients show that $\bar{M}$ values are real and vary from place to place less than previously suspected (Kaspari, 2004).

The rather comparable $\bar{M}$ values are surprising and could make terrestrial 'stable states' questionable: as large-scale fluctuations of $\bar{M}$ values were not observed along the C:N:P gradients (Mulder and Vonk, 2011), we might wonder under which kind of environmental conditions (to be held constant for a certain time span) such 'stable states' might actually occur in the brown world. Moreover, an investigation by Gilljam et al. (2011) consistently shows either underestimations or overestimations of predator–prey systems as soon as the (derived) species-specific $\bar{M}$ averages were used instead of the (original) site-specific weights at individual level m.

6.2. Elemental changes across taxocenes: Community mismatches

Assuming that, at least in the brown world, numerical abundance N matters more for EF than individual mass, we might continue to neglect the below-ground variation of individual body-mass values within one taxon or, possibly, even within the same taxocene—as most soil ecologists currently do (overview in Mulder et al., 2011b). If all taxa absorb energy at constant rate, and the metabolic rate of an individual approximately follows a power law in

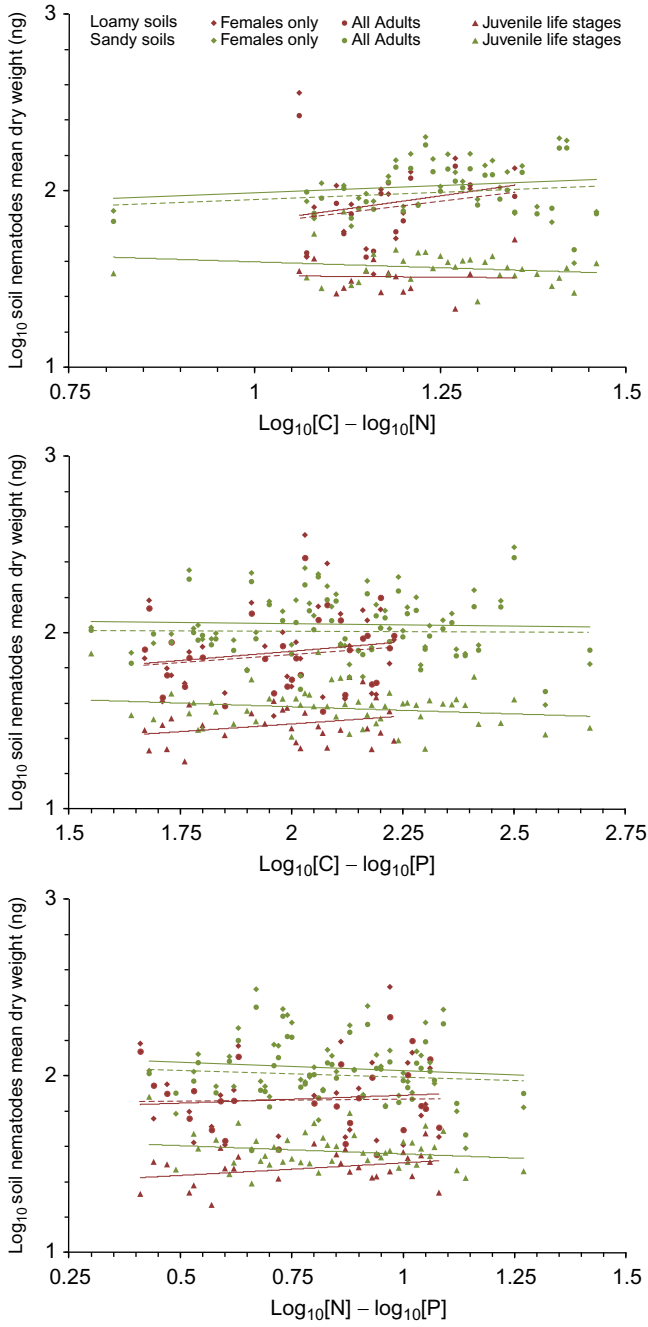


Figure 15 Occurrence of *functional effect* traits in the brown world. The soil types influence the size of individual nematodes more than nutrient ratios do: from top to bottom, the weighted differences in the body mass between the sandy soils (in green)

$\bar{M}$ (Brown et al., 2004; Peters, 1983; Savage et al., 2004), the energetic equivalence hypothesis predicts a mass–abundance slope of −¾. Observing a mass–abundance slope less negative than (respectively, more negative than) −¾ suggests that larger invertebrates absorb more (respectively, less) energy from the environment than smaller invertebrates. However, rather few soil communities scale to the −¾ power (Mulder et al., 2005b, 2009, 2011c), in contrast to species–density scaling (Eq. 2). It should be noted, though, that the scaling power strongly varies between −⅔ and −1 for mass–abundance relationships (Mulder, 2010) and between ⅔ and 1 for metabolic rates (Glazier, 2010) because the scaling exponents are sensitive to which taxa are included (Boit et al., 2012; Glazier, 2005; Mulder et al., 2005b, 2009; Prothero, 1986; Reuman et al., 2008). Still, diverse patterns and clear trends remain recognizable under comparable methodologies.

Few studies on food web manipulation have been performed in the brown world, but Wardle et al. (2011) recently showed that ant exclusion enhanced the first and third trophic level of soil food webs, increasing active microbial biomass and predatory soil nematodes but not bacterial-feeding nematodes (second trophic level). Assuming that larger mites (soil mesofauna) are often predatory, one mesofaunal individual and (at least) one microfaunal individual have to come together. The probability that this happens increases approximately as the product of both population abundances. Thus, if in a nutrient-richer soil both microfauna and mesofauna would be two times more abundant, then the probability of encounter would approximately increase by a factor 4, leading to over-proportionally more feeding opportunities for the predatory mesofauna. But again, directions of the responses need to be specified as in the conceptual framework

and the loamy soils (in brown) of all the occurring nematodes per soil type together fluctuate between 7.9% and 15.0%, implying that nematodes in loamy soils are smaller than those in sandy soils. Averages were consolidated separately for C:N, C:P and N:P ratios and log-transformed. Log–log linear regressions are just plotted for clarity, although they are not significant: from top to bottom, log–log linear regressions for all females (upper solid lines), all adults (dotted lines) and all juveniles (lower solid lines). The cross-product soil type (ST) versus ecosystem type (ET) determines the total abundance of individuals (and hence, the total biomass). This is rather surprising, given that the Atom% Excess (APE) ^{13}C and ^{15}N for nematodes is known to be most sensitive to enrichment (Crotty et al., 2011). Only arable fields and grasslands are shown: loamy soils (41 sites, 1094 adults and 4936 juveniles) versus sandy soils (96 sites, 3504 adults and 10,819 juveniles); *raw data from Mulder and Vonk (2011)*.

(Fig. 12): here, a log-linear decrease of mites and collembolans with decreasing soil fertility (higher nutrient ratios), in contrast to a curvilinear increase of bacterivore nematodes and fungi (cf. Santos et al., 1981). Therefore, regardless of the kind of environmental adversity, soil mesofauna might increase over-proportionally in enriched systems such as the real food web plotted on the background of the four scatter-plots (a reference site marked by a cross) in the composite (Fig. 16).

The results support the stoichiometric theory (Elser, 2006; Mulder and Elser, 2009; Sterner and Elser, 2002) which predicts that animals with higher P demands would suffer a competitive disadvantage due to poor stoichiometric food quality. In Fig. 16, omnivorous species with lower P demands are favoured. This seems to be the case within our soil

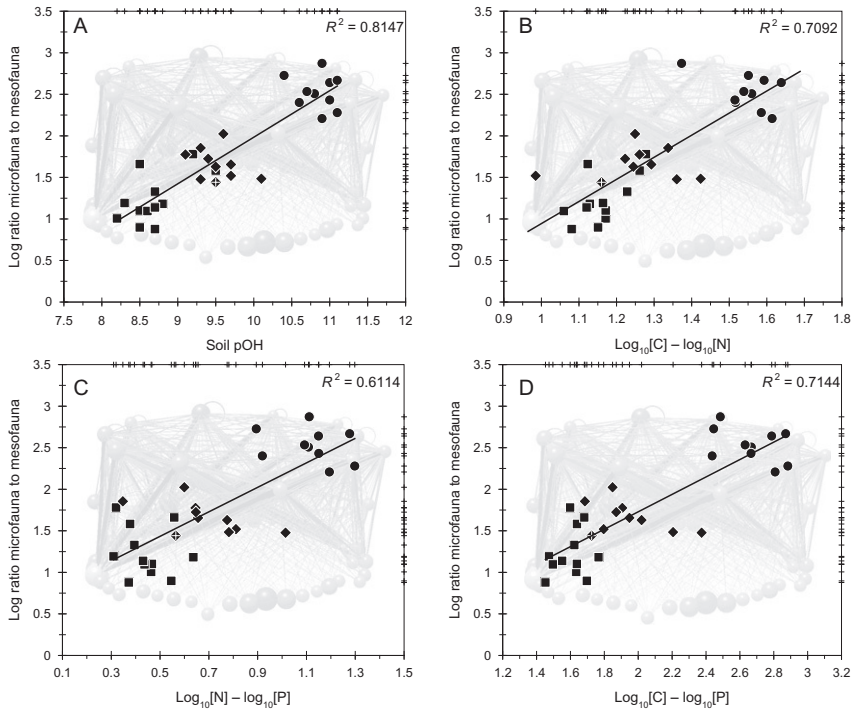


Figure 16 Another example of *trophic effect* and *trophic response* traits (cf. Fig. 13). Logarithmic fits of differently body-size-scaled soil invertebrates across four quantitative gradients of increasing environmental adversity as described by pOH (A), log-transformed C:N ratio (B), N:P ratio (C) and C:P ratio (D) for Dutch dry heathlands (●), abandoned grasslands (◆) and bio-organic farms (■). Lower soil fertility as in the heathlands plotted at the right of the scatters enhances the steepness of the microfauna to mesofauna ratio. Springtails and enchytraeids get eliminated, relative to the overwhelming increase of nematodes, by decreasing [N] and [P].

mesofauna, given that the P contents in the bodies of (predatory) mites are up to three times lower than in detritivorous collembolans (~0.5 body % P-in-Acari vs. 1.4 body % P-in-Collembola; Martinson et al., 2008 and Schneider et al., 2010, respectively). This means that invertebrates at higher trophic levels have a higher P demand than those at lower trophic levels, at least in the brown world. However, during the lifetime of metazoans, the P demand is not necessarily inversely related to the P content as adult (like the aforementioned mites with lower P content than other groupings within the same taxocene); the P demand can, in fact, be needed during growth for structural components like bony skeleton. In the case of fishes, for instance, P demand and P content remain directly correlated with each other (Lauridsen et al., 2012; Sterner and George, 2000).

Therefore, ecological stoichiometry and classical prey–predator chains coexist and contribute to explain apparent difficulties in the application of the Lotka–Volterra model in reality. Still, the possibility of a kind of top-down control has to be taken into account (Wardle, 1999) and causal relationships must be directional and quantitative, such as the pathway analyses performed by Perner and Voigt (2007) and Voigt et al. (2007). Comparing this stoichiometric perspective across soil systems with the large number of terrestrial B–EF studies, it remains surprising that the plea of Chase (2000) to address phosphorus in terrestrial ecosystem types has remained largely ignored by so many soil ecologists (but see Lynch and Ho, 2005).

7. CODA

Macroecology and ecological stoichiometry encompass a wide variety of large-scale phenomena (cf. Gardner et al., 2001; Hall, 2009; Sterner and Elser, 2002), and allometric scaling can link large-scale macroecology to either species- or community levels (Yodzis and Innes, 1992). Together, allometry and ecological stoichiometry are suitable measures to catch the emergent characteristics of large data sets distributed in time and space and offer a reliable tool to outflank difficulties in the environmental assessment of disturbed ecosystems. Like Yodzis and Innes (1992), we argue that allometry and food web theory can be successfully integrated, even if the coupling between biodiversity and EF is less stringent than commonly assumed.

In 2004, the plea for the conservation of ecosystem structure and functioning as priority target came from the United Nations (UNEP/CBD, 2004). Alas, biological findings are often not strengthened for stakeholders and policy-decision makers (Mann, 1991). Many of the studies of the

predominance of quarter-power scaling in biology have remained purely descriptive so far, although there are exciting hints of a mechanistic explanation for observed patterns in EF. The evenness in the structure of a food web can be captured by allometric scaling and when the resulting mass–abundance relationship is close to isometry, its equitability roughly implies biomass evenness across trophic levels. Such 'allometric metrics' can take into account traits like the average body size of given species that may often be independent from environmental predictors, indirectly supporting the historical critique on biodiversity by Hurlbert (1971).

Our survey on the understanding of B–EF relationships includes aspects of taxonomic diversity, functional categorization and metabolic scaling as well as rules for their appropriate use. Given the well-known role of traits as predictors of niche complementarity and community structures, we have considered empirical examples examining how biodiversity supports EF. As model organisms, we chose fishes, plants and invertebrates and highlighted distributional (in)congruences of these organisms, the current state of the field and future challenges. Our review of independent case studies from the blue, the brown and the green worlds shows that biodiversity (at least the taxonomic diversity) as the key predictor for EF and multitrophic interactions like those described in food web theory may be overemphasized. There is an urgent need to galvanize ecologists from different subdisciplines, bringing them together for so many existing questions (Carpenter et al., 2009). A greater synergy between theoretical and empirical disciplines during the construction of null hypotheses is necessary to allow a careful differentiation between experimental design and EF. In the past, research on EF was often diluted by a dichotomy between empirical reports (often as grey literature), novel biology journals and theoretical journals, complicating data mining of disparate data sets. Hence, generalization without oversimplification becomes an important objective in its own right, with the ability to identify traits that underlie species responses and ecological processes (Grime, 1997). Such responses, especially when aggregated up to the biome level, can provide critically important ways to predict ecosystem responses to environmental changes at a global scale (Wall et al., 2008).

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APPENDIX

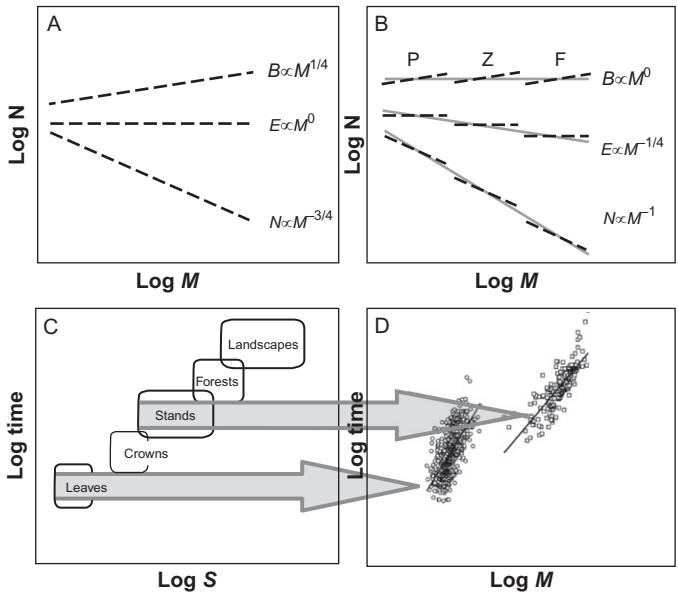

Figure A1 Allometric scaling and diversity–yield relationships. Upper panel: dashed lines describe three log–log relationships between species average weight $\bar{M}$ and species density N for total biomass B, upper line, energy rate E, middle line, and mass–abundance scaling, lower line, as function of $\bar{M}$ for pelagic food webs across trophic levels (A) and within three taxocenes, namely the phytoplankton P, the zooplankton Z and the fishes F (B). Lower panel: dynamic domains of scale (S) in time occupied by different entities enable to address the variation in ecological processes across the discrete boundaries of the investigated domains (C) and allow taking into consideration relationships into a similar space-time domain (D). Adapted from Brown and Gillooly (2003), the upper panels (A, B), and from Kerkhoff and Enquist (2007), the lower panels (C, D).

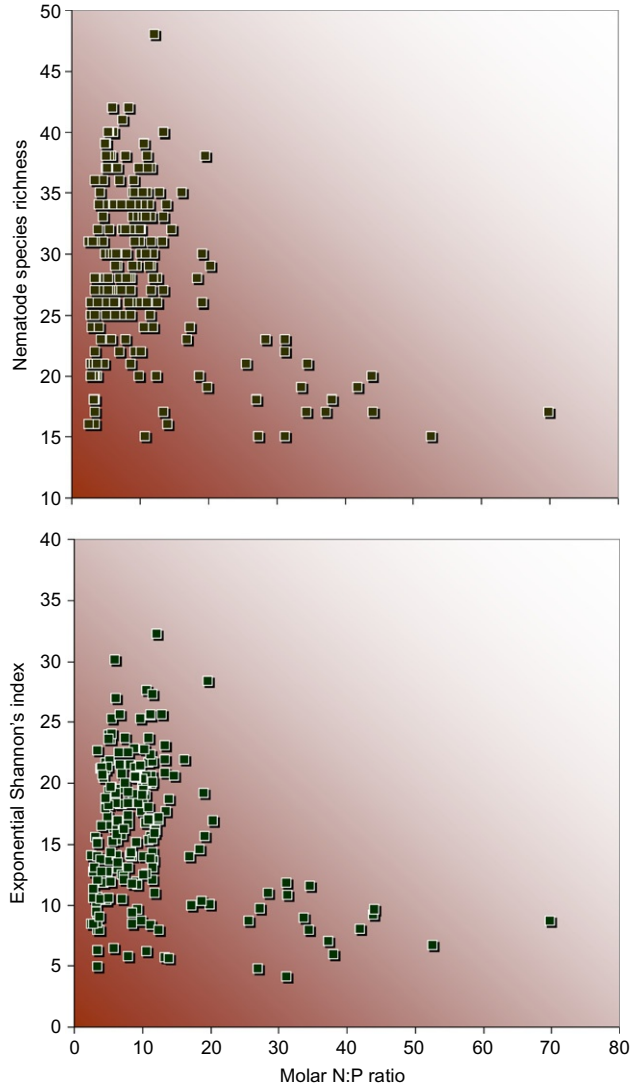

Figure A2 Soil abiotics and diversity–yield relationships for free-living nematodes. Diversity metrics that combine species richness with relative abundance, like the so-called Hill numbers (here the exponential Shannon-Wiener index as in Hill, 1973), are not independent from the (number of) species themselves. We have chosen the molar N:P ratio as proxy for the productivity of agroecosystems (Mulder and Vonk, 2011). If so, productive sites show a higher value of the exponential Shannon-Wiener index (bottom) and a higher amount of nematode species (top). Hence, in more productive sites, species are more even in their spatial distribution than in less productive sites.

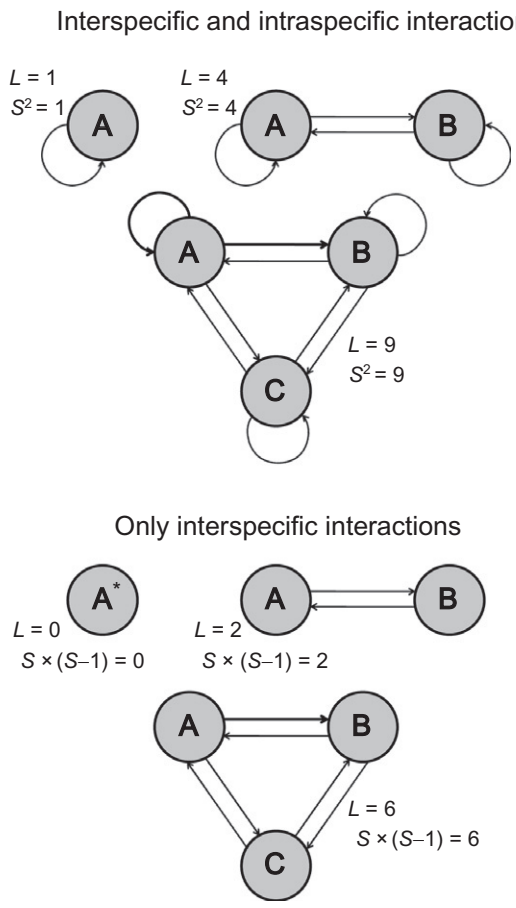

Figure A3 The extent to which one species (A) will feed on other species (here, B and C) can be quantified by species connectivity according to metrical computations (explanations in the text). Within one taxocene, C_t fluctuates between 0% (no trophic links at all) and 100% (maximal aggressive behaviour) for both interspecific and intraspecific interactions (directed connectance, upper panel) as for interspecific interactions only (interactive connectance, no cannibalistic links; lower panel). Here we show the maximal number of possible trophic interactions within the same taxocene ($C_t = 100\%$), besides the unique case of the polar nematode *Scottnema* (this most extreme condition—marked by an asterisk—exhibits $L = 0$, $S \times (S - 1) = 0$ and therefore $C_t = 0\%$ in A*). Many realized trophic links are suggested to reflect a dominance of generalists (high species connectivity implies high omnivory and aggressive feeding behaviour, therefore high resilience at taxocene level), in contrast to a low proportion of realized trophic links, which reflects a skew towards specialists and immature life stages (low species connectivity: low resilience).

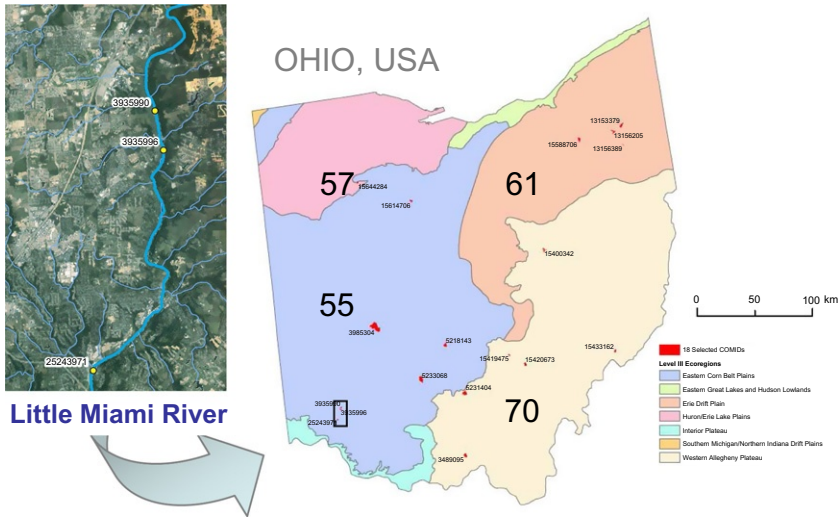

Figure A4 Geographical location of the 18 freshwater assemblages randomly selected after allometric screening (Fig. A5). The rivers Scioto Brush Creek, Hocking (two times), Big Darby Creek, Paint Creek (two times), Blanchard, Duck Creek, Little Miami (three times), Buck Creek, Sandusky, Walhonding, Mahoning (three times) and Cuyahoga were sampled between 2000 and 2007. Many locations (like those in Figs. 10 and A6) are in the Eastern Corn Belt Plains (Ecoregion 55), the most variable in total phosphorus (CV = 88.6%), biochemical oxygen demand (85.5), chemical oxygen demand (118.6), nitrite (125.0), ammonia (231.4) and total suspended solids (153.8), and the least variable in hardness (CV = 22.6%), nitrate (44.4), conductivity (24.6) and total dissolved solids (25.4). Ecoregions as defined in: http://www.eoearth.org/article/Ecoregions_of_Indiana_and_Ohio_%28EPA%29. GIS credit: Katherine Kapo.

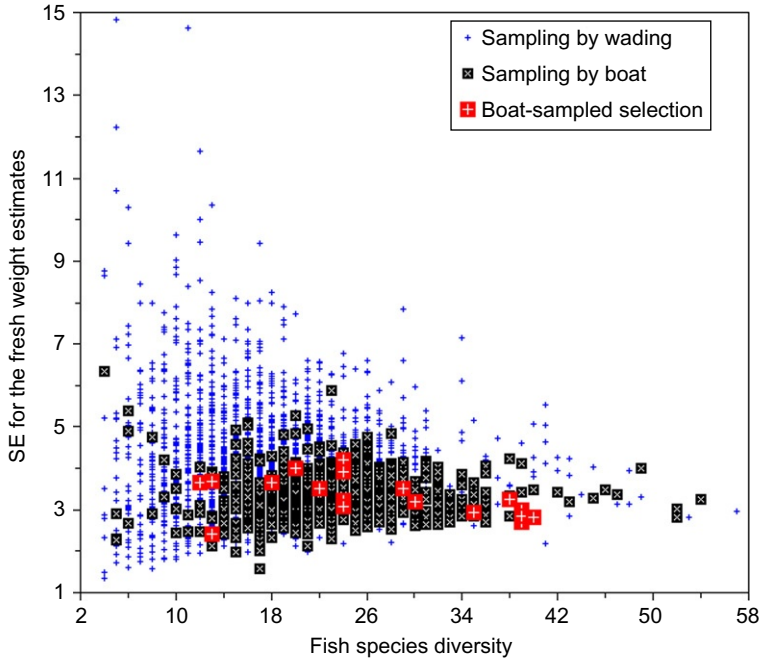

Figure A5 Possible effects of sampling methods associated with the allometric model on uncertainty were investigated by selecting 2656 locations in Ohio sampled either by boat or by wading. The uncertainty in the allometric estimates of the mean fresh biomass (|SE| in grams) of the smallest fish populations in each fish assemblage shows that the kind of sampling (boat or wading) and, indirectly, the river type (large, tributary, etc.), inflates biomass estimates in low-diversity communities, supporting that boat sampling provides the best estimates. As differences in sampling efforts are important for appropriate data mining and computations, we confined our further analyses in the aforementioned boat-sampled locations (Figs. 8 and A6; Table 5).

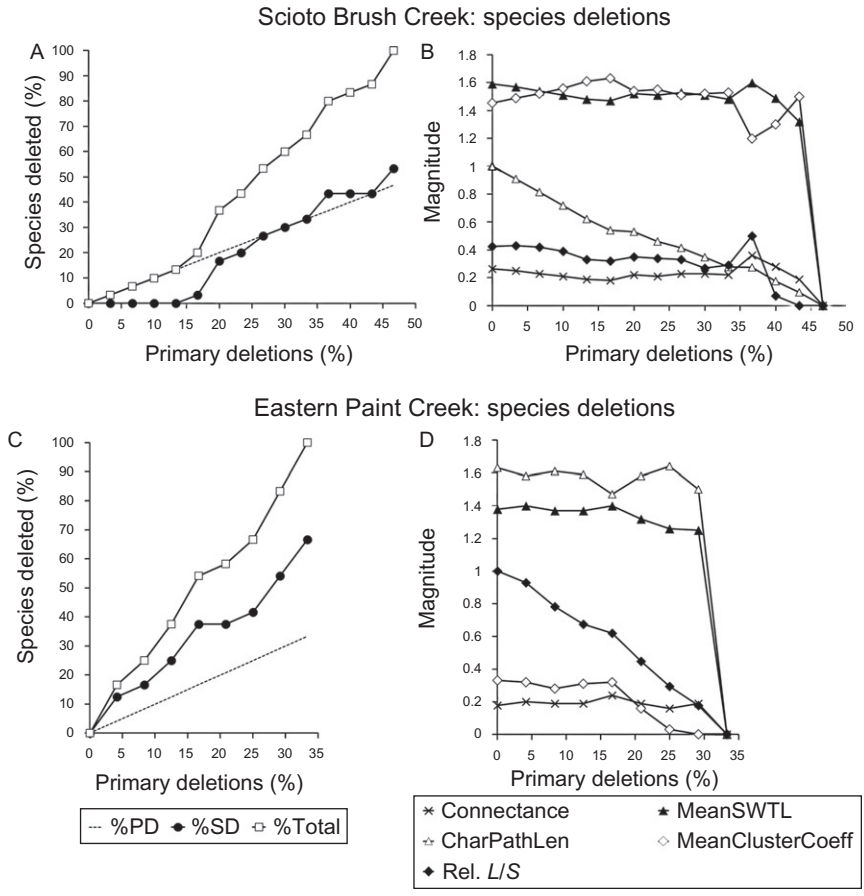

Figure A6 Two case studies in central Ohio on static species deletion scenario 'connectivity descending'. The creeks are both tributaries of the Scioto River. The fish assemblages have different vulnerabilities to secondary deletions (Table 5; Fig 9). Data on the left have been normalized for comparison. (A) The Scioto Brush Creek web with $n = 30$ only shows secondary deletions (% SD) from 15–50% of primary deletions (% PD) until its final collapse. At the beginning, secondary extinctions are less than primary extinctions, becoming equal to (and later more than) primary extinctions (dashed line indicates $x = y$). (B) The Scioto Brush Creek's web properties during the species deletion process, with the relative linkage density L/S quickly decreasing as highly connected nodes disappear from the web. (C) In contrast to the previous river, the Eastern Paint Creek with $n = 24$ immediately shows more secondary extinctions than primary extinctions (line above the 1:1 dashed line). The food web collapses after only 33% of primary extinctions. (D) Most Paint Creek's web properties behave similarly to those in (B).

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio

Weight (average of individual measurements in grams) versus COMID (7- and 8-digit code, GIS location in Fig. A4)

Species (Latin Please check whether the entries are aligned properly in this table. binomial, qualitative) Behavioural Level (**1** or **2**, numeric)																	
3489095	3935990	3935996	3985304	5218143	5231404	5233068	13153379	13156205	13156389	15400342	15419475	15420673	15433162	15588706	15614706	15644284	25243971
Ambloplites rupestris **2**																	
36.0	113.3	115.0	46.7	48.3	32.0	0	25.0	0	0	120.0	90.0	0	62.0	110.0	61.8	93.7	120.0
Ameiurus natalis **2**																	
0	0	0	0	0	0	0	0	0	0	54.0	0	0	0	177.0	0	202.0	0
Amia calva **2**																	
0	0	0	0	0	0	0	0	0	0	1040.0	0	0	0	0	0	0	0
Ammocrypta pellucida **2**																	
0	0	0	0	0	0	0	2.0	0	0	0	0	0	0	0	0	0	0
Aplodinotus grunniens **2**																	
2382.1	865.0	1692.8	0	1100.0	677.2	0	0	0	0	2100.0	0	0	254.5	0	0	545.5	492.1
Campostoma anomalum **1**																	
0	6.3	8.2	20.3	9.2	8.3	0	0	0	0	21.4	0	5.0	0	0	0	0	10.0
Carpiodes carpio **1**																	
0	905.0	1028.0	0	1350.0	601.3	750.0	0	0	0	0	583.3	900.0	0	0	0	0	961.4
Carpiodes cyprinus **2**																	
1400.0	991.7	0	0	1425.0	4.5	0	0	0	0	1100.0	384.2	400.0	140.0	0	0	0	0

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Carpiodes velifer **1**																	
700.0	631.3	0	0	0	261.7	0	0	0	0	650.0	0	0	0	0	0	0	703.0
Catostomus commersonii **1**																	
0	0	0	178.1	0	0	245.0	202.4	242.4	4.0	0	3.0	0	160.0	907.8	154.5	571.4	0
Cottus bairdii **2**																	
0	0	0	9.0	0	0	0	0	0	0	0	2.5	1.0	0	0	0	0	0
Cyprinella spiloptera **2**																	
2.0	4.0	4.6	0	3.0	4.1	2.5	5.0	0	3.3	3.4	3.7	3.5	2.4	0	5.1	4.7	3.5
Cyprinella whipplei **2**																	
0	8.8	4.6	0	0	2.0	0	0	0	0	0	0	6.0	0	0	0	0	3.6
Cyprinus carpio **2**																	
0	2083.3	2511.0	1681.3	2994.4	0	1460.0	0	4911.8	1787.5	1495.7	2317.9	2236.1	3400.0	3012.5	2150.0	2338.5	2366.7
Dorosoma cepedianum **1**																	
135.5	66.0	176.5	0	347.1	247.9	89.4	46.0	5.0	51.7	114.2	422.0	60.9	104.5	0	0	9.0	234.3
Erimystax dissimilis **1**																	
0	0	0	0	8.9	2.0	0	0	0	0	8.6	0	0	0	0	0	0	0
Erimystax x-punctata **1**																	
0	0	8.0	0	0	5.8	0	0	0	0	4.0	0	0	0	0	0	0	0

Continued

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Esox americanus **2**																	
0	0	0	0	0	0	0	52.5	38.6	0	0	12.0	5.0	0	15.0	0	0	0
Esox lucius **2**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2400.0	0	0	0
Esox masquinongy **2**																	
0	0	0	0	0	0	0	0	3991.7	0	0	0	0	0	0	0	0	0
Etheostoma blennioides **1**																	
2.0	8.0	3.9	6.8	3.1	3.3	1.0	0	4.0	0	3.3	4.0	1.0	0	0	0	5.0	5.0
Etheostoma caeruleum **2**																	
0	3.0	1.0	2.8	1.4	1.0	0	0	0	0	0	0	0	0	0	0	0	2.0
Etheostoma camurum **1**																	
0	0	0	0	2.1	1.8	0	0	0	0	4.0	0	0	0	0	0	0	0
Etheostoma flabellare **2**																	
0	0	0	0	0	0	0	7.3	0	0	0	0	0	2.0	0	0	0	0
Etheostoma nigrum **2**																	
2.0	0	0	0	0	0	0	1.4	2.0	0	0	0	0	0	0	0	0	0
Etheostoma tippecanoe **1**																	
0	0	0	0	0.8	1.4	0	0	0	0	0	0	0	0	0	0	0	0
Etheostoma variatum **1**																	
0	4.0	4.9	0	7.5	2.5	0	0	0	0	3.6	0	0	0	0	0	0	5.0

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Etheostoma zonale **1**																	
0	4.0	1.8	2.1	0.8	1.7	0	2.0	0	0	1.0	1.5	1.3	0	0	0	0	1.9
Fundulus notatus **2**																	
2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.0	0
Hiodon tergisus **2**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	217.0
Hypentelium nigricans **1**																	
130.0	203.3	160.9	156.4	178.1	118.7	95.5	94.7	243.3	0	93.6	172.2	108.2	45.7	0	150.0	200.5	88.7
Ichthyomyzon fossor **1**																	
0	0	0	0	0	0	0	12.5	0	0	0	0	0	0	0	0	0	0
Ictalurus punctatus **2**																	
675.0	1512.5	1960.0	0	808.0	1.0	516.7	0	520.0	882.5	1757.1	1450.0	832.0	1115.0	0	0	250.0	1363.5
Ictiobus bubalus **1**																	
0	2252.5	2215.7	0	0	1500.0	0	0	0	0	0	0	0	0	0	0	0	2500.0
Ictiobus cyprinellus **1**																	
0	0	0	0	0	1900.0	0	0	0	0	0	0	0	0	0	0	0	1500.0
Ictiobus niger **1**																	
0	0	0	0	450.0	0	0	0	0	0	0	0	0	0	0	0	0	0

Continued

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Labidesthes sicculus **1**																	
1.3	0	0	0	0	0	0	0	0	2.8	0	0	0	0	0	0	0	0
Lampetra aepyptera **1**																	
0	0	0	0	0	0	0	0	0	0	0	11.0	0	0	0	0	0	0
Lepisosteus osseus **2**																	
1000.0	0	725.5	0	410.0	0	0	0	0	0	0	0	0	0	0	0	0	120.0
Lepomis cyanellus **2**																	
90.0	22.5	0	0	0	20.0	52.5	9.3	9.6	0	0	18.3	0	0	0	6.7	23.9	0
Lepomis gibbosus **2**																	
0	0	0	0	0	0	0	25.0	90.0	0	0	0	0	0	37.4	0	0	0
Lepomis gulosus **2**																	
0	0	0	0	0	0	0	60.0	0	0	0	0	0	0	0	0	0	0
Lepomis macrochirus **1**																	
46.7	21.0	0	9.3	15.4	45.0	11.7	42.2	33.3	135.0	40.0	22.5	36.2	0	25.5	80.0	80.0	76.7
Lepomis megalotis **1**																	
10.2	63.5	32.3	0	20.5	21.8	27.5	0	0	0	0	32.0	0	13.3	0	0	25.9	14.8
Lepomis microlophus **1**																	
0	0	0	0	0	25.0	0	0	0	0	60.0	0	0	0	0	0	0	0
Luxilus chrysocephalus **1**																	
4.3	2.0	2.0	28.0	0	3.0	2.0	0	0	0	2.0	0	0	0	0	0	0	0

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Luxilus cornutus **1**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21.1	0	0
Lythrurus fasciolaris **1**																	
0	0	0	0	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0
Lythrurus umbratilis **1**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.0	0
Micropterus dolomieux **2**																	
712.5	314.3	105.3	124.3	202.7	183.3	326.2	525.0	340.0	168.3	110.3	100.0	159.4	44.0	0	106.7	200.0	124.7
Micropterus punctulatus **2**																	
46.8	140.0	0	0	192.5	49.4	0	0	0	0	187.0	475.0	96.0	170.0	0	0	0	10.0
Micropterus salmoides **2**																	
57.5	90.0	0	0	15.0	0	85.0	70.0	134.3	621.6	233.3	11.3	2.3	169.5	171.8	0	85.7	0
Minytrema melanops **1**																	
96.3	0	0	0	0	0	90.7	60.0	0	0	0	0	0	60.0	697.5	0	167.8	0
Morone chrysops **2**																	
0	190.0	0	0	250.0	0	0	0	0	0	0	0	0	100.0	0	0	0	0
Morone saxatilis **2**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	220.0

Continued

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Moxostoma anisurum **1**																	
379.4	2075.0	2050.0	0	2150.0	1050.0	1240.0	0	0	0	855.3	560.0	728.8	413.9	0	0	0	1866.7
Moxostoma breviceps **1**																	
51.7	296.0	416.3	0	0	285.0	295.0	0	0	0	229.1	0	0	0	0	0	0	215.2
Moxostoma carinatum **1**																	
0	1950.0	0	0	2065.0	0	0	0	0	0	2245.5	0	0	550.0	0	0	0	0
Moxostoma duquesnei **1**																	
78.3	714.5	814.8	476.9	153.8	700.0	650.0	0	0	0	330.0	750.0	0	0	0	0	0	379.3
Moxostoma erythrurum **1**																	
48.6	526.0	559.6	450.0	398.6	7.3	384.5	51.3	0	0	171.5	391.3	331.0	176.8	0	166.2	386.5	372.8
Moxostoma macrolepidotum **1**																	
0	0	0	0	447.5	0	0	0	0	0	0	0	0	100.0	0	0	0	0
Nocomis biguttatus **1**																	
0	0	0	0	0	0	0	0	7.9	0	0	0	0	0	0	0	0	0
Nocomis micropogon **2**																	
0	0	20.0	0	0	0	0	43.2	0	0	6.0	0	0	0	0	0	0	0
Notemigonus crysoleucas **1**																	
0	0	0	0	0	0	0	0	15.0	0	0	0	0	0	17.4	0	0	0

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Notropis amblops **1**																	
0	0	0	0	0	0	0	0	0	0	2.4	0	0	0	0	0	0	0
Notropis atherinoides **1**																	
3.0	2.3	1.7	0	0	2.0	0	0	0	0	0	0	0	1.9	0	0	18.7	1.1
Notropis buccatus **1**																	
0	0	0	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0	0
Notropis photogenis **1**																	
2.0	0	2.0	9.2	5.8	2.0	5.9	0	0	0	8.7	0	0	0	0	0	0	0
Notropis rubellus **2**																	
0	0	2.0	0	0	0	0	0	0	0	2.9	2.0	0	0	0	0	0	0
Notropis stramineus **2**																	
0	0	2.3	0	1.9	1.2	0	0	0	0	2.0	2.0	2.5	0	0	0	3.0	1.5
Notropis volucellus **1**																	
0	3.0	2.3	0	0	0	0	0	0	0	2.0	0	0	0	0	0	0	1.5
Noturus eleutherus **2**																	
0	2.0	3.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Noturus flavus **2**																	
0	30.0	8.2	0	0	7.1	0	0	0	0	6.0	0	0	0	0	40.0	0	10.0
Noturus miurus **2**																	
0	0	0	0	0	5.0	0	0	0	0	0	0	0	0	0	0	0	0

Continued

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Noturus stigmosus **2**																	
0	0	6.0	0	0	5.0	0	0	0	0	0	0	0	0	0	0	0	1.0
Perca flavescens **2**																	
0	0	0	0	0	0	0	70.9	46.4	18.0	0	26.0	0	0	0	0	0	0
Percina caprodes **2**																	
7.6	16.0	8.6	17.0	15.5	12.5	14.9	18.5	0	0	11.0	13.0	0	0	0	0	0	6.3
Percina maculata **2**																	
0	0	0	0	0	0	0	0	0	0	4.0	0	0	0	0	0	0	0
Percina phoxocephala **1**																	
0	4.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.0
Percina sciera **1**																	
0	0	0	0	0	0	0	0	0	0	0	0	12.0	0	0	0	0	0
Percopsis omiscomaycus **2**																	
0	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0	0	0	0
Phenacobius mirabilis **1**																	
0	0	4.5	0	0	3.0	0	0	0	0	0	0	0	0	0	0	0	7.0
Pimephales notatus **1**																	
2.6	2.9	2.7	8.0	3.0	1.4	2.0	3.0	4.0	3.8	2.3	0.8	2.5	0	0	3.0	3.1	1.6
Pimephales vigilax **2**																	
0	2.0	1.0	0	0	2.0	0	0	0	0	0	0	0	0	0	0	0	2.4

Table A1 Occurrence and site-specific body mass (wet weight) of freshwater fishes in the 18 investigated rivers across Ohio—cont'd

Pomoxis annularis **2**																	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80.0	116.0	0
Pomoxis nigromaculatus **2**																	
0	0	200.0	0	0	0	215.0	0	51.8	250.0	280.0	0	0	0	139.7	0	0	0
Pylodictis olivaris **2**																	
2700.0	1747.5	338.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2020.0
Semotilus atromaculatus **2**																	
0	0	0	29.0	0	0	0	0	0	0	0	0	0.9	0	0	0	5.0	0
Stizostedion canadense **2**																	
0	290.0	0	0	388.0	0	0	0	0	0	0	0	0	137.5	0	0	0	379.0
Stizostedion vitreum **2**																	
0	0	484.0	0	0	0	0	150.0	0	455.6	0	0	0	0	0	0	0	0
Umbra limi **2**																	
0	0	0	0	0	0	0	0	4.0	0	0	0	0	0	0	0	0	0

Please note: Occurrence (if present, weight is provided) and behavioural level: 0 = fish species absent in a given site; 1 = all fish species feeding upon preys from other taxocenes; 2 = piscivorous fishes predating within their own taxocene but not within their own population (cannibalism excluded). All feeding traits and fish taxonomy according to www.FishBase.org version June 2011 accessed August 2011.

REFERENCES

Adl, S.M., Simpson, A.G.B., Farmer, M.A., Andersen, R.A., Anderson, O.R., Barta, J.R., Bowser, S.S., Brugerolle, G., Fensome, R.A., Fredericq, S., James, T.Y., Karpov, S., et al., 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. J. Eukaryot. Microbiol. 52, 399–451.

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., et al., 2011. Productivity is a poor predictor of plant species richness. Science 333, 1750–1753.

Allen, A.P., Gillooly, J.F., Brown, J.H., 2005. Linking the global carbon cycle to individual metabolism. Funct. Ecol. 19, 202–213.

Allesina, S., Pascual, M., 2009. Googling food webs: can an Eigenvector measure species' importance for coextinctions? PLoS Comput. Biol. 5, e1000494.

Allison, S.D., 2006. Brown ground: a soil carbon analogue for the green world hypothesis? Am. Nat. 167, 619–627.

Amthor, J.S., 2000. The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. Ann. Bot. 86, 1–20.

Antón, A., Cebrian, J., Heck, K.L., Duarte, C.M., Shhehan, K.L., Miller, M.-E.C., Foster, C.D., 2011. Decoupled effects (positive to negative) of nutrient enrichment on ecosystem services. Ecol. Appl. 21, 991–1009.

Arim, M., Berazategui, M., Barreneche, J.M., Ziegler, L., Zarucki, M., Abades, S.R., 2011. Determinants of density-body size scaling within food webs and tools for their detection. Adv. Ecol. Res. 45, 1–39.

Attrill, M.J., Depledge, M.H., 1997. Community and population indicators of ecosystem health: targeting links between levels of biological organisation. Aquat. Toxicol. 38, 183–197.

Bala, G., Caldeira, K., Wickett, M., Phillips, T.J., Lobell, D.B., Delire, C., Mirin, A., 2007. Combined climate and carbon-cycle effects of large-scale deforestation. Proc. Natl. Acad. Sci. U.S.A. 104, 6550–6555.

Banašek-Richter, C., Bersier, L.F., Cattin, M.F., Baltensperger, R., Gabriel, J.P., Merz, Y., Ulanowicz, R.E., Tavares, A.F., Williams, D.D., De Ruiter, P.C., Winemiller, K.O., Naisbit, R.E., 2009. Complexity in quantitative food webs. Ecology 90, 1470–1477.

Barrett, J.E., Virginia, R.A., Wall, D.H., Cary, S.C., Adams, B.J., Hacker, A.L., Aislabie, J.M., 2006. Co-variation in soil biodiversity and biogeochemistry in northern and southern Victoria Land, Antarctica. Antarct. Sci. 18, 535–548.

Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H., Moorhead, D.L., 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. J. Geophys. Res. 112, G01010.

Beckerman, A.P., Petchey, O.L., Warren, P.H., 2006. Foraging biology predicts food web complexity. Proc. Natl. Acad. Sci. U.S.A. 103, 13745–13749.

Beerling, D.J., Woodward, F.I., 2001. Vegetation and the Terrestrial Carbon Cycle: Modelling the First 400 Million Years. Cambridge University Press, Cambridge, UK.

Benton, T.G., Beckerman, A.P., 2005. Population dynamics in a noisy world: lessons from a mite experimental system. Adv. Ecol. Res. 37, 143–181.

Blackburn, T.M., Gaston, K.J., 1994. Animal body-size distributions—patterns, mechanisms and implications. Trends Ecol. Evol. 9, 471–474.

Blomberg, S., Garland, T., Ives, A., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57, 717–745.

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.

Bongers, T., 1999. The maturity index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. Plant Soil 212, 13–22.

Borgmann, U., 1987. Model on the slope of, and biomass flow up, the biomass size spectrum. Can. J. Fish. Aquat. Sci. 44, 136–140.

Bradford, M.A., Jones, T.H., Bardgett, R.D., Black, H.I.J., Boag, B., Bonkowski, M., Cook, R., Eggers, T., Gange, A.C., Grayston, S.J., Kandeler, E., McCaig, A.E., et al., 2002. Impacts of soil faunal community composition on model grassland ecosystems. Science 298, 615–618.

Briand, F., 1985. Structural singularities of freshwater food webs. Verh. Int. Ver. Theor. Angew. Limnol. 22, 3356–3364.

Brown, J.H., Gillooly, J.F., 2003. Ecological food webs: high-quality data facilitate theoretical unification. Proc. Natl. Acad. Sci. U.S.A. 100, 1467–1468.

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.

Brussaard, L., 2012. Ecosystem services provided by the soil biota. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, H., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press, Oxford, pp. 45–58.

Burton, G.A., De Zwart, D., Diamond, J., Dyer, S., Kapo, K.E., Liess, M., Posthuma, P., 2012. Making ecosystem reality checks the status quo. Environ. Toxicol. Chem. 31, 459–468.

Calder III, W.A., 1984. Size, Function and Life History. Harvard University Press, Cambridge, MA.

Carbone, C., Pettorelli, N., Stephens, P., 2011. The bigger they come, the harder they fall: body size and prey abundance influence predator–prey ratios. Biol. Lett. 7, 312–315.

Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. Nature 472, 86–89.

Cardinale, M., Svedang, H., 2004. Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak-Kattegat (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. Fish. Res. 69, 263–282.

Cardinale, B.J., Srivastava, D.S., Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.

Cardinale, B.J., Bennett, D.M., Nelson, C.E., Gross, K., 2009. Does productivity drive diversity or vice versa? A test of the multivariate productivity–diversity hypothesis in streams. Ecology 90, 1227–1241.

Carpenter, S.R., Kraft, C.E., Wright, R., He, X., Soranno, P.A., Hodgson, J.R., 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. Am. Nat. 140, 781–798.

Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L., Essington, T.E., Houser, J.N., Schindler, D.E., 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecol. Monogr. 71, 163–186.

Carpenter, S.R., Armbrust, E.V., Arzberger, P.W., Chapin III, F.S., Elser, J.J., Hackett, E.J., Ives, A.R., Kareiva, P.M., Leibold, M.A., Lundberg, P., Mangel, M., Merchant, N., et al., 2009. Accelerate synthesis in ecology and environmental sciences. Bioscience 59, 699–701.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell, J.F., Seekel, D.A., Smith, L., Weidell, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. Science 332, 1079–1082.

Castle, M.D., Blanchard, J.L., Jennings, S., 2011. Predicted effects of behavioural movement and passive transport on individual growth and community size structure in marine ecosystems. Adv. Ecol. Res. 45, 41–66.

Caswell, H., Cohen, J.E., 1991. Disturbance, interspecific interaction and diversity in metapopulations. Biol. J. Linn. Soc. 42, 193–218.

Cavalier-Smith, T., 1993. Kingdom protozoa and its 18 phyla. Microbiol. Rev. 57, 953–994.
Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242.
Chase, J.M., 2000. Are there real differences among aquatic and terrestrial food webs? Trends Ecol. Evol. 15, 408–412.
Chown, S.L., Marais, E., Terblanche, J.S., Klok, C.J., Lighton, J.R.B., Blackburn, T.M., 2007. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. Funct. Ecol. 21, 282–290.
Clarke, A., Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. Anim. Ecol. 68, 893–905.
Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85, 235–252.
Cohen, J.E., 1994. Marine and continental food webs: three paradoxes? Philos. Trans. R. Soc. Lond. B 343, 57–69.
Cohen, J.E., Carpenter, S.R., 2005. Species' average body mass and numerical abundance in a community food web: statistical questions in estimating the relationship. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press, San Diego, CA, pp. 137–156.
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. U.S.A. 100, 1781–1786.
Cotner, J.B., Hall, E.K., Scott, J.T., Heldal, M., 2010. Freshwater bacteria are stoichiometrically flexible with a nutrient composition similar to seston. Front. Microbiol. 1, a132.
Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecol. Lett. 4, 72–85.
Courtright, E.M., Wall, D.H., Virginia, R.A., 2001. Determining habitat suitability for soil invertebrates in an extreme environment: the McMurdo Dry Valleys, Antarctica. Antarct. Sci. 13, 9–17.
Cousins, S.H., 1980. A trophic continuum derived from plant structure, animal size and a detritus cascade. J. Theor. Biol. 82, 607–618.
Cousins, S.H., 1996. Food webs: from the Lindeman paradigm to a taxonomic general theory of ecology. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York, pp. 243–251.
Crotty, F.V., Blackshaw, R.P., Murray, P.J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Commun. Mass Spectrom. 25, 1503–1513.
Crutzen, P.J., 2002. Geology of mankind. Nature 415, 23.
Damuth, J., 1981. Population density and body size in mammals. Nature 290, 699–700.
Damuth, J., 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biol. J. Linn. Soc. 31, 193–246.
Damuth, J., 1991. Of size and abundance. Nature 351, 268–269.
Dawson, S.C., Hagen, K.D., 2009. Mapping the protistan 'rare biosphere'. J. Biol. 8, a105.
De Visser, S., Freymann, B., Olff, H., 2011. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. J. Anim. Ecol. 80, 465–475.
De Vries, F.T., Hoffland, E., Van Eekeren, N., Brussaard, L., Bloem, J., 2006. Fungal/bacterial ratios in grasslands with contrasting nitrogen management. Soil Biol. Biochem. 38, 2092–2103.
Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc. Natl. Acad. Sci. U.S.A. 104, 20684–20689.

Dossena, M., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M., Woodward, G., Yvon-Durocher, G., 2012. Warming alters community size structure and ecosystem functioning. Proc. R. Soc. Lond. B 279, 3011–3019.

Du Rietz, G.E., 1931. Life forms of terrestrial flowering plants. Acta Phytogeogr. Suec. 3, 1–95.

Duarte, C.M., Middelburg, J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2, 1–8.

Dukes, J.S., Chiariello, N.R., Cleland, E.E., Moore, L.A., Shaw, M.R., Thayer, S., Tobeck, T., Mooney, H.A., Field, C.B., 2005. Responses of grassland production to single and multiple global environmental changes. PLoS Biol. 3, e319.

Dunne, J.A., 2009. Food webs. In: Meyers, R.A. (Ed.), Complex Networks and Graph Theory—Encyclopedia of Complexity and Systems Science, 3661–3682. http://www.springer.com/978-0-387-75888-6.

Dunne, J.A., Williams, R.J., 2009. Cascading extinctions and community collapse in model food webs. Philos. Trans. R. Soc. Lond. B 364, 1711–1723.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. 5, 558–567.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2004. Network structure and robustness of marine food webs. Mar. Ecol. Prog. Ser. 273, 291–302.

Dunne, J.A., Williams, R.J., Martinez, N.D., Wood, R.A., Erwin, D.H., 2008. Compilation and network analyses of Cambrian food webs. PLoS Biol. 6, e102.

Duplisea, D.E., Drgas, A., 1999. Sensitivity of a benthic, metazoan, biomass size spectrum to differences in sediment granulometry. Mar. Ecol. Prog. Ser. 177, 73–81.

Dyer, S.D., White-Hull, C.E., Wang, X., Johnson, T.D., Carr, G.J., 1998. Determining the influence of habitat and chemical factors on instream biotic integrity for a Southern Ohio watershed. J. Aquat. Ecosyst. Stress Recov. 6, 91–110.

Ebenman, B., Jonsson, T., 2005. Using community viability analysis to identify fragile systems and keystone species. Trends Ecol. Evol. 20, 568–575.

Elser, J., 2006. Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. Am. Nat. 168, S25–S35.

Elser, J.J., Urabe, J., 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology 80, 735–751.

Elser, J.J., Luecke, C., Brett, M.T., Goldman, C.R., 1995. Effects of food web compensation after manipulation of rainbow trout in an oligotrophic lake. Ecology 76, 52–69.

Elser, J.J., Chrzanowski, T.H., Sterner, R.W., Mills, K.H., 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian Shield. Ecosystems 1, 120–136.

Elser, J.J., Sterner, R.W., Galford, A.E., Chrzanowski, T.H., Findlay, D.L., Mills, K.H., Paterson, M.J., Stainton, M.P., Schindler, D.W., 2000. Pelagic C:N:P stoichiometry in a eutrophied lake: responses to a whole-lake food-web manipulation. Ecosystems 3, 293–307.

Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G., Enquist, B.J., 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytol. 186, 593–608.

Enquist, B.J., West, G.B., Charnov, E.L., Brown, J.H., 1999. Allometric scaling of production and life-history variation in vascular plants. Nature 401, 907–911.

Enquist, B.J., Allen, A.P., Brown, J.H., Gillooly, J.F., Kerkhoff, A.J., Niklas, K.J., Price, C.A., West, G.B., 2007. Does the exception prove the rule? Nature 445, E9.

Ernest, S.K.M., Enquist, B.J., Brown, J.H., Charnov, E.L., Gillooly, J.F., Savage, V.M., White, E.P., Smith, F.A., Hadly, E.A., Haskell, J.P., Lyons, S.K., Maurer, B.A., et al., 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecol. Lett. 6, 990–995.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., et al., 2011. Trophic downgrading of planet Earth. Science 333, 301–306.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V., Woodall, C.W., 2010. Forest carbon storage: ecology, management, and policy. Front. Ecol. Environ. 8, 245–252.

FAO, 2000. The State of the World's Fisheries and Aquaculture 2000. Food and Agriculture Organization of the United Nations, Rome.

Feld, C.K., Birk, S., Bradley, D.C., Hering, D., Kail, J., Marzin, A., Melcher, A., Nemitz, D., Pedersen, M.L., Pletterbauer, F., Pont, D., Verdonschot, P.F.M., et al., 2011. From natural to degraded rivers and back again: a test of restoration ecology theory and practice. Adv. Ecol. Res. 44, 119–210.

Fenchel, T., Finlay, B.J., 1983. Respiration rates in heterotrophic, free-living protozoa. Microb. Ecol. 9, 99–122.

Finlay, B.J., 1998. The global diversity of protozoa and other small species. Intern. J. Parasitol. 28, 29–48.

Finlay, B.J., 2002. Global dispersal of free-living microbial eukaryote species. Science 296, 1061–1063.

Flombaum, P., Sala, O.E., 2012. Effects of plant species traits on ecosystem processes: experiments in the Patagonian steppe. Ecology 93, 227–234.

Flotemersch, J.E., 2001. Fish assessment methods. In: Flotemersch, J.E., Autrey, B.C., Cormier, S.M. (Eds.), Comparisons of Boating and Wading Methods Used to Assess the Status of Flowing Waters. EPA/600/R-00/108. U.S. Environmental Protection Agency, Cincinnati, OH, pp. 68–82.

Foissner, W., 2006. Biogeography and dispersal of micro-organisms: a review emphasizing protists. Acta Protozool. 45, 111–136.

Foissner, W., 2008. Protist diversity and distribution: some basic considerations. Biodivers. Conserv. 17, 235–242.

Forster, J., Hirst, A.G., Woodward, G., 2011. Growth and development rates have different thermal responses. Am. Nat. 178, 668–678.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O., et al., 2009. Plant functional traits capture the effects of land use change and climate on litter decomposability of herbaceous communities in Europe and Israel. Ecology 90, 598–611.

Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B., Hildrew, A.G., Lamouroux, N., Trimmer, M., Woodward, G., 2011. Biomonitoring of human impacts in freshwater ecosystems: the good, the bad, and the ugly. Adv. Ecol. Res. 44, 2–68.

Fridley, J.D., 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93, 514–526.

Froese, R., Pauly, D. (Eds.), 2005. FishBase, http://www.fishbase.org.

Fry, B., Quiñones, R.B., 1994. Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. Mar. Ecol. Prog. Ser. 112, 201–204.

Gams, W., 1992. The analysis of communities of saprophytic microfungi with special reference to soil fungi. In: Winterhoff, W. (Ed.), Fungi in Vegetation Science. Kluwer Academic Publishers, Dordrecht, pp. 183–223.

Gardner, R.H., Kemp, W.M., Kennedy, V.S., Petersen, J.E. (Eds.), 2001. Scaling Relations in Experimental Ecology. Columbia University Press, New York.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gerritsen, J., Barbour, M.T., King, K., 2000. Apples, oranges, and ecoregions: on determining pattern in aquatic assemblages. J. N. Am. Benthol. Soc. 19, 487–496.
Ghilarov, A.M., 2000. Ecosystem functioning and intrinsic value of biodiversity. Oikos 90, 408–412.
Gilljam, D., Thierry, A., Edwards, F.K., Figueroa, D., Ibbotson, A.T., Jones, J.I., Lauridsen, R.B., Petchey, O.L., Woodward, G., Ebenman, B., 2011. Seeing double: size-based and taxonomic views of food web structure. Adv. Ecol. Res. 45, 67–133.
Glazier, D.S., 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biol. Rev. 80, 611–662.
Glazier, D.S., 2010. A unifying explanation for diverse metabolic scaling in animals and plants. Biol. Rev. 85, 111–138.
Glibert, P.M., Harrison, J., Heil, C., Seitzinger, S., 2006. Escalating worldwide use of urea: a global change contributing to coastal eutrophication. Biogeochemistry 77, 441–463.
Goldbogen, J.A., Calambokidis, J., Croll, D.A., McKenna, M.F., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G., Shadwick, R.E., Tershy, B.R., 2012. Scaling of lunge-feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. Funct. Ecol. 26, 216–226.
Goldstein, R.M., Meador, M.R., 2004. Comparisons of fish species traits from small streams to large rivers. Trans. Am. Fish. Soc. 133, 971–983.
Goldstein, R.M., Simon, T.P., 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. In: Simon, T.P. (Ed.), Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press, Boca Raton, FL, pp. 123–202.
Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., Evans-Freke, I.I., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281, 2045–2047.
González, A.L., Fariña, J.M., Kay, A.D., Pinto, R., Marquet, P.A., 2011. Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers. Oikos 120, 1247–1255.
Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.
Grime, J.P., 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.
Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester, UK.
Grime, J.P., 1997. Biodiversity and ecosystem function: the debate deepens. Science 277, 1260–1261.
Gross, K., Cardinale, B.J., 2007. Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. Am. Nat. 170, 207–220.
Guénard, G., Von Der Ohe, P.C., De Zwart, D., Legendre, P., Lek, S., 2011. Using phylogenetic information to predict species tolerances to toxic chemicals. Ecol. Appl. 21, 3178–3190.
Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L., Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimarães Jr., P.K., Jenkins, G.B., et al., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Adv. Ecol. Res. 46, 89–210.
Hall, S.R., 2009. Stoichiometrically explicit food webs: feedbacks between resource supply, elemental constraints, and species diversity. Annu. Rev. Ecol. Evol. Syst. 40, 503–528.
Hartnett, D.C., Wilson, G.W.T., 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80, 1187–1195.
Havens, K.E., 1992. Scale and structure in natural food webs. Science 257, 1107–1109.
Hawkins, C.P., 2006. Quantifying biological integrity by taxonomic completeness: its utility in regional and global assessments. Ecol. Appl. 16, 1277–1294.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., et al., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123–1127.

Hector, A., Loreau, M., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., 2002. Biodiversity manipulation experiments: studies replicated at multiple sites. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp. 36–46.

Hedin, L.O., 2006. Plants on a different scale. Nature 436, 399–400.

Hein, M., Pedersen, M.F., Sandjensen, K., 1995. Size-dependent nitrogen uptake in micro- and macroalgae. Mar. Ecol. Prog. Ser. 118, 247–253.

Hendriks, A.J., Mulder, C., 2008. Scaling of offspring number and mass to plant and animal size: model and meta-analysis. Oecologia 155, 705–716.

Hendriks, A.J., Mulder, C., 2012. Delayed logistic and Rosenzweig–MacArthur models with allometric parameter setting estimate population cycles at lower trophic levels well. Ecol. Complex. 9, 43–54.

Hendrixson, H.A., Sterner, R.W., Kay, A.D., 2007. Elemental stoichiometry of freshwater fish in relation to phylogeny, allometry and ecology. J. Fish Biol. 70, 121–140.

Hildrew, A.G., 2009. Sustained research on stream communities: a model system and the comparative approach. Adv. Ecol. Res. 41, 175–312.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Hirose, T., Werger, M.J.A., 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72, 520–526.

Hladyz, S., Gessner, M.O., Giller, P.S., Pozo, J., Woodward, G., 2009. Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshw. Biol. 54, 957–970.

Hladyz, S., Åbjörnsson, K., Cariss, H., Chauvet, E., Dobson, M., Elosegi, A., Ferreira, V., Fleituch, T., Gessner, M.O., Giller, P.S., Graça, M.A.S., Gulis, V., et al., 2011. Stream ecosystem functioning in an agricultural landscape: the importance of terrestrial-aquatic linkages. Adv. Ecol. Res. 44, 211–276.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P., Thompson, K., 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos 85, 282–294.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. Ecol. Monogr. 75, 3–35.

Höppener-Ogawa, S., Leveau, J.H., Hundscheid, M.P., van Veen, J.A., de Boer, W., 2009. Impact of *Collimonas* bacteria on community composition of soil fungi. Environ. Microbiol. 11, 1444–1452.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Hunt, H.W., Wall, D.H., 2002. Modeling the effects of loss of soil biodiversity on ecosystem function. Glob. Change Biol. 8, 32–49.

Hunting, E.R., Whatley, M.H., Van der Geest, H.G., Mulder, C., Kraak, M.H.S., Breure, A.M., Admiraal, W., 2012. Invertebrate footprints on detritus processing, bacterial community structure and spatiotemporal redox profiles. Freshw. Sci. 31, 724–732.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Hurlbert, A.H., Jetz, W., 2010. More than "More Individuals": the nonequivalence of area and energy in the scaling of species richness. Am. Nat. 176, E50–E65.

Huston, M.A., 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.
Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110, 449–460.
Huston, M.A., Wolverton, S., 2009. The global distribution of net primary production: resolving the paradox. Ecol. Monogr. 79, 343–377.
Huston, M.A., Wolverton, S., 2011. Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. Ecol. Monogr. 81, 349–405.
Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., Grime, J.P., Hodgson, J., Lauenroth, W.K., Thompson, K., Vandermeer, J.H., Wardle, D.A., 2000. No consistent effect of plant diversity on productivity. Science 289, 1255a.
Hutchinson, G., 1978. An Introduction to Population Ecology. Yale University Press, New Haven, CT.
Isaac, N.J.B., Carbone, C., 2010. Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. Ecol. Lett. 13, 728–735.
Ives, A.R., Carpenter, S.R., Dennis, B., 1999. Community interaction webs and zooplankton responses to planktivory manipulations. Ecology 80, 1405–1421.
Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., et al., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.
Jacob, U., Thierry, A., Brose, U., Arntz, W.E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O., Riede, J.O., et al., 2011. The role of body size in complex food webs: a cold case. Adv. Ecol. Res. 45, 181–223.
Jenkins, D.G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., Lyon, B.N., Metzger, O.G.A., Olandese, M.L., Pepe, D., Silvers, G.A., et al., 2007. Does size matter for dispersal distance? Glob. Ecol. Biogeogr. 16, 415–425.
Jennings, S., 2005. Size-based analyses of aquatic food webs. In: Belgrano, A., Scharler, U., Dunne, J., Ulanowicz, R.E. (Eds.), Aquatic Food Webs: An Ecosystem Approach. Oxford University Press, Oxford, pp. 86–97.
Jennings, S., Blanchard, J., 2004. Fish abundance with no fishing: predictions based on macroecological theory. J. Anim. Ecol. 73, 632–642.
Jennings, S., Mackinson, S., 2003. Abundance–body mass relationships in size-structured food webs. Ecol. Lett. 6, 971–974.
Jennings, S., Greenstreet, S.P.R., Reynolds, J.D., 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. J. Anim. Ecol. 68, 617–627.
Jeschke, J.M., Kopp, M., Tollrian, R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol. Rev. 79, 337–349.
Johnson, N.C., 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. New Phytol. 185, 631–647.
Jonsson, T., Cohen, J.E., Carpenter, S.R., 2005. Food webs, body size and species abundance in ecological community description. Adv. Ecol. Res. 36, 1–84.
Jørgensen, C.B., 1966. Biology of Suspension Feeding. Pergamon Press, Oxford.
Kaspari, M., 2001. Taxonomic level, trophic biology and the regulation of local abundance. Glob. Ecol. Biogeogr. 10, 229–244.
Kaspari, M., 2004. Using the metabolic theory of ecology to predict global patterns of abundance. Ecology 85, 1800–1802.
Kaspari, M., 2005. Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. Proc. Natl. Acad. Sci. U.S.A. 102, 5079–5083.

Kaspari, M., Weiser, M.D., 2012. Energy, taxonomic aggregation, and the geography of ant abundance. Ecography 35, 65–72.
Kaspari, M., Pickering, J., Longino, J.T., Windsor, D., 2001. The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. Behav. Ecol. Sociobiol. 50, 382–390.
Kaspari, M., Yuan, M., Alonso, L., 2003. Spatial grain and the causes of regional diversity gradients in ants. Am. Nat. 161, 459–477.
Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., et al., 2011. TRY—a global database of plant traits. Glob. Change Biol. 17, 2905–2935.
Kerkhoff, A.J., Enquist, B.J., 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. Bioscience 57, 489–499.
Kerkhoff, A.J., Enquist, B.J., Elser, J.J., Fagan, W.F., 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. Glob. Ecol. Biogeogr. 14, 585–598.
Killen, S.S., Atkinson, D., Glazier, D.S., 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecol. Lett. 13, 184–193.
Klironomos, J.N., McCune, J., Hart, M., Neville, J., 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. Ecol. Lett. 3, 137–141.
Krivtsov, V., Griffiths, B., Liddell, K., Garside, A., Salmond, R., Bezginova, T., Thompson, J., 2011. Soil nitrogen availability is reflected in the bacterial pathway. Pedosphere 21, 26–30.
Lack, D., 1954. The Natural Regulation of Animal Numbers. Clarendon, Oxford.
Ladygina, N., Hedlund, K., 2010. Plant species influence microbial diversity and carbon allocation in the rhizosphere. Soil Biol. Biochem. 42, 162–168.
Larrañaga, A., Layer, K., Basaguren, A., Pozo, J., Woodward, G., 2010. Consumer body composition and community structure in a stream is altered by pH. Freshw. Biol. 55, 670–680.
Lauridsen, R.B., Edwards, F.K., Bowes, M.J., Woodward, G., Hildrew, A.G., Ibbotson, A.T., Jones, J.I., 2012. Consumer-resource elemental imbalances in a nutrient rich stream. Freshw. Sci. 31, 408–422.
Lavorel, S., Garnier, E., 2002. Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.
Lavorel, S., McIntyreb, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol. 12, 474–478.
Lavorel, S., Harrington, R., Storkey, J., Díaz, S., De Bello, F., Bardgett, R.D., Dolédec, S., Feld, C., Roux, X.L., Berg, M.P., Cornelissen, J.H., Hance, T., et al., 2009. RUBICODE—how trait linkages within and across trophic levels underlie the vulnerability of ecosystem services. FP6, Thematic Area: Global Change and Ecosystems. European Commission, DG Research, Bruxelles.
Layer, K., Riede, J.O., Hildrew, A.G., Woodward, G., 2010. Food web structure and stability in 20 streams across a wide pH gradient. Adv. Ecol. Res. 42, 265–299.
Layer, K., Hildrew, A.G., Jenkins, G.B., Riede, J., Rossiter, S.J., Townsend, C.R., Woodward, G., 2011. Long-term dynamics of a well-characterised food web: four decades of acidification and recovery in the Broadstone Stream model system. Adv. Ecol. Res. 44, 69–117.
Leaper, R., Raffaelli, D., 1999. Defining the abundance body-size constraint space: data from a real food web. Ecol. Lett. 2, 191–199.
Ledger, M.E., Harris, R.M.L., Armitage, P.D., Milner, A.M., 2012. Climate change impacts on community resilience: evidence from a drought disturbance experiment. Adv. Ecol. Res. 46, 211–258.

Lepš, J., 2001. Species-pool hypothesis: limits to its testing. Folia Geobot. 36, 45–52.
Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.
Lipton, D.S., Blanchar, R.W., Blevins, D.G., 1987. Citrate, malate, and succinate concentration in exudates from P-sufficient and P-stressed *Medicago sativa* L. seedlings. Plant Physiol. 85, 315–317.
Loreau, M., 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Philos. Trans. R. Soc. Lond. B 365, 49–60.
Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.
Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. Am. Nat. 156, 201–219.
Lynch, J.P., Ho, M.D., 2005. Rhizoeconomics: carbon costs of phosphorus acquisition. Plant Soil 269, 45–56.
Lynch, J.M., Whipps, J.M., 1990. Substrate flow in the rhizosphere. Plant Soil 129, 1–10.
Lyons, J., 1989. Correspondence between the distribution of fish assemblages in Wisconsin streams and Omernik ecoregions. Am. Midl. Nat. 122, 163–182.
Lyons, K.G., Schwartz, M.W., 2001. Rare species loss alters ecosystem function–invasion resistance. Ecol. Lett. 4, 358–365.
MacArthur, R., 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36, 533–536.
Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., et al., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335, 214–218.
Makarieva, A.M., Gorshkov, V.G., Li, B.L., Chown, S.L., Reich, P.B., Gavrilov, V.M., 2008. Mean mass-specific metabolic rates are strikingly similar across life's major domains: evidence for life's metabolic optimum. Proc. Natl. Acad. Sci. U.S.A. 105, 16994–16999.
Makino, W., Cotner, J.B., Sterner, R.W., Elser, J.J., 2003. Are bacteria more like plants or animals? Growth rate and resource dependence of bacterial C:N:P stoichiometry. Funct. Ecol. 17, 121–130.
Mann, C.C., 1991. Extinction: are ecologists crying wolf? Science 253, 736–738.
Marquet, P.A., Labra, F.A., Maurer, B.A., 2004. Metabolic ecology: linking individuals to ecosystems. Ecology 85, 1794–1796.
Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M., Rivadeneira, M., 2005. Scaling and power-laws in ecological systems. J. Exp. Biol. 208, 1749–1769.
Martinez, N.D., 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecol. Monogr. 61, 367–392.
Martinez, N.D., 1992. Constant connectance in community food webs. Am. Nat. 139, 1208–1218.
Martinez, N.D., 1993. Effects of scale on food web structure. Science 260, 242–243.
Martinson, H.M., Schneider, K., Gilbert, J., Hines, J.E., Hambäck, P.A., Fagan, W.F., 2008. Detritivory: stoichiometry of a neglected trophic level. Ecol. Res. 23, 487–491.
May, R.M., 1972. Will a large complex system be stable? Nature 238, 413–414.
McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.
Meehan, T.D., 2006. Energy use and animal abundance in litter and soil communities. Ecology 87, 1650–1658.

Menge, D.N.L., Field, C.B., 2007. Simulated global changes alter phosphorus demand in annual grassland. Glob. Change Biol. 13, 2582–2591.
Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well Being. Island Press. Encyclopedia of Earth. http://www.eoearth.org/article/Millennium_Ecosystem_Assessment_Synthesis_Reports (Retrieved 10 December 2010).
Mohr, C.D., 1940. Comparative populations of game, fur and other mammals. Am. Midl. Nat. 24, 581–584.
Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. Nature 442, 259–264.
Moore, J.C., Berlow, E.L., Coleman, D.C., De Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., et al., 2004. Detritus, trophic dynamics and biodiversity. Ecol. Lett. 7, 584–600.
Moorhead, D.L., Wall, D.H., Virginia, R.A., Parsons, A.N., 2002. Distribution and life-cycle of *Scottnema lindsayae* (Nematoda) in Antarctic soils: a modeling analysis of temperature responses. Polar Biol. 25, 118–125.
Mori, S., Yamaji, K., Ishida, A., Prokushkin, S.G., Masyagina, O.V., Hagihara, A., Hoque, A.T.M.R., Suwa, R., Osawa, A., Nishizono, T., Ueda, T., Kinjo, M., et al., 2010. Mixed-power scaling of whole-plant respiration from seedlings to giant trees. Proc. Natl. Acad. Sci. U.S.A. 107, 1447–1451.
Mulder, C., 2010. Soil fertility controls the size-specific distribution of eukaryotes. Ann. N.Y. Acad. Sci. 1195, E74–E81.
Mulder, C., Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Glob. Change Biol. 15, 2730–2738.
Mulder, C., Vonk, J.A., 2011. Nematode traits and environmental constraints in 200 soil systems: scaling within the 60–6,000 μm body size range. Ecology 92, 2004 [Ecological Archives E092-171].
Mulder, C., Van Wijnen, H.J., Van Wezel, A.P., 2005a. Numerical abundance and biodiversity of below-ground taxocenes along a pH gradient across the Netherlands. J. Biogeogr. 32, 1775–1790.
Mulder, C., Cohen, J.E., Setälä, H., Bloem, J., Breure, A.M., 2005b. Bacterial traits, organism mass, and numerical abundance in the detrital soil food web of Dutch agricultural grasslands. Ecol. Lett. 8, 80–90.
Mulder, C., Den Hollander, H.A., Hendriks, A.J., 2008. Aboveground herbivory shapes the biomass distribution and flux of soil invertebrates. PLoS One 3, e3573.
Mulder, C., Den Hollander, H.A., Vonk, J.A., Rossberg, A.G., Jagers op Akkerhuis, G.A.J.M., Yeates, G.W., 2009. Soil resource supply influences faunal size-specific distributions in natural food webs. Naturwissenschaften 96, 813–826.
Mulder, C., Helder, J., Vervoort, M.T.W., Vonk, J.A., 2011a. Gender matters more than intraspecific trait variation. Ecol. Evol. 1, 386–391.
Mulder, C., Boit, A., Bonkowski, M., De Ruiter, P.C., Mancinelli, G., Van der Heijden, M.G.A., Van Wijnen, H.J., Vonk, J.A., Rutgers, M., 2011b. A below-ground perspective on Dutch agroecosystems: how soil organisms interact to support ecosystem services. Adv. Ecol. Res. 44, 277–357.
Mulder, C., Vonk, J.A., Den Hollander, H.A., Hendriks, A.J., Breure, A.M., 2011c. How allometric scaling relates to soil abiotics. Oikos 120, 529–536.
Naeem, S., 2008. Advancing realism in biodiversity research. Trends Ecol. Evol. 23, 414–416.
Naeem, S., Chapin III, F.S., Costanza, R., Ehrlich, P., Golley, F., Hooper, D., Lawton, J.H., O'Neill, R., Mooney, H., Sala, O., Symstad, A., Tilman, D., 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. Issues Ecol. 4, 4–12.

Nakazawa, T., Ushio, M., Kondoh, M., 2011. Scale dependence of predator-prey mass ratio: determinants and applications. Adv. Ecol. Res. 45, 269–302.
O'Gorman, E.J., Emmerson, M.C., 2010. Manipulating interaction strengths and the consequences for trivariate patterns in a marine food web. Adv. Ecol. Res. 42, 301–419.
O'Gorman, E.J., Enright, R.A., Emmerson, M.C., 2008. Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. Oecologia 158, 557–567.
OHIO-EPA, 2008. Biological and Water Quality Survey of the Scioto Brush Creek Basin. State of Ohio Environmental Protection Agency, Division of Surface Water, Columbus, OH. OEPA Report DSW/EAS 2008-4-6.
Olesen, J.M., Dupont, Y.L., O'Gorman, E., Ings, T.C., Layer, K., Melian, C.J., Troejelsgaard, K., Pichler, D.E., Rasmussen, C., Woodward, G., 2010. From Broadstone to Zackenberg: space, time and hierarchies in ecological networks. Adv. Ecol. Res. 42, 1–71.
Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., et al., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996.
Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S.G., Reiss, J., Woodward, G., 2010. Environmental warming and biodiversity-ecosystem functioning in freshwater microcosms: partitioning the effects of species identity, richness and metabolism. Adv. Ecol. Res. 43, 177–209.
Perner, J., Voigt, W., 2007. Measuring the complexity of interaction webs using vertical links between functional groups. Agric. Ecosyst. Environ. 120, 192–200.
Perrings, C., Folke, C., Mäler, K.-G., 1992. The ecology and economics of biodiversity loss: the research agenda. Ambio 21, 201–211.
Perrings, C., Naeem, S., Ahrestani, F.S., Bunker, D.E., Burkill, P., Canziani, G., Elmqvist, T., Fuhrman, J.A., Jaksic, F.M., Kawabata, Z., Kinzig, A., Mace, G.M., et al., 2011. Ecosystem services, targets, and indicators for the conservation and sustainable use of biodiversity. Front. Ecol. Environ. 9, 512–520.
Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge, UK.
Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416, 84–86.
Pimm, S.L., 1980. Food web design and the effect of species deletion. Oikos 35, 139–149.
Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food web patterns and their consequences. Nature 350, 669–674.
Polis, G.A., 1998. Stability is woven by complex webs. Nature 395, 744–745.
Polis, G.A., 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86, 3–15.
Pope, J.G., Shepherd, J.G., Webb, J., 1994. Successful surf-riding on size spectra: the secret of survival in the sea. Philos. Trans. R. Soc. Lond. B 343, 41–49.
Pope, J.G., Rice, J.C., Daan, N., Jennings, S., Gislason, H., 2006. Modelling an exploited marine fish community with 15 parameters: results from a simple size-based model. ICES J. Mar. Sci. 63, 1029–1044.
Posthuma, L., De Zwart, D., 2006. Predicted effects of toxicant mixtures are confirmed by changes in fish species assemblages in Ohio, USA, rivers. Environ. Toxicol. Chem. 25, 1094–1105.
Prothero, J., 1986. Scaling of energy metabolism in unicellular organisms: a re-analysis. Comp. Biochem. Physiol. 83A, 243–248.
Ptacnik, R., Moorthi, S.D., Hillebrand, H., 2010. Hutchinson reversed, or why there need to be so many species. Adv. Ecol. Res. 43, 1–43.

Purdy, K.J., Hurd, P.J., Moya-Larano, J., Trimmer, M., Woodward, G., 2010. Systems biology for ecology: from molecules to ecosystems. Adv. Ecol. Res. 43, 87–149.
Quince, C., Higgs, P.G., McKane, A.J., 2005. Deleting species from model food webs. Oikos 110, 283–296.
Raunkiaer, C., 1934. The Life Forms of Plants and Statistical Plant Geography. Oxford University Press, Oxford.
Redfield, A.C., 1958. The biological control of chemical factors in the environment. Am. Sci. 46, 205–221.
Reich, P.B., 2000. Do tall trees scale physiological heights? Trends Ecol. Evol. 15, 41–42.
Reich, P.B., Tjoelker, M.G., Machado, J.-L., Oleksyn, J., 2006. Universal scaling of respiratory metabolism, size and nitrogen in plants. Nature 439, 457–461.
Reich, P.B., Oleksyn, J., Wright, I.J., Niklas, K.J., Hedin, L., Elser, J.J., 2010. Evidence of a general 2/3-power law of scaling leaf nitrogen to phosphorus among major plant groups and biomes. Proc. R. Soc. Lond. B 277, 877–883.
Reiss, J., Bridle, J., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24, 505–514.
Reiss, J., Bailey, R.A., Cássio, F., Woodward, G., Pascoal, C., 2010. Assessing the contribution of micro-organisms and macrofauna to biodiversity-ecosystem functioning relationships in freshwater microcosms. Adv. Ecol. Res. 43, 150–176.
Reiss, J., Bailey, R.A., Perkins, D.M., Pluchinotta, A., Woodward, G., 2011. Testing effects of consumer richness, evenness and body size on ecosystem functioning. J. Anim. Ecol. 80, 1145–1154.
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.
Reuman, D.C., Mulder, C., Banašek-Richter, C., Cattin Blandenier, M.-F., Breure, A.M., Den Hollander, H., Kneitel, J.M., Raffaelli, D., Woodward, G., Cohen, J.E., 2009. Allometry of body size and abundance in 166 food webs. Adv. Ecol. Res. 41, 1–44.
Richardson, A.E., Barea, J.M., McNeill, A.M., Prigent-Combaret, C., 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321, 305–339.
Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J., Martinez, N.D., 2009. Predicting invasion success in complex ecological networks. Philos. Trans. R. Soc. Lond. B 364, 1743–1754.
Roscher, C., Thein, S., Schmid, B., Scherer-Lorenzen, M., 2008. Complementary nitrogen use among potentially dominant species in a biodiversity experiment varies between two years. J. Ecol. 96, 477–488.
Rossberg, A.G., Ishii, R., Amemiya, T., Itoh, K., 2008. The top-down mechanism for body-mass-abundance scaling. Ecology 89, 567–580.
Rossberg, A.G., Farnsworth, K.D., Satoh, K., Pinnegar, J.K., 2011. Universal power-law diet partitioning by marine fish and squid with surprising stability—diversity implications. Proc. R. Soc. Lond. B 278, 1617–1625.
Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., et al., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.
Samanta, A., Ganguly, S., Hashimoto, H., Devadiga, S., Vermote, E., Knyazikhin, Y., Nemami, R.R., Myneni, R.B., 2010. Amazon forests did not green-up during the 2005 drought. Geophys. Res. Lett. 37, L05401.
Santos, P.F., Phillips, J., Whitford, W.G., 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62, 664–669.

Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J., Brown, J.H., 2004. The predominance of quarter-power scaling in biology. Funct. Ecol. 18, 257–282.

Schmid, B., Balvanera, P., Cardinale, B.J., Godbold, J., Pfisterer, A.B., Raffaelli, D., Solan, M., Srivastava, D.S., 2009. Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective. Oxford University Press, Oxford, pp. 14–29.

Schneider, K., Kay, A.D., Fagan, W.F., 2010. Adaptation to a limiting environment: the phosphorus content of terrestrial cave arthropods. Ecol. Res. 25, 565–577.

Schneider, F.D., Scheu, S., Brose, U., 2012. Body mass constraints on feeding rates determine the consequences of predator loss. Ecol. Lett. 15, 436–443.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J. Mar. Sci. 62, 384–396.

Short, F.T., Duarte, C.M., 2001. Methods for the measurement of seagrass growth and production. In: Short, F.T., Coles, R.G. (Eds.), Global Seagrass Research Methods. Elsevier, Amsterdam, pp. 155–182.

Simon, T.P. (Ed.), 1999. Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press, Boca Raton, FL.

Solé, R.V., Montoya, J.M., 2006. Ecological network meltdown from habitat loss and fragmentation. In: Pascual, M., Dunne, J.A. (Eds.), Ecological Networks: Linking Structure to Dynamics in Food Webs. Oxford University Press, New York, pp. 305–323.

Solé, R.V., Manrubia, S.C., Benton, M., Kauffman, S., Bak, P., 1999. Criticality and scaling in evolutionary ecology. Trends Ecol. Evol. 14, 156–160.

Srinivasan, U.T., Dunne, J.A., Harte, J., Martinez, N.D., 2007. Response of complex food webs to realistic extinction sequences. Ecology 88, 671–682.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am. Nat. 152, 510–529.

Stachowicz, J.J., Best, R.J., Bracken, M.E., Graham, M.H., 2008. Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. Proc. Natl. Acad. Sci. U.S.A. 105, 18842–18847.

Standen, V., 1980. Factors affecting the distribution of Enchytraeidae (Oligochaeta) in associations at peat and mineral sites in northern England. Bull. Ecol. 11, 599–608.

Standen, V., 1982. Associations of Enchytraeidae (Oligochaeta) in experimentally fertilized grasslands. J. Anim. Ecol. 51, 501–522.

Sterner, R.W., 2004. A one-resource "stoichiometry"? Ecology 85, 1813–1816.

Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press, Princeton, NJ.

Sterner, R.W., George, N.B., 2000. Carbon, nitrogen and phosphorus stoichiometry of cyprinid fishes. Ecology 81, 127–140.

Storch, D., Marquet, P.A., Brown, J.H. (Eds.), 2007. Scaling Biodiversity. Cambridge University Press, Cambridge, UK.

Suding, K.N., Goldberg, D.E., Hartman, K.M., 2003. Relationship among species traits: separating levels of response and indentifying linkages to abundance. Ecology 84, 1–16.

Sultan, S.E., Spencer, H.G., 2002. Metapopulation structure favors plasticity over local adaptation. Am. Nat. 160, 271–283.

Thingstad, T.F., 2000. Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. Limnol. Oceanogr. 45, 1320–1328.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., Lawton, J.H., 2004a. Comparative losses of British butterflies, birds, and plants and the Global Extinction Crisis. Science 303, 1879–1881.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqiuera, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., et al., 2004b. Extinction risk from climate change. Nature 427, 145–148.

Thornley, J.H.M., 2011. Plant growth and respiration re-visited: maintenance respiration defined—it is an emergent property of, not a separate process within, the system—and why the respiration: photosynthesis ratio is conservative. Ann. Bot. 108, 1365–1380.

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ.

Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C., Lehman, C., 2004. Does metabolic theory apply to community ecology? It's a matter of scale. Ecology 85, 1797–1799.

Toepfer, C.S., Williams, L.R., Martinez, A.D., Fisher, W.L., 1998. Fish and habitat heterogeneity in four streams in the central Oklahoma/Texas Plains Ecoregion. Proc. Okla. Acad. Sci. 78, 41–48.

Tomas, F., Abbott, J.M., Steinberg, C., Balk, M., Williams, S.L., Stachowicz, J.J., 2011. Plant genotype and nitrogen loading influence seagrass productivity, biochemistry, and plant-herbivore interactions. Ecology 92, 1807–1817.

Treonis, A.M., Wall, D.H., Virginia, R.A., 1999. Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. Ecosystems 2, 482–492.

Treonis, A.M., Wall, D.H., Virginia, R.A., 2000. The use of anhydrobiosis by soil nematodes in the Antarctic Dry Valleys. Funct. Ecol. 14, 460–467.

Ulrich, W., Buszko, J., Czarnecki, A., 2005. The local interspecific abundance—body weight relationship of ground beetles: a counterexample to the common pattern. Pol. J. Ecol. 53, 585–589.

UNEP/CBD, 2004. Convention on Biological Diversity: Decisions Adopted by the Conference of the Parties to the Convention of Biological Diversity at Its Seventh Meeting. Kuala Lumpur, Malaysia. http://www.cbd.int/decisions/.

Valcu, M., Dale, J., Kempenaers, B., 2012. rangeMapper: a platform for the study of macroecology of life-history traits. Glob. Ecol. Biogeogr. 21, 945–951.

Voigt, W., Perner, J., Jones, T.H., 2007. Using functional groups to investigate community response to environmental changes: two grassland case studies. Glob. Change Biol. 13, 1710–1721.

Vonk, J.A., Stapel, J., 2008. Regeneration of nitrogen (^{15}N) from seagrass litter in tropical Indo-Pacific meadows. Mar. Ecol. Prog. Ser. 368, 165–175.

Vonk, J.A., Pijnappels, M.H.J., Stapel, J., 2008. *In situ* quantification of *Tripneustes gratilla* grazing and its effects on three co-occurring tropical seagrass species. Mar. Ecol. Prog. Ser. 360, 107–114.

Wagner, T., Bremigan, M.T., Cheruvelil, K.S., Soranno, P.A., Nate, N.A., Breck, J.E., 2007. A multilevel modeling approach to assessing regional and local landscape features for lake classification and assessment of fish growth rates. Environ. Monit. Assess. 130, 437–454.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30, 257–300.

Walker, G., Dorrell, R.G., Schlacht, A., Dacks, J.B., 2011. Eukaryotic systematics: a user's guide for cell biologists and parasitologists. Parasitology 138, 1638–1663.

Wall, D.H., 2007. Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. Philos. Trans. R. Soc. Lond. B 362, 2291–2306.
Wall, D.H., 2008. Biodiversity: extracting lessons from extreme soils. Soil Biol. 13, 71–84.
Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., Dangerfield, J.M., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z., et al., 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob. Change Biol. 14, 2661–2677.
Walter, H., 1964. Die Vegetation der Erde in Öko-physiologischer Betrachtung. Gustav Fischer Verlag, Jena.
Walters, C.J., Maguire, J.J., 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. 6, 125–137.
Wardle, D.A., 1999. How soil food webs make plants grow. Trends Ecol. Evol. 14, 418–420.
Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton, NJ.
Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecol. Lett. 9, 870–886.
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633.
Wardle, D.A., Hyodo, F., Bardgett, R.D., Yeates, G.W., Nilsson, M.-C., 2011. Long-term aboveground and belowground consequences of red wood ant exclusion in boreal forest. Ecology 92, 645–656.
Watkinson, A.R., Freckleton, R.P., 1997. Quantifying the impact of arbuscular mycorrhiza on plant competition. J. Ecol. 85, 541–546.
Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck Jr., K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., et al., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. U.S.A. 106, 12377–12381.
Weiser, M.D., Sanders, N.J., Agosti, D., Andersen, A.N., Ellison, A.M., Fisher, B.L., Gibb, H., Gotelli, N.J., Gove, A.D., Gross, K., Guénard, B., Janda, M., et al., 2011. Canopy and litter ant assemblages share similar climate–species density relationships. Biol. Lett. 6, 769–772.
Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425.
West, G.B., Brown, J.H., 2004. Life's universal scaling laws. Phys. Today 57, 36–43.
White, C.R., 2010. There is no single *p*. Nature 464, 691–692.
White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between body size and abundance in ecology. Trends Ecol. Evol. 22, 323–330.
White, C., Kendall, B.E., Gaines, S., Siegel, D.A., Costello, C., 2008. Marine reserve effects on fishery profit. Ecol. Lett. 11, 370–379.
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.
Winemiller, K.O., 1989. Must connectance decrease with species richness? Am. Nat. 134, 960–968.
Woodward, G., Hildrew, A.G., 2002. The impact of a sit-and-wait predator: separating consumption and prey emigration. Oikos 99, 409–418.
Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005a. Body size in ecological networks. Trends Ecol. Evol. 20, 402–409.
Woodward, G., Speirs, D.C., Hildrew, A.G., 2005b. Quantification and resolution of a complex, size-structured food web. Adv. Ecol. Res. 36, 85–135.

Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, J.I., Figueroa, D., Warren, P.H., Petchey, O.L., 2010a. Individual-based food webs: species identity, body size and sampling effects. Adv. Ecol. Res. 43, 211–266.

Woodward, G., Perkins, D.M., Brown, L.E., 2010b. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philos. Trans. R. Soc. Lond. B 365, 2093–2106.

Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Elosegi, A., et al., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. Science 336, 1438–1440.

Wu, T., Ayres, E., Bardgett, R.D., Wall, D.H., Garey, J.R., 2011. Molecular study of world-wide distribution and diversity of soil animals. Proc. Natl. Acad. Sci. U.S.A. 108, 17720–17725.

Xu, L., Samanta, A., Costa, M.H., Ganguly, S., Nemani, R.R., Myneni, R.B., 2011. Wide-spread decline in greenness of Amazonian vegetation due to the 2010 drought. Geophys. Res. Lett. 38, L07402.

Yee, D.A., Juliano, S.A., 2007. Abundance matters: a field experiment testing the More Individuals Hypothesis for richness–productivity relationships. Oecologia 153, 153–162.

Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. Am. Nat. 139, 1151–1175.

Yoneyama, K., Xie, X., Kusumoto, D., Sekimoto, H., Sugimoto, Y., Takeuchi, Y., 2007. Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. Planta 227, 125–132.

Yoon, I., Williams, R.J., Levine, E., Yoon, S., Dunne, J.A., Martinez, N.D., 2004. Webs on the Web (WOW): 3D visualization of ecological networks on the WWW for collaborative research and education. SPIE 5295, 124–132.

Yvon-Durocher, G., Allen, A.P., Montoya, J.M., Trimmer, M., Woodward, G., 2010. The temperature dependence of the carbon cycle in aquatic systems. Adv. Ecol. Res. 43, 267–313.

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

Yvon-Durocher, G., Reiss, J., Blanchard, J., Ebenman, B., Perkins, D.M., Reuman, D.C., Thierry, A., Woodward, G., Petchey, O.L., 2011b. Across ecosystem comparisons of size structure: methods, approaches, and prospects. Oikos 120, 550–563.

Yvon-Durocher, G., Caffrey, J.M., Cescatti, A., Dossena, M., Del Giorgio, P., Gasol, J.M., Montoya, J.M., Pumpanen, J., Staehr, P.A., Trimmer, M., Woodward, G., Allen, A.P., 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature 487, 472–476.

Zobel, M., 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends Ecol. Evol. 12, 266–269.