

Towards a size-structured biodiversity science

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Abstract

We compare traditional biodiversity approaches treating species as trait-free, taxonomic units with novel allometric and size-spectrum concepts including body mass as a primary trait at the
45 levels of populations and individuals, respectively. While traditional biodiversity research is necessarily characterizing species' extinctions and associated biodiversity decreases as random, the size-structured approaches (allometric or size-spectrum) address the consequences of the higher extinction probability of large species. Assuming that biodiversity changes are caused by species
50 extinctions, we re-assess three classic debates on the relationships between biodiversity and complexity, stability and ecosystem functioning. Contrasting current expectations, size-structured approaches suggest that species loss may lead to future food-webs that are less interwoven and more structured by chains of interactions and compartments. The disruption of natural body-mass distributions maintaining food-web stability may trigger avalanches of secondary extinctions and strong trophic cascades with expected knock-on effects on the functionality of the ecosystems.
55 Overall, size-structured approaches thus suggest that the consequences of species loss for ecological communities may be much more severe than anticipated. The ecological advances by size-structured approaches provide an integrative ecological concept that enables a better understanding of each species' unique role across communities and the causes and consequences of biodiversity loss.

60 **Introduction**

The world's ecosystems are currently exposed to species extinctions at a rate higher than ever before (Barnosky *et al.* 2011) leading to projected strong decreases in their biodiversity (Pereira *et al.* 2010). This biodiversity crisis has motivated intensive debates about how biodiversity losses will affect natural species communities concerning their food-web structure (*biocomplexity*), stability
65 (*biostability*), functioning (*biofunctioning*) and the subsequent provisioning of ecosystem services. Over decades understanding generalities in the structuring principles of natural species communities has been hampered by a dichotomy between biodiversity sciences treating species as numbers and natural history approaches assigning each species its unique combination of characteristic traits that is coded by the taxonomic latin binomials. Taxonomic characterizations of species have formed the
70 core of biodiversity sciences ever since and numerous approaches emphasizing differences in species richness across ecosystems have been deployed. This research unraveled natural constraints and anthropogenic effects on biodiversity, but the uniqueness of every species and every interaction between pairs of species often hindered generalizations across ecosystems and mechanistic understanding of the consequences of biodiversity loss (“the curse of the Latin binomial” -
75 Raffaelli 2007). Moreover, the lack of a generalized trait-based concept has led to theoretical approaches that are based on neutral, random-trait species, which often hampered direct connections to empirical data. Hence, biodiversity research is suffering from a chronic lack of generalized empirical approaches and non-neutral theories linking patterns across phylogenetic groups and ecosystem types by accounting for species functional traits.

80 One of the key questions in biodiversity research is thus how to include general species traits. Species are characterized by the specific set of traits that they possess, and these traits determine their biological rates of metabolism, feeding and biomass production that drive ecosystem

functions. Biodiversity decreases thus cause loss of specific traits from communities which translates into changes in their structure, stability and functioning (Cardinale *et al.* 2012). Facing the enormous complexity of possible different trait combinations and their various and interactive effects on ecological communities, biologists have been debating the positive, negative or neutral effects of biodiversity loss on community stability and ecosystem functioning controversially (Curtisdotter *et al.* 2011; Schneider *et al.* 2012; Harvey *et al.* 2013). Traditional approaches grouped individuals by taxon names according to their species identity (Fig. 1a), which reduces quantitative variation in traits across species to species identity categories as characterized by the Latin binomials. This leads to interaction networks (networks connecting species by their interaction such as feeding) with random, undefined or uniform trait distributions (Fig. 1b). Traditional biodiversity research thus addresses relationships between species diversity and community characteristics (e.g., ecosystem functions) by averaging across species without accounting for their traits. To give an example, the functional consequences of losing five species from a community of 40 species is described as the difference in functionality between communities of 35 and 40 species when averaging across all combinations of five species that could potentially be lost. However, many species' biological rates can be predicted by allometric scaling relationships that use body size as a super-trait (Brown *et al.* 2004). This provides an opportunity for developing allometric biodiversity concepts that are based on two foundations: the taxonomic identity of species and their average body masses (Fig. 1c). As the functional role (and other traits) depends on body masses (Fig. 1c) this yields interaction networks with species that are ordered according to their body size (Fig. 1d). These allometric biodiversity concepts assume the consequences of species loss or gain differ depending on species characteristics that can be predicted by the average body size of these species. A third category of concepts, that is progressing further in this direction, is represented by size-spectrum approaches lumping individuals in size classes independent of their taxonomic identity,

which increases the resolution of size distributions across individuals (Fig. 1e, grey dots). They also account for within-species differences in body size, as for instance caused by ontogenetic growth from juvenile to adult life stages, but they mostly ignore trait differences between species of varying taxonomy that are not described by body size (Blanchard *et al.* 2009, 2012). Novel approaches, however, have started to include taxonomic information and trait variance within size classes in size-spectra (e.g., Hartvig *et al.* 2011- Fig. 1e, colored dots). The functional roles of individuals depend on body mass (ordered in size classes) and the taxonomic identity (Fig. 1e) yielding interaction networks in which species occur several times according to their size classes that occupy different functional roles (Fig. 1f). Despite this re-thinking across biological disciplines biodiversity science is still lacking a general integration of these trait-based approaches.

In this review, we provide a brief overview of allometric and size-spectrum approaches and how body size correlates with vulnerability to extinction. Subsequently, we review the three major debates addressing the consequences of biodiversity loss for the structure (*biocomplexity*), stability (*biostability*) and functioning (*biofunctioning*) of natural communities. We add a novel aspect to these debates by integrating each of these sections across the so far separated disciplines of traditional (species identities), allometric (species identities and average body size) and size-spectrum (distribution of individuals across size classes) concepts. It has been argued that enhanced collaboration and cross-fertilization between these different schools and concepts that have been traditionally isolated due to departmental borders should present an auspicious way for community ecology and biodiversity research (Raffaelli 2007; Webb 2012). Effectively, adhering to these earlier recommendations has resulted in recent advances in our understanding of community patterns and biodiversity ecosystem-function relationships. Synthesizing these concepts illustrates the potential for integrating functional ecology with biodiversity studies and highlights novel

130 research agendas at their intersections.

Body size and species' traits: the allometric approach

Three decades ago, Peters (1983) documented how various physiological and ecological parameters scale allometrically with body size. Many of these patterns are driven by the allometric scaling of metabolism as the energy processing rate of organisms (Brown *et al.* 2004). Despite
135 intensive debates on the exact scaling exponents and how they vary across phylogenetic groups (Ehnes *et al.* 2011), there is a general agreement that metabolic rates constrain the allometric scaling of other physiological processes such as individual growth, mortality and biomass production and the resulting population characteristics such as abundance, age of sexual maturity, reproductive rate and life span (Peters 1983; Brown *et al.* 2004). Hence, many of the individual
140 species traits are closely correlated with body sizes. To balance the metabolic energy requirements, the overall feeding rates (across all interactions) of many organisms also follow similar allometric scaling relationships (e.g., Brose *et al.* 2008; Rall *et al.* 2012) and consequently, the feeding links (who consumes whom) in natural food webs (Petchey *et al.* 2008; Eklöf *et al.* 2013) and strengths of pair-wise interactions among species (how much is consumed through specific interactions) also
145 depend on their body sizes (Brose *et al.* 2008; Kalinkat *et al.* 2013). Together, these allometries cause systematic relationships between population abundances (i.e., the number of individuals) or biomasses with population-averaged body sizes (Reuman *et al.* 2008; Ehnes *et al.* 2014) explaining the general pattern that populations of large-bodied species have fewer individuals than small-bodied species.

150 Overall, these studies have illustrated that the majority of traits at the levels of individual organisms, interactions and populations scale closely with species' body sizes (see Fig. 1c, where

“functional role” represents species traits). The allometric approach uses this scaling of functional traits with body masses (Fig. 1c) to predict the network structure of food webs (who feeds on whom) and species' energy processing rates as well interaction strengths between species (Fig. 1d).
155 We will describe below how this provides critically important predictions of how species loss translates into modified community structures and functions depending on the size of the species lost.

Individual body size, traits, and life-history: the size-spectrum approach

The size-spectrum approach that is mainly employed in marine ecology has been based on the
160 notion that body size is an individual property, and not a property of a species. Consequently, species grow across several size classes from offspring to adult size (indicated in Fig. 1e by color coded species occurring in several size classes). Species with large adult to offspring size ratio may experience ontogenetic niche shifts and life-history omnivory, with transitions between markedly different functional and trophic roles (e.g., Rudolf & Rasmussen 2013). For these organisms it may
165 be inappropriate to ascribe a characteristic body size for the species as it is the individual size that determines characteristics such as the metabolic rate and predator-prey relationships. Hence, size-spectra are used at two levels of organization: (1) the community-level, where all individuals irrespective of species identity in a community are pooled into a single community size-spectrum (e.g., Reuman *et al.* 2008; Yvon-Durocher *et al.* 2011a), and (2) the species level, where the size-
170 spectrum shows the body mass distribution within a species (e.g., Hartvig *et al.* 2011).

The simplistic community size-spectrum approach may be seen as a short-cut for studying community-level properties and patterns as they include only individual-level body size while disregarding both explicit food web structure and differences across species. Both, empirical and

theoretical studies, have shown the pattern of how marine biomass is distributed equally when body
175 masses are pooled in logarithmically evenly sized bins (Andersen & Beyer 2006). Both species-
resolved size-spectra models and allometric food web models naturally yield equivalent results
when analysed at the community-level (Hartvig *et al.* 2011). This shows that communities organise
to preserve certain community-level properties independently of the explicit food web structure and
species composition.

180 The species-resolved size-spectrum approach accounts for ontogenetic niche shifts such as
changes in niche breadth or trophic position during the life of individuals. These are important in
shaping trophic relationships when the difference between offspring and adult size is large (Hartvig
& Andersen 2013; Rudolf & Rasmussen 2013). In these cases, modeling of the within species size-
spectrum is important, which has been addressed with physiologically structured population models
185 (de Roos & Persson 2013). While being mathematically more challenging, this approach is
ecologically more simple and reasonable as the life-history from birth, through maturation, and
ultimately death is modeled explicitly instead of assuming instantaneous population increase upon
food intake as in traditional food web models. To study large dynamic food webs of size-structured
species populations a trait-based approach has been employed to characterize species (Hartvig *et al.*
190 2011). In these systems, topology is more complex as the connection between species depends on
both the traditional taxonomic interaction matrix and the body-sizes or life-stages of the interacting
individuals (Fig 1f).

Overall size-spectrum approaches thus address patterns at different levels of ecological
organization including (1) the simplistic community size-spectrum approach where species identity
195 is ignored, and (2) the ecologically detailed food web approach with size-structured species
populations. The first approach is surprisingly capable of describing many community-level

patterns in spite of the fact that it completely disregards natural-history knowledge. The latter approach bridges individual-level properties and processes with natural history knowledge through a trait-based description to achieve descriptions of population- and community-level dynamics.

200 Throughout this review, we will separate the predictions of community and species-level size spectrum approaches (in Fig. 2-4, however, we focus on species-level size spectra).

Body size and vulnerability to extinction

Species loss is a highly non-random process where the vulnerability to extinction depends on the interaction between the biology and environment of the species (Cardillo *et al.* 2005). Species

205 extinctions often stem from anthropogenic activities, such as overharvesting, destruction of habitats and pollution (Purvis *et al.* 2000) and species abilities to cope with these threats are in turn dictated by their biological traits. Certain key traits are likely to influence extinction vulnerability: in particular large body size, high trophic level and low density all increase the probability of extinction (Purvis *et al.* 2000; Cardillo *et al.* 2005; Olden *et al.* 2007; Binzer *et al.* 2011). Moreover,

210 species with a large body size are positioned at high trophic levels and therefore they are more prone to go secondarily extinct (i.e., extinct following an initial loss of another species) due to the dependencies on species at lower levels (Dunne *et al.* 2002; Eklöf & Ebenman 2006; Curtsdotter *et al.* 2011). For instance, a global study of about 4000 mammal species showed there was a clear increase in the effect of extinction risk-promoting factors for species with a body mass over a

215 certain threshold: while small bodied species were only affected by environmental factors, large bodied species were also strongly affected by intrinsic factors (Cardillo *et al.* 2005). Similarly, in fish communities a clear relationship between the size and vulnerability to extinction has been shown (Olden *et al.* 2007). Interestingly, this particular study showed there is a variation in the effect depending on if the focus is on marine or freshwater communities: in marine communities

220 large species are at a higher risk of facing extinctions whereas in fresh water communities smaller
species are more vulnerable (Olden *et al.* 2007). This highlights that there is a combination of body
size and environmental parameters influencing extinction risk.

Overall, these recent findings illustrate that biodiversity loss should be a non-random process
during which the extinction likelihood increases with body size. Large body size is also a well-
225 known predictor of past extinctions, with size-dependent extinctions causing far-reaching ecological
consequences in prehistoric time. There are examples from the Pleistocene in both Australia and
North America where the loss of megafauna (large vertebrates) caused a complete replacement of
one vegetation type with another due to the decline in herbivory (Rule *et al.* 2012). Similarly, the
current extinction wave may cause a deconstruction of natural communities removing species from
230 the largest to the smallest species. We will subsequently review and explore the consequences of
this non-random biodiversity loss under the assumption that extinction risk is inversely correlated to
body size.

Biocomplexity

Diversity-complexity relationships

235 There is quite obviously much more to living communities than the dictum "eat or be eaten", but
in order to understand ecological systems, this simple point of view provides a mechanistic
backbone. In this vein, the structural complexity of ecological communities is often described
mainly by two parameters: the number of species and the number of trophic (i.e., feeding)
interactions. Here, we refer to the number of species as biodiversity, and to the number of feeding
240 interactions as biocomplexity of the community. The key role of trophic interactions as one of the
most central organizing concepts in community ecology explains the continuous interest in

topological community descriptions among ecologists. Pioneering food-web studies described how trophic links among species compose complex networks (Cohen 1978). Since then, many network variables have been proposed based on the number of nodes and the number of links between them
245 to allow for ecologically meaningful comparisons between different food webs across a variety of systems (Cohen 1978; Martinez 1991; Thompson *et al.* 2012). While classic studies assumed that linkage density (i.e. the number of links per species; Cohen & Briand 1984) or connectance (i.e. the proportion of possible links realized; Martinez 1992) should be constant, recent comparisons, using more detailed data on food webs, suggested that both complexity parameters vary with diversity
250 (Schmid-Araya *et al.* 2002). In these across ecosystem comparisons, decreasing diversity is associated with reductions in linkage density and subsequent increases in connectance. In consequence, this suggests that species loss (illustrated by the randomly chosen red node in Fig. 2a) is associated with the loss of links (red links in Fig. 2a), and the remaining species (white nodes in Fig. 2a) should on average have fewer links to other species, whereas the food web has a higher
255 connectance (Fig. 2a). However, these studies compare empirical food webs of different species richness, and their predictions are based on averages across all species and do not account for unequal extinction probabilities. Hence, these predictions are unlikely to hold for the deconstruction of biocomplexity following real species losses.

Allometric concepts of biocomplexity

260 Trophic interactions are to a large extent dictated by species traits. Pioneering studies documented the explicit importance of species body masses for the formation of predator-prey interactions across ecosystems (Cohen *et al.* 1993). These patterns were later generalized across ecosystems and different species groups to show that (1) predator and prey masses are systematically correlated (Brose *et al.* 2006a; Barnes *et al.* 2010; Riede *et al.* 2011b), (2) predator body masses increase with

265 trophic level, and (3) the ratio between predator and prey body masses decreases with trophic level
(Riede *et al.* 2011b). Together, these findings suggest that consumers become progressively larger
from the base to the top of food webs but more similarly sized to their prey (Fig. 2b). The loss of
large top predators thus decreases the average body masses, but surprisingly it should also increase
the average predator-prey body-mass ratios. Despite aggregating knowledge how the community
270 body-size structure determines food-web stability (Brose *et al.* 2006b; Brose 2008; Heckmann *et al.*
2012), the structural and dynamic consequences of these combined changes in allometric patterns
have not been addressed yet.

Moreover, the number of interactions a species possesses tends to vary with body size. The linkage
density of a species can be described using different measurements: generality describes the number
275 of prey species, vulnerability describes the number of consumer species, and degree (linkedness)
describes the sum of all ingoing and outgoing links. Allometric degree distributions describe how
these measurements of linkage density (generality, vulnerability and degree) scale with species
body mass, irrespective of taxonomy or other traits (Otto *et al.* 2007). Several generalities have
been revealed from analyses of a large number of empirical food webs, such as increasing
280 generality and decreasing vulnerability with the average body mass of a species (Otto *et al.* 2007;
Digel *et al.* 2011; Thierry *et al.* 2011b). This implies that natural food webs possess a specific
architecture: large top predators have a wide prey spectrum and small basal species have a wide
consumer spectrum. Despite some exceptions, this body-mass signature seems to be consistent
across both different ecosystem types and organism groups (Riede *et al.* 2011b). These empirical
285 patterns across communities thus suggest that the loss of the largest species with the highest linkage
density (red node in Fig. 2b) should result in a decrease of food-web complexity (red links in Fig.
2b). Additionally, these large top predators usually distribute their trophic links across prey of

different trophic levels (Fig. 2b, red links) thus creating a web-like network structure with short pathways between different populations. In consequence of their loss, future food-webs may thus be
290 less interwoven, more structured by chains of interactions and compartments and generally have lower trophic levels (Fig. 2b).

Not only the number but also the identities of feeding interactions are strongly dependent on species body masses (Eklöf *et al.* 2013). Understanding the role of body mass distributions in defining species interactions can therefore give us valuable insights into the organization of ecological
295 networks (Stouffer *et al.* 2011). A community wide structural measurement that has gained a lot of interest in food web research is intervality. If a food web exhibits intervality all species can be ordered in such a way that all consumers prey on a consecutive range of prey species. This characteristic has been employed as a central rule in commonly used models for food web structure (Cohen & Briand 1984; Williams & Martinez 2000). While subsequent models dropped this
300 assumption (Allesina *et al.* 2008), empirical analyses showed that natural food webs are close to (but not fully) interval (Stouffer *et al.* 2006) and identified body size as an important factor underlying this intervality (Cohen *et al.* 2003; Stouffer *et al.* 2011; Zook *et al.* 2011). Laboratory experiments documented that predators feed within size ranges of potential prey that are limited by decreasing success rates towards smaller prey (lower chances of catching prey) and larger prey
305 (lower chances of subduing prey; Brose *et al.* 2008; Brose 2010). Consequently, rigorous empirical tests documented that consumer and resource body size are often the most important, although not the only, species-specific traits explaining the largest proportion of trophic linkages between species (Eklöf *et al.* 2012, 2013). In this vein, some recent approaches used the systematic relationships between consumer and resource body masses and optimal foraging theory to develop mechanistic
310 models predicting the trophic links between species (Petchey *et al.* 2008, 2011). These trait-based models can predict the food-web linkages among populations following the loss of specific species

such as large top predators (Thierry *et al.* 2011a). One advantage over prior static food-web models is that they can account for the re-wiring of trophic links when consumers switch to new resources after losing others. While pioneering studies addressed the risk of secondary extinctions (Curtsdotter *et al.* 2011; Riede *et al.* 2011a; Thierry *et al.* 2011a) the structural consequences of species loss for natural communities remains to be explored.

Size-spectrum concepts of biocomplexity

As discussed above, recent explorations of food web intervality have shown that characteristic species-specific body masses significantly explain the optimal ordering of species for contiguity in their diets, highlighting the importance of organism size in structuring natural communities (Stouffer *et al.* 2011; Zook *et al.* 2011). Yet, the range of *intraspecific* variation in body size for many species may muddy the waters when exploring trends in taxonomically defined networks. An analysis of highly resolved food webs showed that species-based analysis may obscure patterns that only emerge when within species individual body-sizes are employed (Gilljam *et al.* 2011). Additionally, relationships between predator body mass and (1) prey body mass, and (2) predator-prey mass ratio were more accurately represented when considering individual size over taxonomy (Gilljam *et al.* 2011). Adopting an individual-based approach may thus improve the predictability of empirically observed community structures. The allometric diet breadth model (ADBM) employs allometries of foraging variables to predict the structure of real food webs (Petchey *et al.* 2008). An investigation of four highly resolved empirical food webs found that the ADBM more accurately predicted the structure of individual-based food webs in all cases, with over 80% of links correctly predicted for Broadstone Stream (Woodward *et al.* 2010). However, while it is now recognized that allometric approaches more accurately describe predator-prey interactions than their taxonomic counterparts, taxonomy still reveals important mechanistic insights into predator-prey strategies

335 (Rall *et al.* 2011). Thus, as both species identity and individual body size matter, a logical next step is to analyze and model communities by taking both components into consideration simultaneously (Woodward *et al.* 2010; Rall *et al.* 2011).

The framework for food webs of size-structured populations takes both components into account, as it resolves the body size and abundance of each species with a size-spectrum while modeling
340 physiological processes and interactions as a function of both individual body size and species-level traits (Hartvig *et al.* 2011). Thus, topology is more complex compared to the case of classical food webs of unstructured populations, as interactions are dependent on both taxonomy and individual body sizes. This poses a challenge when comparing food web topologies from systems with size-structured populations to classical food webs, as the classical interaction matrix topology in the
345 structured communities depends on how the body-mass composition of the individual species are sampled (Woodward *et al.* 2010; Hartvig 2011). To overcome a need for high dimensional interaction matrices we need to focus on the ecology of interactions and describe individual interaction probabilities (and other individual processes) as a function of species-level traits and individual body size and document these in databases. This sets out a new trait-based paradigm of
350 biocomplexity, where topology is an emergent property of individual-level processes, which has fundamental advantages compared to the current approach where a topology is ascribed a priori. Having emergent food web topologies allows for predictions of future community structures when species move around due to climate change and form new and novel communities (Lurgi *et al.* 2012). In this vein, size-spectrum models of community structures may provide a fruitful yet so far
355 unexplored possibility for forecasting the consequences of perturbations and anthropogenic stressors.

Summary: Consequences of non-random species loss for biocomplexity

Traditional studies of changes in biocomplexity with biodiversity employ data across communities that differ in these two characteristics and demonstrate power-law increases in connectance with decreasing species richness (Schmid-Araya *et al.* 2002). This would imply that species loss should lead to higher connectance communities, in which species are more interwoven with each other by their trophic interactions (Fig. 2a). Accounting for the fact that species with large body masses are most vulnerable to extinctions allometric concepts of biodiversity loss suggest different conclusions. Given that large species often feed on prey from a wide size range and thus have a higher number of interactions than small species, their loss should result in a decrease of food-web complexity and trophic levels (Fig. 2b). The trophic role and position of species in size-spectra concepts are less well defined as species may grow through different trophic and functional roles with size- or stage-dependent interactions (Fig. 3c; Hartvig & Andersen 2013). Accordingly, the loss of species with the largest adult individuals will also lead to the loss of the juvenile nodes with smaller body sizes and lower trophic levels (Fig. 2c). Consequently, this should yield losses of links across trophic levels with the most pronounced effect at the highest trophic levels where species are less redundant (Fig. 2c). Contrasting traditional approaches, allometric and size-spectrum approaches both suggest that the loss of biodiversity should lead to future food-webs that may be less interwoven and more structured by chains of interactions and compartments (Fig. 2b, c).

Biostability

Diversity-stability relationships

Over several decades, the relationship between the diversity of food webs and their stability has

been central to ecology (May 1972; McCann 2000). May's seminal study (1972) demonstrated that
380 random networks are destabilized by increasing complexity, diversity and average interaction
strengths, which imposed a scientific conundrum on community ecology. Ecologists faced this
challenge by documenting that natural food webs possess a non-random structure in their topology
(Williams & Martinez 2000) and distribution of interaction strengths across species (de Ruiter *et al.*
1995) which both increase network stability (Neutel *et al.* 2002; Rooney *et al.* 2006). In addition,
385 many natural ecosystems possess multiple sub-habitats such as benthic-pelagic or below-
aboveground compartments, and their dynamic coupling increases the community stability (Rooney
et al. 2006). Overall, these studies documented some surprising regularities in the way food webs
are structured across different ecosystem types, but the question of how they are constrained into
those stable configurations remained unanswered. In addition, several theoretical studies have
390 shown that diversity can have a stabilizing effect on the variance at the community level (i.e. lower
temporal variation of aggregated biomass or density), while having a destabilizing effect at the
species level (Thébault & Loreau 2005; Ives & Carpenter 2007). Such instabilities at the species
level can increase the risk of secondary extinctions after species primary extinctions or
experimental deletions (Thébault *et al.* 2007). To the contrary, experimental studies most
395 commonly report positive diversity-stability relationships, but they mostly focus on two measures
of stability, that is community temporal variability and resistance to species invasion (Ives &
Carpenter 2007). While all these studies highlighted some important mechanisms behind diversity-
stability relationships, theoretical approaches were based on randomly-parametrized species, and
models as well as experiments often focused on only one or two-trophic level food webs (e.g., only
400 plants or plant-herbivore communities). However, meta-analyses of empirical studies suggest that
mechanisms underlying biostability relationships differ between single- and multi-trophic
communities (Jiang & Pu 2009). Incorporating food web complexity and realistic species traits has

thus remained a centrally important challenge to tackle consequences of species loss on stability in realistically diverse and complex ecological communities.

405 **Allometric concepts of biostability**

While traditional taxonomic models of complex food webs exhibit a chronic instability, adding size structure to these complex networks yielded a surprising persistence of the populations (Brose *et al.* 2006b; Otto *et al.* 2007; Heckmann *et al.* 2012). In complex food webs, the risk of extinction generally increases with the trophic level of the species (Eklöf & Ebenman 2006; Binzer *et al.* 410 2011). Empirically documented increases in body masses with the trophic position of a species (Riede *et al.* 2011b) cause simultaneous decreases in the per unit biomass rates of respiration and consumption, which are responsible for the stabilizing effects of allometry. Interestingly, the stability of complex natural food webs might be a simple by-product of physical constraints on foraging interactions without implying any network level evolution towards stability (Brose 2010). 415 Consistently, evolutionary food web models based on body size and allometric rules also documented emergence of stable food webs with a realistic topology (Loeuille & Loreau 2005). In addition, size-based traits of species are also correlated to interaction strength and hence to the stability of ecological networks (Brose *et al.* 2006b; Heckmann *et al.* 2012), and consequently the loss of large-bodied species is also most likely to trigger avalanches of secondary extinctions 420 (Curtsdotter *et al.* 2011; Riede *et al.* 2011a). Moreover, even small changes in the mortality or growth rates of large top predators or decreases in their body size can also cause trophic cascades and secondary extinctions (Jochum *et al.* 2012; Säterberg *et al.* 2013). Ultimately, these extinction avalanches are again most likely to undermine the energetic support of large-bodied top predators thus increasing their extinction risk (Binzer *et al.* 2011). This affects the predictability of 425 extinctions, since bottom-up extinctions are most often driven by the network topology, whereas

extinctions of large bodied species at higher trophic positions in the network will be dependent on the dynamics of the systems which is usually less straight forward to predict due to numerous possible indirect effects. So far, accounting for species-averaged body masses in allometric models has thus allowed to understand the constraints on ecological stability in realistically diverse and
430 complex communities.

Size-spectrum concepts of biostability

Mathematical models of the community size spectrum have shed light on important properties like the stability and resilience of ecosystems to perturbations. Recent studies using community spectrum models have shown that size spectra can be either remarkably stable or oscillate around a
435 steady state (Law *et al.* 2009). Faster returns following small perturbations close to steady states have been shown to be influenced by ecological properties. Modeled community size spectra with lower mean preferred predator-to-prey mass ratios, wider diet breadth of predators and higher growth conversion efficiency, and larger maturation size all result in faster recovery from perturbations (Blanchard *et al.* 2009; Law *et al.* 2009). Perturbations further away from steady state,
440 driven by changing productivity and fishing can also alter the properties of these size spectra as well – truncating them, propagating cascades and making them less resilient. For instance, fishing intensity and selectivity can drive instabilities, with highly selective fishing patterns resulting in high amplitude traveling waves (Rochet & Benoît 2012). Different sub-communities such as the benthic and pelagic parts of marine ecosystems possess their separate size spectra, and Blanchard et
445 al. (2011) demonstrated that benthic-pelagic coupling of size-based communities increases stability in a similar fashion to asymmetry of energy channels in traditional food webs (Rooney *et al.* 2006).

The community size-spectrum is the sum of all species size-spectra, and as species of different asymptotic sizes have different life-history trade-offs individuals of equal size across species may

have different growth rates. Interestingly, the diversity in growth rates across the community size-
450 spectrum at a given body size plays an important role in enhancing stability (Zhang *et al.* 2013).
Species resolved size spectrum models have also shown that mortality perturbations (e.g. from
fishing) can ignite damped trophic cascades that propagate both up and down in trophic levels due
to a combination of changes in predation mortality and prey availability (Andersen & Pedersen
2010). Yet, conservation of the overall slope of the community size spectra may reveal a stabilizing
455 property in the face of cascading effects. Similar observations have been made from natural
communities where the arrival of new species to fill available size niches helps to preserve the flow
of energy through the community (O’Gorman *et al.* 2011).

While size-spectrum approaches have provided substantial insights in community dynamics and
structure, their traditional focus on size of individuals irrespective of their taxonomic identity has
460 precluded conclusions concerning biodiversity effects. Recently, this limitation has been removed
by novel approaches that explicitly model species-level size-spectra. Interestingly, they found that
using just a single trait (e.g. size at maturation) to characterize functional species identity is
insufficient for assembling species-rich food webs of size-structured populations (Hartvig &
Andersen 2013). Coexistence requires a low niche overlap (determined by the overlap of both prey
465 and predators) or a decreasing difference in relative fitness between species when their niche
overlap increases. For instance, a low niche overlap may be obtained by increasing niche space
dimensionality through increasing the number of traits that determine interactions between species
(Eklöf *et al.* 2013). Such increasing trait dimensionality accounts for more of the details that make
up each species as it allows them to have similar prey, but different predators - or vice versa. It has
470 indeed been demonstrated that species rich systems may be achieved for higher trait-dimensionality
in both size-structured (Hartvig *et al.* 2011) and unstructured systems. Obvious trait candidates for
increased dimensionality include preferred predator–prey mass ratios that vary across predator and

prey groups (Brose *et al.* 2008) as this allows transfer of energy from different trophic levels for predators of equal sizes.

475 **Summary: Consequences of non-random species loss for biostability**

Traditional models of complex species communities suggested a chronic instability undermined by severe extinction waves that accelerated with species diversity, whereas empirical studies experienced a high stability of diverse communities. The stability of these complex communities was increased by natural network topologies, specific distributions of interactions strengths and
480 coupling of energy channels (Neutel *et al.* 2002; Rooney *et al.* 2006). Species deletion studies unraveled that in particular the loss of the most connected species (i.e., those that have most interactions with other species) would severely undermine the structural integrity of the communities (Dunne *et al.* 2002). In these taxonomic food-web models, however, all species have equal or randomly-assigned traits and the likelihood of extinction does not predictably differ
485 between them. This suggests that effects of extinctions can potentially occur anywhere in the community while on average the indirect effects on other directly linked species may often occur locally (Fig. 3a).

In contrast, allometric concepts identified aspects of natural body-mass distributions such as the increase in body masses with trophic levels as the crucially important structures that maintain food-
490 web stability (Brose *et al.* 2006b; Otto *et al.* 2007; Heckmann *et al.* 2012). This suggests that the loss of large-bodied species will most likely imply the most severe consequences for the stability of natural communities and also indirect effects on other species may be distributed across trophic levels (Fig. 3b), which found partial support in modeling studies addressing the risk of secondary extinction avalanches (Curtsdotter *et al.* 2011; Riede *et al.* 2011a).

495 Interestingly, size-spectrum approaches have demonstrated that even much more subtle changes
in the size structure of populations that do not include complete extinctions can have severe
consequences for ecological communities. For instance, predatory species shape the size-spectra of
their prey populations, and changes of predator size-spectra through disturbances such as fishing
can render the predator incapable of controlling the prey size-distribution. This may lock the system
500 in a state where competition between prey and small predators drives the predator population to a
low-density state or even extinction (Persson *et al.* 2007). Moreover, disrupting the slope of size
spectra (e.g. steepening due to more small and fewer large individuals, as demonstrated through
overfishing or warming) can lead to a less stable system due to inefficient transfer of energy
through the food web and a shift towards faster growth rates and an increase in abundance
505 fluctuations of the overall community (Yvon-Durocher *et al.* 2011a; Blanchard *et al.* 2012).
Ultimately, the loss of large-bodied individuals will reduce the size structure of the community and
likely trigger avalanches of secondary extinctions that are distributed across the entire networks
(Fig. 3c). Hence, the intra-specific size structure of natural populations can be critically important
for driving the stability and persistence of species across trophic levels.

510 **Biofunctioning**

Biodiversity and ecosystem functioning

The relationship between biodiversity and ecosystem functioning has been addressed by
numerous experimental studies (see Balvanera *et al.* 2006 for an overview). While decreases in
species richness are usually associated with lower ecosystem functions such as primary
515 productivity, litter decomposition and nutrient recycling, these relationships are most often better
explained by the diversity of species functional traits (Flynn *et al.* 2011), and they are not

necessarily simple and linear (Reiss *et al.* 2009). Compared to work on isolated trophic levels, assessments of changing biodiversity within a food-web context reveal a greater variability in the effects of species loss, as these are mediated by trophic interactions (Thébault & Loreau 2003; 520 Duffy *et al.* 2007). In naturally complex communities the biofunctioning relationships thus often appear idiosyncratic (Emmerson *et al.* 2001; Harvey *et al.* 2013) rendering predictions on the consequences of biodiversity loss fraught with uncertainty. Hence, there is increasing recognition that simple inventories of species richness are not sufficient to predict consequences of species loss, because species differ in traits such as body size and communities differ in structure.

525 **Allometric concepts of biofunctioning**

In communities organized in multiple trophic levels, the functional consequences of losing a particular species depend strongly on network structure and species traits such as body size (Solan *et al.* 2004; Schneider *et al.* 2012; Poisot *et al.* 2013). Even in communities exhibiting strong average increases in ecosystem functions with species diversity, the loss of a species from the full 530 community can have positive, negative or neutral effects on this function depending on the community context (Schneider & Brose 2013). In multi-trophic predator communities with a clear size structure, large predators have their strongest interactions with other predators in intraguild links, whereas smaller predators mainly impose top-down control on basal primary producers or decomposers (Schneider *et al.* 2012). These systematic relationships allow understanding and 535 predicting the differences between the loss of large-bodied and small-bodied predators. For example, in three trophic level systems, the loss of large species should often cause decreases in the functions maintained by basal species (that are now exposed to stronger top-down control by the smaller intraguild predators), while the opposite should follow the loss of small predators (Schneider *et al.* 2012). Similarly, the loss of the largest top predator in four trophic level systems

540 can release smaller intermediate predators, suppressing primary consumers and leading to an
increase in functions carried out at the bottom of the web. As this concept was largely developed
and tested by employing food-web motifs of few species, empirical studies scaling-up these
findings to more complex and more diverse communities are needed.

Size-spectra and biofunctioning

545 Changes to community-level size spectra can have dramatic consequences for biofunctioning.
For instance, warming is expected to alter the shape of size spectra, with steeper slopes (more small
individuals, fewer large individuals) predicted from metabolic theory and temperature-size rules
(Brown *et al.* 2004; Daufresne *et al.* 2009). These effects have been demonstrated experimentally,
with a shift towards smaller and more abundant phytoplankton in pond mesocosms (Yvon-Durocher
550 *et al.* 2011a). The associated increase in gross primary productivity was not sufficient to offset the
rise in ecosystem respiration and methane efflux, which have much higher activation energies,
leading to a net input of CO₂ and CH₄ to the atmosphere (Yvon-Durocher *et al.* 2011b). Even in
some naturally heated stream systems, where warming has unexpected effects on community size
spectra (fewer small individuals, more large individuals), lower standing stock biomass of diatoms
555 belies more rapid energy and nutrient cycling (O’Gorman *et al.* 2012) and greater overall primary
productivity (Demars *et al.* 2011). Thus, linking community size spectra to biofunctioning requires
insight into individual-level performance traits, such as growth and reproductive rates.

Furthermore, many human pressures that are often thought to be acting at the species level may
be more appropriately described as community-level actions that affect sub-populations of multiple
560 species. For instance, fishery may be seen as a size-selective pressure on most fish species, which
can trigger community-wide biomass changes through a trophic cascade to size ranges both larger
and smaller than the targeted individuals (Andersen & Pedersen 2010). Some survey data show that

exploitation may change the overall slope of the community size-spectrum (Daan *et al.* 2005),
although this is not always the case (Boldt *et al.* 2012). In consequence of these community-level
565 changes, altered energy flow and biomass ratios at opposite ends of the size spectrum following
fishing activity may lead to similar changes in ecosystem functioning as those described for
environmental stressors such as warming.

Predatory species shape the size-spectra of prey populations, and changes in predator size-
spectra (e.g. through warming or fishing) can render the predator incapable of controlling the prey
570 size-distribution. Recent experimental manipulations of species-level size spectra also suggest that
loss of a species is not required to modify top-down control, with altered size structure of a predator
population capable of causing trophic cascades affecting primary productivity (Jochum *et al.* 2012).
Similarly, manipulating the life stage structure of a keystone predator in pond communities altered
its functional role, with concurrent changes in community structure, primary producer biomass, and
575 ultimately net primary productivity and ecosystem respiration (Rudolf & Rasmussen 2013). Thus,
the intraspecific size structure of natural populations can be critically important for driving
ecosystem functioning.

Summary: Consequences of non-random species loss for biofunctioning

Impaired functionality due to reduced biodiversity was initially shown through manipulations
580 mainly restricted to altering species richness at single trophic levels. Furthermore, species loss was
treated as random, *i.e.* focus was on reduced biodiversity *per se* rather than the identity or traits of
the species going extinct and, consequently, the response was largely idiosyncratic (Emmerson *et al.*
al. 2001). Hence, the effects of species loss on ecosystem functions can potentially emerge at
different levels of the food webs, but there is a high likelihood that redundancy of species of the
585 same trophic level or functional group can compensate for this loss (Fig. 4a). In contrast, the non-

random sequence of species loss seen in natural communities under anthropogenic pressure highlights the relationship between species traits and ecological processes (Solan *et al.* 2004). Large-bodied taxa are more vulnerable and prone to extinction; making traits linked to body size not only directly important for ecological processes, but particularly significant if they covary with extinction risk. Non-random loss of individuals within a species or large taxa across a community is expected to affect ecosystem functionality. Modeling studies demonstrated that the loss of large species is expected to accelerate competitive exclusion among basal species (Brose 2008) and trigger the strongest trophic cascades and indirect effects in natural ecosystems (Berlow *et al.* 2009), which may alter their functionality dramatically. While these indirect effects and trophic cascades are often hard to predict, allometric approaches predict a high likelihood of losing upper trophic levels where the redundancy of species is low (Fig. 4b). Size-spectrum approaches suggest that these effects may be less focused on upper trophic levels (Fig. 4c). In addition, they have shown that even without losing species, subtle size-specific changes in population structures such as those introduced by size-selective fishing can impose severe trophic cascades and alterations to ecosystem functioning (Jochum *et al.* 2012). Moreover, the targeted removal or loss of larger individuals alters the mass-abundance scaling in the community with modifications of the ratio of autotrophic to heterotrophic biomass, which has knock-on effects on gross primary production, ecosystem respiration, and carbon sequestration.

Conclusions

Over several decades, biodiversity research has been dominated by several important debates of how the loss of species from natural communities affects their structural complexity, dynamic stability and ecosystem functioning. While traditional studies averaged across species, novel size-structured approaches include body size as a super trait to predict the consequences of non-random

species loss. Concerning structural complexity, allometric and size-spectrum approaches both
610 suggest that future food-webs may be less interwoven and more structured by chains of interactions
and compartments than predicted by traditional taxonomic concepts. These changes in the
community structure are likely to cause severe knock-on effects on their stability. In particular, the
loss of large-bodied species will most likely strongly undermine ecological stability and increase
the risk of secondary extinction avalanches. Furthermore, even much more subtle reductions in the
615 average body size of individuals within populations that do not include complete extinctions can
yield strong trophic cascades that undermine dynamic stability and cause secondary extinctions. In
consequence, allometric and size-spectrum approaches both suggest that species loss should have
strong effects on ecosystem functions and their reliability. Just as the discovery of the fundamental
interactions in particle physics or the invention of the periodic table of elements by Mendeleev
620 provided an integrative backbone for physics and chemistry, these ecological advances by size-
structured approaches provide an integrative ecological concept that enables a better understanding
of each species' unique role across communities and the causes and consequences of biodiversity
loss.

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Figure Labels

Fig. 1: Three approaches of ecological community description assign species' functional roles (latin numbers representing functional traits such as trophic levels): **a)** The **taxonomic approach** categorizes functional roles of species according to taxonomy (unique colour code) yielding **b)** networks of species (nodes) and their interactions (links between nodes) with randomly distributed functional roles. **c)** The **allometric approach** orders species according to their body mass based on allometric (often power-law) scaling of their functional roles (or traits) creating **d)** interaction networks exhibiting increasing body masses (and scaling of associated traits) with trophic levels. **e)** The **size-spectrum approach** either lumps all individuals across species in distinct size bins (community-level size spectra, grey dots) or separates species according to taxonomy and size class (species-level size spectra, coloured dots) resulting in **f)** networks with species occupying different trophic levels across size classes. Note that all panels have the same number of (colored) non-basal species.

Fig. 2: Biocomplexity changes following species loss. Species loss (red node) causes loss of links (red links) to other species, which changes the biocomplexity (number of links and connection probability) of the networks differently under the **a)** taxonomic approach, **b)** allometric approach and **c)** size-spectrum approach.

Fig. 3: Biostability changes following species loss. Primary species loss (red node) has effects (red links) on other species (red circles) that can go secondarily extinct. The identity and distribution of these secondarily affected species differs between the **a)** taxonomic approach, **b)** allometric approach and **c)** size-spectrum approach.

Fig. 4: Biofunctioning changes following species loss. Species loss (red node) eliminates its

875 contribution to an ecosystem function (e.g., primary or secondary production, predation).

Ecosystem functions after extinctions (coloured boxes) are thus lower than those in the intact community (dashed lines around boxes). The expected losses of ecosystem functions differ between the **a)** taxonomic approach, **b)** allometric approach and **c)** size-spectrum approach.

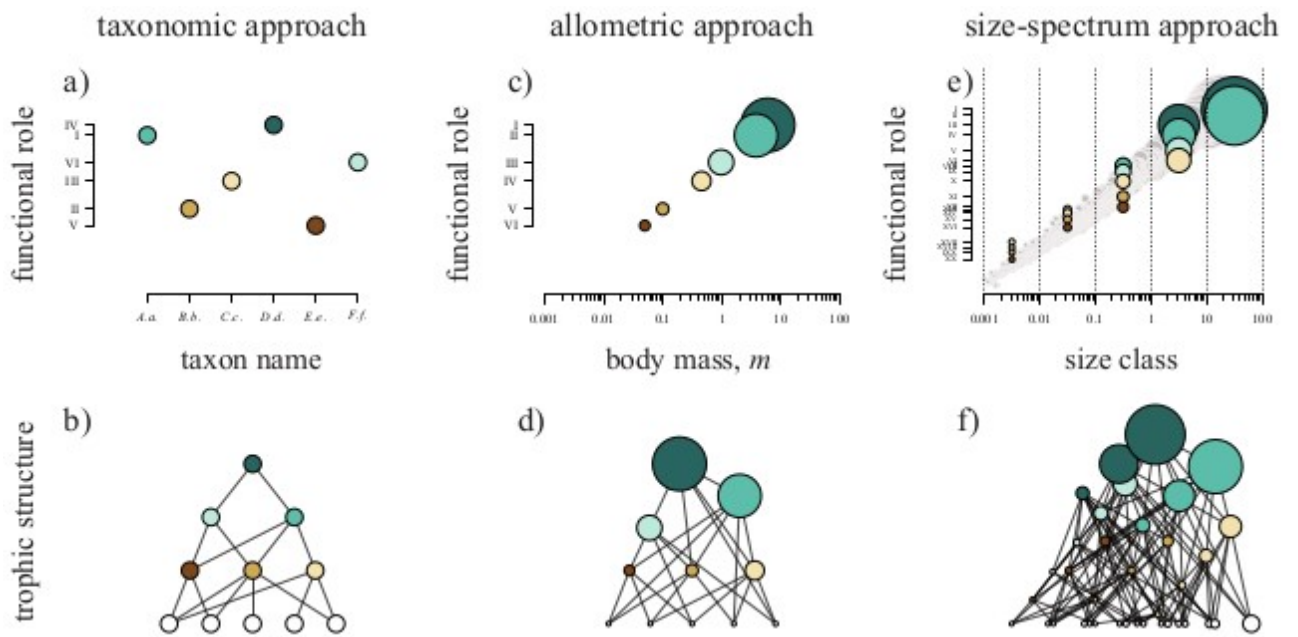
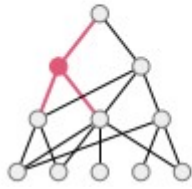


Fig. 2

taxonomic approach

a)



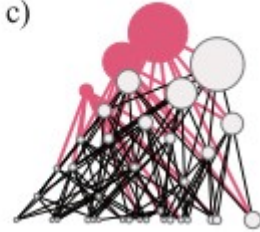
allometric approach

b)



size-spectrum approach

c)



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Fig. 3

taxonomic approach

a)



allometric approach

b)



size-spectrum approach

c)

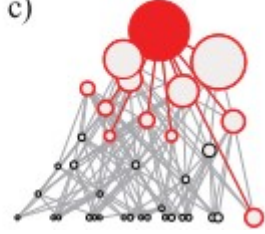
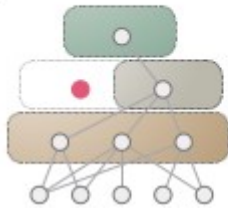


Fig. 4

taxonomic approach

a)



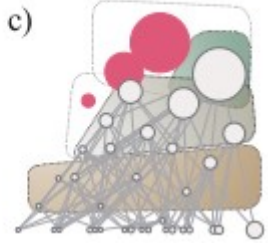
allometric approach

b)



size-spectrum approach

c)



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