Oikos 120: 503–509, 2011
doi: 10.1111/j.1600-0706.2010.18862.x

Subject Editor: Bo Ebenman. Accepted 18 November 2010

Body sizes, cumulative and allometric degree distributions across natural food webs

Christoph Digel, Jens O. Riede and Ulrich Brose

C. Digel, J. O. Riede and U. Brose (ubrose@gwdg.de), J.F. Blumenbach Inst. of Zoology and Anthropology, Georg-August-Univ. Goettingen, Germany.

The distributions of body masses and degrees (i.e. the number of trophic links) across species are key determinants of food-web structure and dynamics. In particular, allometric degree distributions combining both aspects in the relationship between degrees and body masses are of critical importance for the stability of these complex ecological networks. They describe decreases in vulnerability (i.e. the number of predators) and increases in generality (i.e. the number of prey) with increasing species' body masses. We used an entirely new global body-mass database containing 94 food webs from four different ecosystem types (17 terrestrial, 7 marine, 54 lake, 16 stream ecosystems) to analyze (1) body mass distributions, (2) cumulative degree distributions (vulnerability, generality, linkedness), and (3) allometric degree distributions (e.g. generality – body mass relationships) for significant differences among ecosystem types. Our results demonstrate some general patterns across ecosystems: (1) the body masses are often roughly log-normally (terrestrial and stream ecosystems) or multi-modally (lake and marine ecosystems) distributed, and (2) most networks exhibit exponential cumulative degree distributions except stream networks that most often possess uniform degree distributions. Additionally, with increasing species body masses we found significant decreases in vulnerability in 70% of the food webs and significant increases in generality in 80% of the food webs. Surprisingly, the slopes of these allometric degree distributions were roughly three times steeper in streams than in the other ecosystem types, which implies that streams exhibit a more pronounced body mass structure. Overall, our analyses documented some striking generalities in the body-mass (allometric degree distributions of generality and vulnerability) and degree structure (exponential degree distributions) across ecosystem types as well as surprising exceptions (uniform degree distributions in stream ecosystems). This suggests general constraints of body masses on the link structure of natural food webs irrespective of ecosystem characteristics.

Complex food webs depict energy flows from producer (e.g. photoautotroph) and other basal species to higher trophic levels. They provide an integrated understanding of the diversity, organization and functioning of natural communities. Challenged by the ecological complexity of natural ecosystems, recent theoretical advances in our understanding of food-web structure and their dynamic stability have documented the importance of body mass, degree and allometric degree distributions (Woodward et al. 2005, Montoya et al. 2006, Otto et al. 2007, Berlow et al. 2008). These new approaches offer possibilities of reducible complexity via allometric scaling relationships as a proxy of structural and dynamic aspects of complex food webs that unravel regularities across ecosystem types.

Body mass is among the most fundamental traits of organisms with strong implications for most of their other physiological and ecological characteristics including metabolic rates, ingestion rates, interaction strength with other species, the ability to handle prey and the risk of being attacked by predators (Peters 1983, Brown et al. 2004, Emmerson and Raffaelli 2004, Brose et al. 2006, 2008, O'Gorman and Emmerson 2009, Rall et al. 2010, Vucic-Pestic et al. 2010). In consequence, a species body mass determines its trophic position in the food web (Jennings et al. 2001, Woodward and Hildrew 2002, Cohen et al. 2003, Woodward et al. 2005). Recently, interest in classic body-mass patterns of natural food webs (Elton 1927) has been invigorated by allometric scaling models that successfully predict the binary link structure and the interaction strengths between species across complex natural food webs (Brose et al. 2008, Petchey et al. 2008, Berlow et al. 2009, Vucic-Pestic et al. 2010). To allow detecting generalities across ecosystems, these theoretical advancements trigger an urgent need for comprehensive quantitative descriptions of natural body-mass distributions. Pioneering studies documented that the body mass distributions of natural food webs can be approximated by log normal distributions (Jonsson et al. 2005, Woodward et al. 2005), but generalizations of these findings across ecosystem types are lacking.

In complex natural food webs, the energy, produced by plants and other basal species is distributed across the species by trophic interactions (Allesina and Bodini 2004). The links and their distribution across the food web describe the generalities in energy fluxes. These generalities across food webs are conceptualized in degree distributions for linkedness (total number of links of a species), generality (number of links to prey), and vulnerability (number of links to predators). Degree distributions describe the frequency (f(l)) of one of these linkedness variables (l) across all populations in the network, whereas the more often employed cumulative degree distributions characterize the cumulative frequency of all populations with a linkedness variables higher than a threshold ($f(l > k)$). While most biological networks exhibit scale-free power-law cumulative degree distributions (i.e. cumulative frequency decreases linearly with an increasing number of links on a log-log scale) (Albert and Barabasi 2002), food webs are best characterized by exponential (i.e. cumulative frequency decreases linearly with an increasing number of links on a lin-log scale) or uniform (i.e. cumulative frequency is constant across the number of links) degree distributions (Camacho et al. 2002, Dunne et al. 2002). Power-law cumulative degree distributions have been documented only in small food webs with unusually low connectance (Dunne 2006, Dunne et al. 2002). Mathematically, however, a specific cumulative degree distribution does not necessarily imply that the non-cumulative distribution follows the same form (Tomas Jonsson pers. comm.). Interestingly, the predictive success of recent topological food-web models (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008) is closely related to their built-in assumption of approximately exponential degree distributions (Stouffer et al. 2005).

While studies addressing the distributions of body masses and degrees across food webs have a long tradition in ecology (Schoener 1989), interest in their relationship as conceptualized in allometric degree distributions has emerged recently (Jonsson et al. 2005, Otto et al. 2007). Allometric degree distributions describe how linkedness, generality and vulnerability scale with species' body masses irrespective of their taxonomy or other traits. In this context, we employ the term 'allometric' in a broad sense to refer to the scaling of a degree property with the population-averaged body mass, whereas this does not imply a power-law scaling. Across five natural food webs, the vulnerability increased and generality decreased with increasing body mass (Otto et al. 2007). Interestingly, these specific allometric degree distributions are crucially important for the stability of complex food webs (Otto et al. 2007), but empirical analyses of their generality across ecosystems are lacking.

In this study, we present novel findings that generalize the work of previous studies on the distributions of body masses, cumulative degrees and allometric degrees across a much larger data set of 94 natural food webs. Our analyses address systematic differences in these relationships between marine, lake, stream and terrestrial ecosystems.

Material and methods

We gathered a data set comprising 94 natural food webs from different ecosystems. Each of these food webs contains information on (1) the consumer-resource links (who is eating whom), and (2) the body masses of all species. The consumer-resource link were published in the original sources, and the body masses were taken from a data base (Brose et al. 2005) and other published sources (Supplementary material Appendix 1). Food webs were grouped by four ecosystem types: marine, stream, lake and terrestrial (Table A1). For our analyses, we removed some taxa representing trophic species that aggregate taxonomic species of different body masses (e.g. Gastropoda).

For each taxon, we used the food-web matrices to calculate (1) the vulnerability as the number of its consumer taxa (2) the generality as the number of its resource taxa and (3) the linkedness as the total number of links (equal to the sum of vulnerability and generality).

To analyze the body-mass distributions across the four ecosystem types, we used the pooled species list for each ecosystem type and calculated histograms with a class width of 1 on a $\log_{10}$ body mass [g] scale. Subsequently, we calculated the cumulative degree distributions as the fraction of species P(k) that have k or more trophic links. Independent cumulative degree distributions were calculated for vulnerability, generality and linkedness for each of the ecosystem types. After $\log_{10}$ transformation of the cumulative degrees, the data was fitted with linear least square regressions in R 2.9 (R Development Core Team 2009). While linear relationships in this semi-log plot indicate exponential cumulative distributions, uniform and power-law cumulative distributions exhibit downward (i.e. linear on lin-lin scale) and upward curves (i.e. linear on a log-log scale), respectively. This first graphical impression was subsequently tested by fitting linear models to lin-lin, lin-log and log-log data. Additionally the cumulative degree distributions were calculated for each single food web. The goodness of fit (i.e. the coefficient of determination, r^2) of linear least square regressions to log-log plots (power-law relationships), semi-log plots (exponential distributions) and untransformed plots (uniform distributions) was calculated and used to compare the effects of species richness and connectance on the goodness of fit of the different distributions. This was tested by linear least squares regressions of the ratios of goodness of fits of (1) exponential to power law (r^2_{exp}/r^2_{pl}) and (2) exponential to uniform (r^2_{exp}/r^2_{univ}) against species richness and connectance.

To study allometric degree distributions we calculated the linear least square regressions of the number of predators (vulnerability), the number of prey (generality) and the number of links (linkedness) per species (y) on the $\log_{10}$ body mass (x) of the species for each of the 94 food webs independently. Subsequently, we tested for significant differences in the slopes of the allometric degree distributions between the ecosystem types by employing a linear mixed effect model with body mass (continuous explanatory variable) and ecosystem type (categorical explanatory variable) as fixed effects and the food webs as a random factor.

Results

Body masses were approximately log-normally distributed in stream and terrestrial ecosystems, whereas they were multi-modal for lake and marine ecosystems (Fig. 1). Body masses from stream and terrestrial ecosystems had the highest frequency in the category between 10^{-3} and 10^{-2} g. Terrestrial ecosystems were dominated by invertebrate species with the addition of some birds and vertebrates (e.g. coyotes, foxes and birds). The largest individuals were coyotes (4550 g) of the sand community food web from Coachella

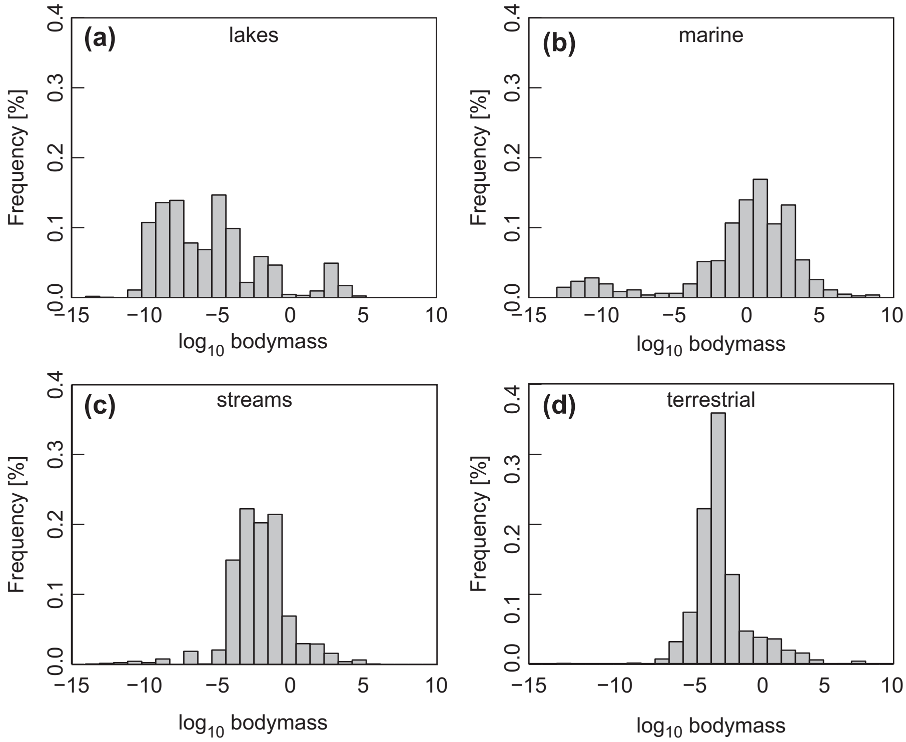

Figure 1. The body-mass structure of natural food webs: histograms of body masses for (a) lake, (b) marine, (c) stream and (d) terrestrial ecosystems.

Valley, and the smallest species were soil microbes (10^{-8} g) of the Coachella food web. Stream ecosystems were also dominated by invertebrate species, whereas also few fish species occurred. The size range of the stream food webs spanned from algae (10^{-15} g) to trouts (12 000 g).

In contrast to the terrestrial and stream ecosystems, the body-mass distributions of lakes and marine ecosystems clearly exhibited multiple peaks (Fig. 1). For lake ecosystems, we found a high frequency of body masses in the category between 10^{-10} and 10^{-8} g, which corresponds to the body-mass range of phytoplankton. The second peak occurred in the category between 10^{-6} and 10^{-4} g representing zooplankton species. A third smaller peak occurred in the category between 10^2 and 10^3 g corresponding to the largest trouts. We found the largest range in body masses in the marine food webs. Here the smallest individuals are diatoms with a mass of 10^{-13} g and the largest individuals in the food webs are baleen whales with a body mass of 80 tonnes. Marine systems exhibited the inverse pattern to lake systems with the highest frequency of body masses in the category between 10 and 10^3 g representing small birds (preying on fish in marine ecosystems), fishes and invertebrates such as sponges, sea urchins and starfishes, and a second smaller peak in the body-mass category between 10^{-12} and 10^{-10} g corresponding to phytoplankton and zooplankton (e.g. algae and foraminiferans).

Analyses at the meta-community level lumping all data for each of the ecosystem types indicate that food webs of lakes, marine and terrestrial ecosystems should have exponential cumulative degree distributions for vulnerability, generality and linkedness (indicated by roughly linear relationships in Fig. 2), whereas stream food webs exhibited downward curved relationships for generality and linkedness indicative of more uniform degree distributions (Fig. 2). Statistical tests of these relationships are carried out for each of the food webs independently. Additionally, the food webs of the four ecosystems differed in the maximum linkedness for a single species: 45 for lakes, 300 for marine, 138 for stream and 201 for terrestrial ecosystems.

Subsequent analyses at the local-community level with individual data sets for each of the 94 food webs studied generally confirmed these findings. In 54% of the individual food webs cumulative degree distributions were best characterized by exponential regressions using the r^2 as an estimate of goodness of fit , whereas a better goodness of fit of uniform and power-law cumulative distributions occurred in 45% and 1% of the webs, respectively (Supplementary material Appendix 1, Table A1). Some differences in the relative frequency of the different distributions (indicated by the highest r^2 of the regressions) between the ecosystem types were detected: lake food webs exhibited exponential cumulative degree distributions in 57% (30 of 53) of the food webs, uniform cumulative degree distributions in 43% (23 of 53) and one food web with a power law cumulative degree distribution; in marine food webs we found 57% (4 of 7) uniform cumulative distributions and 43% (3 of 7) exponential cumulative distributions; stream food webs exhibited uniform cumulative distributions in 87.5% (14 of 16) of the food webs and exponential cumulative distributions in 12.5% (2 of 16) of the food webs; terrestrial food webs exhibited exponential cumulative distributions in 94% (16 of 17) of the food webs, and uniform cumulative distributions in only one (6%) of the 17 terrestrial food webs.

Across all ecosystem types, the goodness of fit plots demonstrate that power law cumulative degree distributions occurred only in very few food webs with low species richness

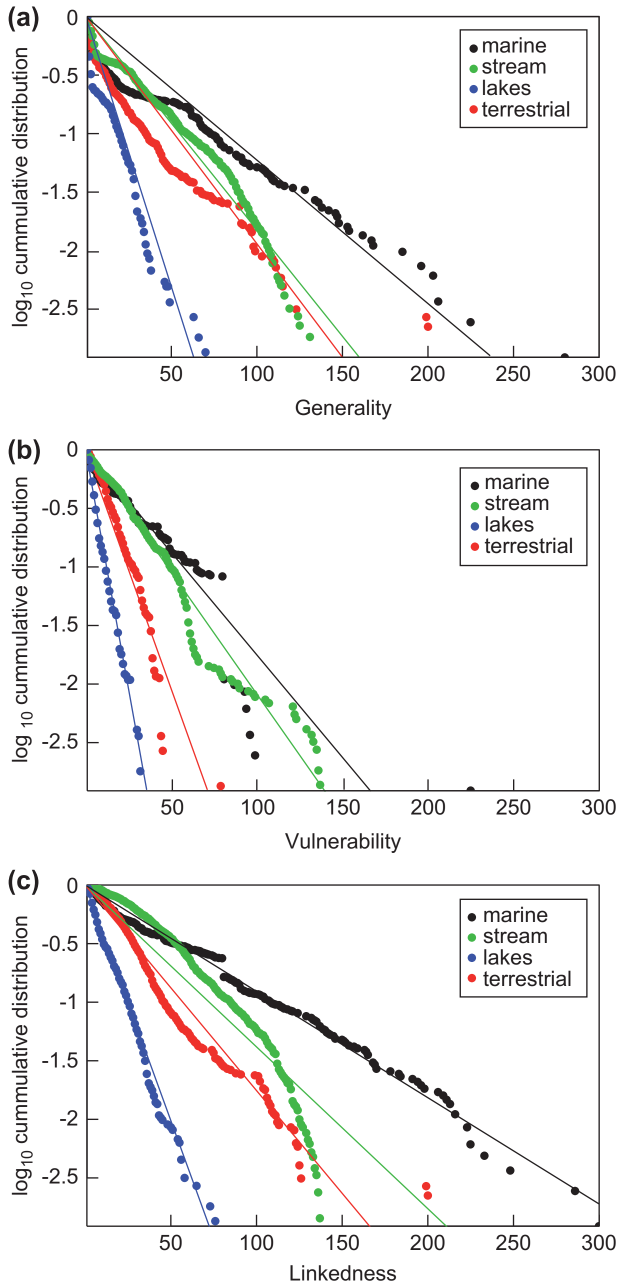

Figure 2. (a) Linear-log plots of cumulative degree distributions in the different ecosystems of the number of predator links per species (generality; $p < 0.001$, $r^2 = 0.97$ for lake; $p < 0.001$, $r^2 = 0.97$ for marine; $p < 0.001$, $r^2 = 0.98$ for stream and $p < 0.001$, $r^2 = 0.94$ for terrestrial ecosystems); (b) the number of prey links per species (vulnerability; $p < 0.001$, $r^2 = 0.99$ for lake; $p < 0.001$, $r^2 = 0.94$ for marine; $p < 0.001$, $r^2 = 0.99$ for stream and $p < 0.001$, $r^2 = 0.98$ for terrestrial ecosystems); (c) the total number of links per species (linkedness; $p < 0.001$, $r^2 = 0.99$ for lake; $p < 0.001$, $r^2 > 0.99$ for marine; $p < 0.001$, $r^2 = 0.95$ for stream and $p < 0.001$, $r^2 = 0.98$ for terrestrial ecosystems).

and low connectance (Fig. 3a, b, data points with goodness of fit ratio exponential to power law lower than one). Generally, the fit of exponential cumulative degree distributions improved over that of power-law cumulative degree distributions with increasing species richness and connectance. In contrast, uniform cumulative degree distributions occurred in the food webs with the highest connectance (Fig. 3d, data points with goodness of fit ratio exponential to uniform lower than one), whereas species richness did not affect the probability of encountering uniform cumulative degree distributions (Fig 3c).

Our analyses suggest that allometric degree distributions are wide spread across all ecosystem types. For instance, in the food web of the Mondego Estuary *Zostera* seagrass bed we found a significant decrease in vulnerability and a significant increase in generality with the $\log_{10}$ body masses of the species (Fig. 4a, b). In contrast, the linkedness (the total number of links equal to the sum of vulnerability and generality) did not vary significantly with the $\log_{10}$ body masses of the species (Fig. 4 c). Consistent with this pattern, we found a significant decrease in vulnerability in 70% (66 food webs) and a significant increase in generality in 80% (75 food webs) of the 94 food webs analyzed (significant increases or decreases indicated by linear least squares regressions with slopes significantly different from zero, $p < 0.05$, data in Supplementary material Appendix). Furthermore, we found a slightly significant effect (negative or positive) of body masses on linkedness in 40% (38 of 94) of the food webs (Supplementary material Appendix 1).

The slopes of the allometric degree distributions quantify the strength of the decrease and increase in vulnerability and generality, respectively, with the $\log_{10}$ body masses. These slopes differed significantly between the ecosystem types (Fig. 5). Linear mixed effects models indicated significant differences between the four ecosystems. The vulnerability slopes of stream ecosystems were the steepest, whereas the slopes of terrestrial systems were the shallowest. The slopes of marine and lake systems ranged between these two groups (Fig. 5a, Supplementary material Appendix 1, Table A1). Linear mixed effects models indicated the same pattern for generality, with the steepest slopes in stream food webs, the shallowest slopes in terrestrial food webs and intermediate slopes in marine and lake ecosystems (Fig. 4b, Supplementary material Appendix 1, Table A1). The steeper slopes in stream food webs indicate a stronger relationships between the body mass and the number of predator or prey links. Thus, in stream ecosystems individuals with higher body mass have on average less predators and more prey than large species in other ecosystems. The shallow slopes of terrestrial food webs indicate a weak relationship between body mass and degree suggesting that the influence of body masses on the vulnerability or generality is weaker than in the other ecosystems. The slopes of linkedness were shallower ranging around zero and exhibited only little differences among ecosystems (Fig. 5c).

Discussion

In this study, we analyzed a new allometric food-web data base containing data from 94 natural communities across four ecosystem types. Despite substantial variation in ecosystem and species characteristics, some regularities across ecosystem types were identified: exponential degree distributions dominated the food-web topologies across all ecosystem types except for streams, and allometric degree distributions of vulnerability and generality occurred in most food

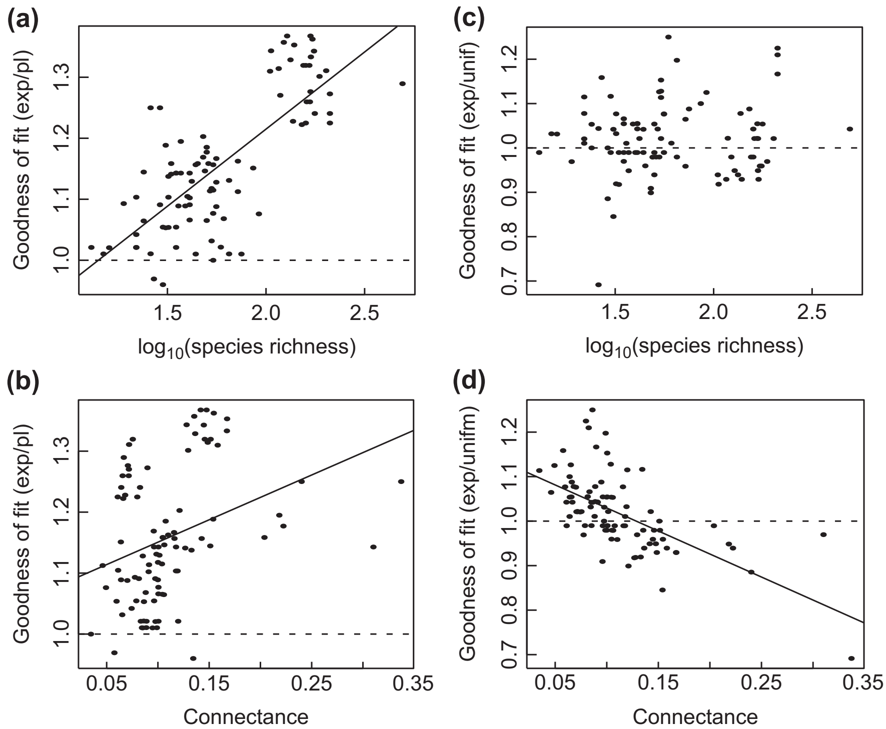

Figure 3. Goodness of fit ratio plots with r^2 values of exponential degree distributions (exp) over r^2 values of power-law (pl; a, c) or uniform degree distributions (unif; b, d) depending on $\log_{10}$ species richness (a, b) and food-web connectance (c, d). Points under the dashed lines indicate a better fit of uniform or power-law distributions, whereas points above the dashed line suggest a better fit of exponential degree distributions. Linear least square regressions: (a) $p < 0.001$, $r^2 = 0.58$; (b) $p < 0.001$, $r^2 = 0.11$; (c) not significant; (d) $p < 0.001$, $r^2 = 0.38$.

webs studied. Our novel results generalize previous findings (Camacho et al. 2002, Dunne et al. 2002, Otto et al. 2007) to cover marine, freshwater and terrestrial food webs using a new extensive global data base of 94 food webs.

Our analyses documented some systematic differences in the body-mass distributions between ecosystem types. We found approximately log-normally distributed body masses in stream and terrestrial food webs, whereas the body-mass distributions of lakes and marine ecosystems exhibited multiple peaks. This corresponds to the occurrence of multiple dominant species groups in these ecosystems: phytoplankton, zooplankton and fish species in lakes and phytoplankton, zooplankton and birds, fishes and large invertebrates in marine ecosystems.

Consistent with prior studies (Dunne et al. 2002), our analyses indicate that in contrast to other biological networks, food webs rarely exhibit power-law degree distributions. While the topology of most biological networks is well predicted by preferential attachment algorithms (Barabasi and Albert 1999), food-web structure follows more complex models (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008). These food-web models have two common features: (1) the species are hierarchically ordered according to a set of arbitrary niche values, and (2) each species has a specific exponentially decaying probability of preying on a given fraction of the species with lower niche values (Stouffer et al. 2005). Our analyses support the interpretation that body masses can serve as a proxy for the ordered set

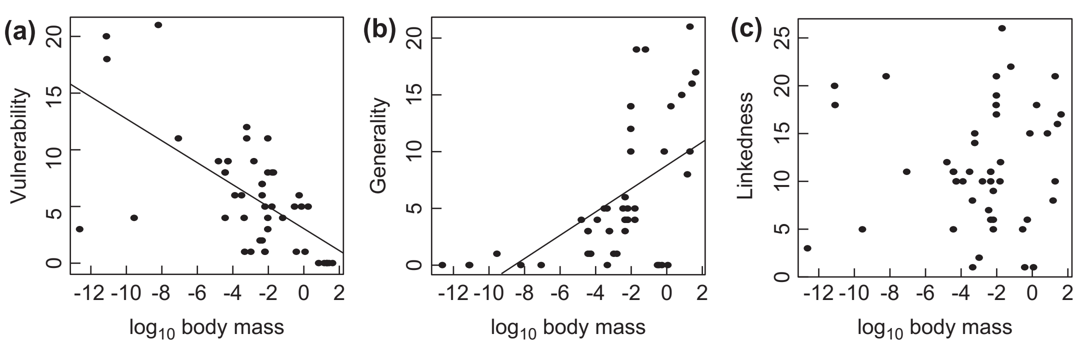

Figure 4. Allometric degree distributions of the food web of the Mondego Estuary *Zostera* seagrass bed: (a) vulnerability (i.e. number of predators) depending on $\log_{10}$ body mass ($p < 0.001$, $r^2 = 0.39$); (b) generality (i.e. number of prey) depending on $\log_{10}$ body mass ($p < 0.001$, $r^2 = 0.32$); (c) linkedness (i.e. total number of links) depending on $\log_{10}$ body mass ($p = 0.78$).

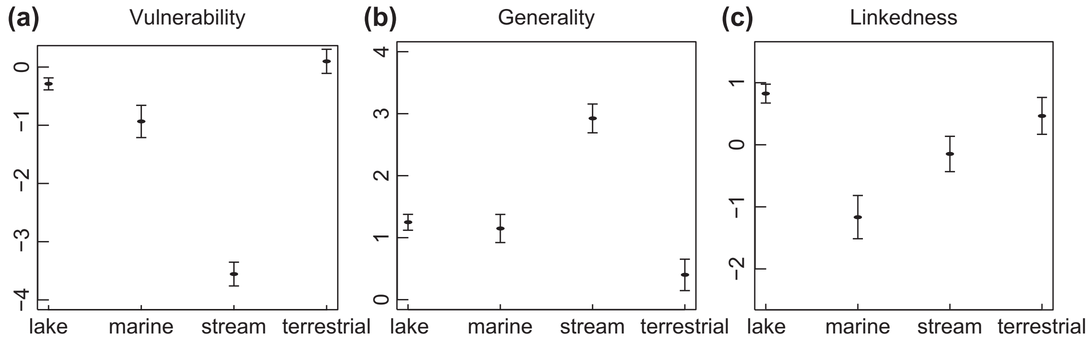

Figure 5. Slopes of the linear mixed effect models of the allometric degree distributions in the different ecosystems: (a) vulnerability slopes, with $F_{1,7345} = 114.30$ and $p < 0.001$ for $\log_{10}$(body mass), $F_{3,90} = 25.22$ and $p < 0.001$ for ecosystem type and $F_{1,7345} = 97.71$ and $p < 0.001$ for $\log_{10}$(body mass) × ecosystem type; (b) generality slopes, with $F_{1,7345} = 329.35$ and $p < 0.001$ for $\log_{10}$(body mass), $F_{3,90} = 22.19$ and $p < 0.001$ for ecosystem type and $F_{1,7345} = 28.60$ and $p < 0.001$ for $\log_{10}$(body mass) × ecosystem type; (c) linkedness slopes, with $F_{1,7345} = 19.76$ and $p < 0.001$ for $\log_{10}$(body mass), $F_{3,90} = 38.84$ and $p < 0.001$ for ecosystem type and $F_{1,7345} = 12.52$ and $p < 0.001$ for $\log_{10}$(body mass) × ecosystem type.

of niche values, and they suggest that exponential degree distributions are a generality across lake, marine and terrestrial food webs. Surprisingly, stream food webs exhibited more uniform degree distributions suggesting that taxa with an average linkedness are more frequent than in food webs of the other ecosystem types. Consistent with this pattern, the generality of the stream consumers was higher than in the other ecosystem types. One biological interpretation of this pattern is that the strong drift of stream ecosystems prevents the occurrence of highly specialized consumers, because consumer-resource interactions are more driven by random encounters than by specific search (Hildrew 2009). Interestingly, the lack of an exponential degree distribution for stream food webs suggests that their topology might be less well predicted by the current structural models than food webs of other ecosystem types (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008). However, this suggestion remains a hypothesis to be tested. Consistent with previous findings (Dunne et al. 2002), we found that power law degree distributions only occurred in food webs with very low species richness and with low connectance (<0.1). In contrast, uniform degree distributions occurred in few food webs with a high connectance, but high species richness had no influence on the occurrence of uniform distributions. In the present data set, most of the high connectance food webs with uniform degree distributions are streams, and it is difficult to determine whether the high connectance or the ecosystem type stream are responsible for this result. Until more terrestrial, lake and marine food webs of higher connectance are sampled, our analyses generally confirm the conclusion that exponential degree distributions best characterize most natural food webs except for stream ecosystems.

Our analyses demonstrate that allometric degree distributions occur in the majority of the food webs studied. These allometric degree distributions hold that generality (the number of links to resources) increases and vulnerability (the number of links to consumers) decreases with a species' population-averaged body mass. Interestingly, under the assumption that body masses are a proxy of the topological models' niche values (Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008), the hierarchical ordering of species predominantly preying on lower ranked species (i.e. those of smaller body masses) in these models would imply similar allometric degree distributions. Empirically, these relationships were first documented for the food webs of Tuesday Lake (Jonsson et al. 2005). A subsequent study (Otto et al. 2007) has identified these allometric degree distributions as a characteristic of natural food webs that is crucially important for their stability. While food webs with allometric degree distributions as documented in the present study constrain their food chains in a domain of parameter combinations that yields species persistence, topological randomizations only reduce persistence if allometric degree distributions are disrupted (Otto et al. 2007). The results of the present study now demonstrate the generality of these allometric degree distributions across a much larger data set of 94 natural food webs suggesting that based on theoretical arguments stability might be a more general property of complex food webs than previously anticipated.

Together, our results document the body-mass and link structure of natural food webs across ecosystem types as well as surprising deviations such as the occurrence of uniform degree distributions in stream food webs. This stresses the need for more detailed topological analyses of stream food webs to provide a better understanding whether and why they deviate from other ecosystems' food webs. Moreover, the present data set is lacking data of terrestrial soil food webs, and data for marine pelagic communities is scarce. Urgently, future empirical studies should fill these gaps. Nevertheless, the regularities documented here suggest that allometric scaling models may provide a useful tool for building abstract ecosystem models. Generally, these models should employ exponential degree distributions and allometric degree distributions for generality and vulnerability. These abstract models will certainly not allow mimicking quantitative dynamics or exact topologies of natural food webs, but they will enable a deepened understanding of the general physical and biological principles that govern natural ecosystems.

Acknowledgements – We are particularly grateful to Julia Blancard and the members of the sizemic steering committee for organizing the sizemic meetings and promote this special issue. We thank Tomas Jonsson and Mark Emmerson for providing very helpful reviews. Tomas Jonsson has provided derivations that the form of cumulative and non-cumulative degree distributions cannot necessarily be inferred from each other. We thank Ute Jacob, Denise Piechnik, Kateri Harrison and Neo Martinez for providing data. Franziska Grischkat has been a tremendous help in unearthing body-mass data. Helpful suggestions have been provided by Jennifer Dunne and Neo Martinez. Financial support for this study is provided by funds to CD, JR and UB by the German Research Foundation (BR 2315/4-1, 9-1), and by the European Science Foundation Research Network SIZEMIC.

References

Albert, R. and Barabasi, A. L. 2002. Statistical mechanics of complex networks. – Rev. Modern Physics 74: 47–97.

Allesina, S. and Bodini, A. 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. – J. Theor. Biol. 230: 351–358.

Allesina, S. et al. 2008. A general model for food web structure. – Science 320: 658–661.

Barabasi, A.-L. and Albert, R. 1999. Emergence of scaling in random networks. – Science 286: 509–512.

Berlow, E. L. et al. 2008. The "Goldilocks factor" in food webs. – Proc. Natl Acad. Sci. USA 105: 4079–4080.

Berlow, E. L. et al. 2009. Simple prediction of interaction strengths in complex food webs. – Proc. Natl Acad Sci. USA 106: 187–191.

Brose, U. et al. 2005. Body sizes of consumers and their resources. – Ecology 86: 25–45.

Brose, U. et al. 2006. Consumer–resource body-size relationships in natural food webs. – Ecology 87: 2411–2417.

Brose, U. et al. 2008. Foraging theory predicts predator–prey energy fluxes. – J. Anim. Ecol. 77: 1072–1078.

Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Camacho, J. et al. 2002. Robust patterns in food web structure. – Phys. Rev. Lett. 88: 228102.

Cattin, M. F. et al. 2004. Phylogenetic constraints and adaptation explain food-web structure. – Nature 427: 835–839.

Cohen, J. E. et al. 2003. Ecological community description using the food web, species abundance and body size. – Proc. Natl Acad. Sci. USA 100: 1781–1786.

Dunne, J. A. 2006. The network structure of food webs. – In: Pascual, M. and Dunne, J. A. (eds), Ecological networks: linking structure to dynamics in food webs. Oxford Univ. Press, pp. 27–86.

Supplementary material (available as Appendix o18862 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Dunne, J. A. et al. 2002. Food-web structure and network theory: the role of connectance and size. – Proc. Natl Acad. Sci. USA 99: 12917–12922.

Elton, C. 1927. Animal ecology. – Sidgewick and Jackson.

Emmerson, M. C. and Raffaelli, D. 2004. Predator–prey body size, interaction strength and the stability of a real food web. – J. Anim. Ecol. 73: 399–409.

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

Jennings, S. et al. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. – J. Anim. Ecol. 70: 934–944.

Jonsson, T. et al. 2005. Food webs, body size, and species abundance in ecological community description. – Adv. Ecol. Res. 36: 1–84.

Montoya, J. M. et al. 2006. Ecological networks and their fragility. – Nature 442: 259–264.

O'Gorman, E. J. and Emmerson, M. C. 2009. Perturbations to trophic interactions and the stability of complex food webs. – Proc. Natl Acad. Sci. USA 106: 13393–13398.

Otto, S. B. et al. 2007. Allometric degree distributions facilitate food-web stability. – Nature 450: 1226–1229.

Petchey, O. L. et al. 2008. Size, foraging, and food web structure. – Proc. Natl Acad. Sci. USA 105: 4191–4196.

Peters, R. H. 1983. The ecological implications of body size. – Cambridge Univ. Press.

Schoener, T. 1989. Food webs from the small to the large. – Ecology 70: 1559–1589.

Stouffer, D. B. et al. 2005. Quantitative patterns in the structure of model and empirical food webs. – Ecology 86: 1301–1311.

Rall, B. C. et al. 2010. Temperature, predator–prey interaction strength and population stability. – Global Change Biol. doi: 10.1111/j.1365-2486.2009.02124.x

Vucic-Pestic, O. et al. 2010. Allometric functional response model: body masses constrain interaction strengths. – J. Anim. Ecol. 79: 249–256.

Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – Nature 404: 180–183.

Woodward, G. and Hildrew, A. G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. – J. Anim. Ecol. 71: 1063–1074.

Woodward, G. et al. 2005. Quantification and resolution of a complex, size-structured food web. – Adv. Ecol. Res. 36: 85–135.