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Robustness to secondary extinctions: comparing trait-based sequential deletions in static and dynamic food webs

Alva Curtsdotter^{a, *}, Amrei Binzer^b, Ulrich Brose^b, Francisco de Castro^c, Bo Ebenman^a, Anna Eklöf^d, Jens O Riede^b, Aaron Thierry^{e, f}, Björn C Rall^b

^aDepartment of Physics, Chemistry and Biology, Linköping University, Sweden

^bJ.F. Blumenbach Institute of Zoology and Anthropology, Georg-August University Göttingen, Germany

^cDepartment of Ecology and Ecological Modelling, University of Potsdam, Germany

^dDepartment of Ecology and Evolution, University of Chicago, United States

^eDepartment of Animal and Plant Sciences, University of Sheffield, United Kingdom

^fMicrosoft Research, JJ Thompson Avenue, Cambridge, CB3 0FB, UK.

*Corresponding author. Tel.: +46 (0)13 281 331; fax: +46 (0)13 282 611.

E-mail address: alvka@ifm.liu.se.

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Abstract

The loss of species from ecological communities can unleash a cascade of secondary extinctions, the risk and extent of which are likely to depend on the traits of the species that are lost from the community. To identify species traits that have the greatest impact on food web robustness to species loss we here subject allometrically scaled, dynamical food web models to several deletion sequences based on species' connectivity, generality, vulnerability or body mass. Further, to evaluate the relative importance of dynamical to topological effects we compare robustness between dynamical and purely topological models. This comparison reveals that the topological approach overestimates robustness in general and for certain sequences in particular. Top-down directed sequences have no or very low impact on robustness in topological analyses, while the dynamical analysis reveals that they may be as important as high-impact bottom-up directed sequences. Moreover, there are no deletion sequences that result, on average, in no or very few secondary extinctions in the dynamical approach. Instead, the *least* detrimental sequence in the dynamical approach yields an average robustness similar to the *most* detrimental (non-basal) deletion sequence in the topological approach. Hence, a topological analysis may lead to erroneous conclusions concerning both the relative and the absolute importance of different species traits for robustness. The dynamical sequential deletion analysis shows that food webs are least robust to the loss of species that have many trophic links or that occupy low trophic levels. In contrast to previous studies we can infer, albeit indirectly, that secondary extinctions were triggered by both bottom-up and top-down cascades.

Key words: species loss, extinction cascades, top-down effect, bottom-up effect, stability, body size, trophic interactions, vulnerability, generality, keystone species

Introduction

The current rate of extinctions matches those of previous mass extinction events (Brook, Sodhi & Ng 2003; Barnosky, Matzke, Tomiya, Wogan, Swartz et al. 2011). As we depend on functioning communities to provide ecosystem services, it becomes increasingly important to understand the consequences of species' extinctions. This includes biological degradation by cascades of secondary extinctions (Pimm 1980; Dunne, Williams & Martinez 2002; Ebenman, Law & Borrvall 2004), which in turn may make the system even more sensitive to further disturbance (Ives & Cardinale 2004; Thebault, Huber & Loreau 2007). A system where the risk and extent of secondary extinctions is low has been termed a robust system (Dunne et al. 2002). This robustness of a community to species loss is likely to depend on the traits of the species that is lost from the community (Solé & Montoya 2001; Dunne & Williams 2009; Staniczenko, Lewis, Jones & Reed-Tsochas 2010). This renders it crucially important to identify species traits associated with secondary extinction risk.

Community robustness has been studied by subjecting species interaction networks to different deletion sequences. Species are deleted from the network in an order defined by species traits and after each deletion (or “primary extinction”) the number of resulting secondary extinctions is recorded. Deletion sequences that remove the most connected species cause substantially more secondary extinctions than random removals (Solé et al. 2001; Dunne et al. 2002). This result has been corroborated by later research, subjecting both empirical and model generated networks to deletion sequences based on, among other things, connectivity to other species, geographical prevalence, trophic level and IUCN Red List status (Srinivasan, Dunne, Harte & Martinez 2007; Dunne et al. 2009; Staniczenko et al. 2010; de Visser, Freymann & Olf 2011; Ebenman 2011; but see Allesina & Pascual 2009 for an exception). These studies suggest that conservation efforts should focus on “network hubs”, those species with most interactions.

The above-mentioned studies are topological: they only considered the link structure of the networks and omitted population dynamics. In such approaches, secondary extinctions occur when a

consumer has lost all of its resources (but see Thierry, Beckerman, Warren, Williams, Cole et al. 2011, this special feature for a different topological approach). Thus, all secondary extinctions emerge from bottom-up cascades. However, empirical observations show that the loss of a species can also cause top-down extinction cascades (Paine 1966; Elmhagen & Rushton 2007). For example, the loss of a top-predator can cause meso-predator release with the subsequent overexploitation of a basal prey (Estes & Palmisano 1974; Johnson, Isaac & Fisher 2007; Elmhagen et al. 2007). Likewise the loss of top-down control on strongly competitive species can result in subsequent competitive exclusion (Paine 1966; van Veen, Holland & Godfray 2005). Together, these examples illustrate the importance of top-down induced secondary extinctions for food web robustness. Hence, bottom-up cascades studied in traditional topological analyses of robustness only represent a minimum, or “best case”, scenario of secondary extinctions.

The combination of bottom-up and top-down effects on secondary extinctions can be addressed by dynamical approaches. In such approaches we take into account, not only the link structure of a food web, but also the changes in species abundance through time, as well as the indirect effects that these changes have on the abundances of other species. While there have been several topological studies investigating food web robustness by performing sequential deletions based on species traits, there have been no such studies with a dynamical approach. However, there have been several dynamical studies looking at cascading secondary extinctions after the deletion of *a single species* (Borrvall, Ebenman & Jonsson 2000; Ebenman et al. 2004; Eklöf & Ebenman 2006; Petchey, Eklöf & Ebenman 2008; Sahasrabudhe & Motter 2011; see also Riede, Brose, de Castro, Rall, Binzer et al. 2011, this special feature for a detailed introduction to single species deletions). These studies clearly showed the capacity of the dynamical approach to capture the bottom-up as well as the top-down effects, as secondary extinction cascades occurred when primary producers as well as top-level consumers were removed from the food web. Notwithstanding, only one of these dynamical single species deletion studies looked at the importance of a species' connectivity for food web robustness

(Eklöf et al. 2006). As with the topological studies, this study points to the importance of highly connected species.

In addition to species connectivity, body size may be a species trait with implications for robustness. A dynamical species deletion experiment investigating interaction strengths found that the deletion of large-bodied species led to big changes in the biomass densities of the remaining species in the food web (Berlow, Dunne, Martinez, Stark, Williams et al. 2009). Further, sensitivity analysis has demonstrated the importance of body size for the food web response to other types of press perturbations (Berg, Christianou, Jonsson & Ebenman, 2011). The importance of large-bodied species for the dynamical stability of food webs in these studies thus suggests that large-bodied species could also play an important role for food web robustness.

The method of subjecting interaction networks to sequential deletions can help identify the traits defining species pivotal for food web robustness. Here we aim to fill a knowledge-gap by investigating the robustness of food webs in a dynamical setting. Further, we compare the food web responses in the dynamical setting to the responses in a topological setting.

Methods

Food web structure and dynamics

The dynamic food web models are built in a three step process (see Binzer, Brose, Curtsdotter, Eklöf, Rall et al. 2011, this special feature for a more detailed model description). First, the food web structure is created by the niche model (Williams & Martinez 2000) with species richness, S , and connectance, C (i.e., the connection probability of species' pairs in the web), as input parameters. S and C were sampled from truncated normal distributions ranging from 20 to 60 and from 0.05 to 0.25, respectively. Second, the body-masses are distributed across species according to trophic level – body mass relationships, such that body masses increase with trophic level by a factor sampled from a normal distribution with a mean of 10 and a standard deviation of 100. This factor is sampled

independently for each of the species in a food web (see Berlow et al. 2009), which implies that some consumers can be smaller than their average prey. Third, the species' body masses are employed to parameterize a bioenergetic predator-prey model with negative-quarter power-law scaling of the per unit biomass biological rates of respiration, biomass production and maximum consumption (see Rall, Guill & Brose 2008; Brose 2008 for a detailed description). Consistent with prior work, this model includes logistically growing basal species and non-linear functional responses. The predator-interference term and the Hill exponent, parameters of the functional response, are both sampled from normal distributions (interference: mean = 0.1, sd = 0.05; hill: mean = 1.1, sd = 0.5). The sampled range of the Hill exponent yields functional responses from Holling type II (Hill exponent = 1) to increasingly sigmoidal, Holling type III-like curves with increasing values of the exponent (see Rall et al. 2008 for a detailed description of functional responses).

Sequential deletion simulations

We created 1000 food webs and simulated them dynamically for 5000 time steps, without any species deletions to remove initial transient dynamics and transient species doomed to extinction. Initial biomass densities, B_i , were drawn independently from a uniform distribution ranging 0.1 - 1. During simulations, species with a biomass density less than 10^{-30} were considered extinct. For each of the resulting food webs, network statistics, e.g. S and C, were recalculated. Each food web was then subjected to dynamical as well as topological sequential deletions.

The deletion sequences removed species in trait defined order, starting with the species with the (a) highest connectivity (total number of trophic interactions), (b) lowest connectivity, (c) highest vulnerability (number of consumers), (d) lowest vulnerability, (e) highest generality (number of resources), (f) lowest generality, (g) largest body mass or (h) smallest body mass. In case of a tie, i.e. two or more species had the highest (or lowest) trait value, the one removed was randomly chosen among them. In these sequences, only consumer species were involved; basal species were never deleted. We complement these sequences by two sequences removing, at random, consumers only

or basal species only. The latter is expected to provide a worst case scenario, as removing all primary producers generally should be the fastest route to complete eradication of the system.

The sequential deletion can be seen as a stepwise process, where a step always starts with the deletion of the first species in the deletion sequence. After the deletion, secondary extinctions are recorded. In the topological approach a species was considered secondarily extinct if it had lost all of its prey species. In the dynamical approach a species was considered secondarily extinct if its biomass density diminished to less than 10^{-30} during a simulation period of 5000 time steps after the species deletion. Before adding a new step the deletion sequence was updated, as extinctions in the previous step could have changed species' trait values and thus their rank. Sequential deletion steps were added until there were no more species that could be deleted, i.e. there were no consumer species left in the food web or, in the case of random basal species removal, no basal species left.

Statistics

Robustness is measured as R_{50} : the proportion of species that has to be deleted to cause the extinction of 50% of the species in the food web. Maximum robustness thus corresponds to a R_{50} of 50%, in which case 50% of the species have been deleted and no secondary extinctions have occurred. Lower values of R_{50} mean more secondary extinctions and, thus, lower robustness. As species are discrete units, the exact R_{50} is often overshoot. To address this issue, R_{50} is estimated by linear interpolation between the P_{DEL} (the proportion of deleted species to the original species richness) immediately below and above the R_{50} . Three food webs were excluded from further analysis; two of them contained trophic loops allowing consumers in the topological approach to survive without pathways to the primary production base and the third web had more than 50% basal species, hence not reaching R_{50} for nine of the ten deletion sequences.

To evaluate, within a given approach, what species traits are most important for food web robustness, the R_{50} values from the respective approach were analysed, using an ANOVA followed by

a Tukey HSD post hoc test. For each of the 10 deletion sequences, a t-test was applied to test for differences in mean robustness, measured as mean R_{50} , between the dynamical and the topological approach. Additionally, for each sequence, a correlation was made between the individual food webs' R_{50} values in the topological and dynamical approach. The correlation will be strong for sequences that predict similar robustness in both approaches, while being low if the two approaches differ in robustness.

Results

The 1000 model food webs include a large variation in structural as well as dynamical parameters. Species richness varies from 10 to 60 species, connectance from 0.05 to 0.30 and maximum trophic level from 2.5 to 7.3. The food webs also differ in body size structure, as measured by the slopes of the relationships between body mass and generality (slopes ranging from -0.9 to 3.3), vulnerability (-3.1 to 0.4), trophic level (-0.1 to 5.0) and abundance (-4.9 to 1.1) (see Riede et al. 2011, this special feature for further details). The functional response varies among the webs from a pure Holling type II (Hill exponent = 1) to one dynamically similar to the Holling type III (approx. at Hill exponent \approx 1.2; see (Williams & Martinez 2004; Rall et al. 2008)). This large variation among the food webs ensures that our results are quite general and not dependent on one specific food web configuration.

The raw data from the dynamical sequential deletions is presented in Fig. 1. The high amount of scatter shows that there is substantial variation among the food webs as to how they respond to a certain deletion sequence. However, as exemplified by the extinction sequences from food web 125, the response of a specific food web may differ substantially depending on the deletion sequence to which it is subjected. To analyse the variation in robustness, we begin by looking at the effects of the different deletion sequences on the R_{50} values in the dynamical approach, and to infer the mechanisms behind these effects we contrast the effects of the sequences in the dynamical and the topological approach.

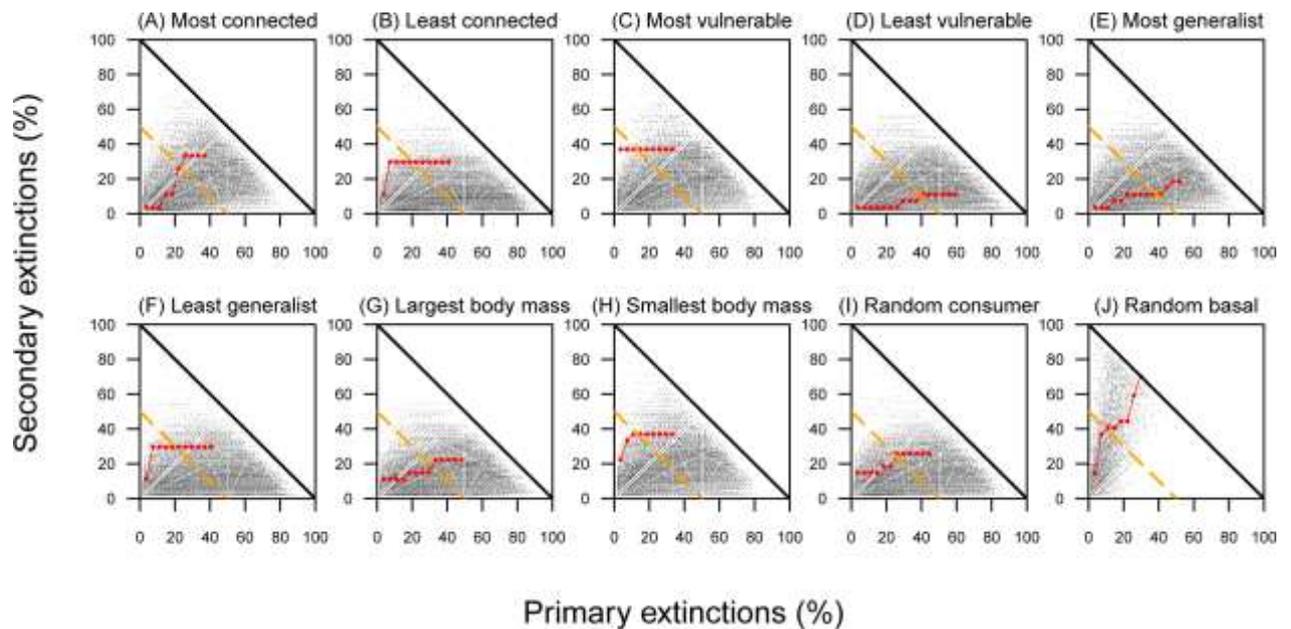


Fig. 1. Extinction sequences from the dynamical approach. Each subplot shows the data from all 997 food webs for one of the 10 deletion sequences: (A) most connected, (B) least connected, (C) most vulnerable, (D) least vulnerable, (E) most generalist, (F) least generalist, (G) largest body mass, (H) smallest body mass, (I) random consumer and (J) random basal. The x-axis shows the proportion of the original species richness in a food web that has been deleted. The y-axis shows the cumulative proportion of the original species richness that as a result has gone secondarily extinct. The continuous diagonal line corresponds to 100% species loss; the dashed diagonal line corresponds to 50% species loss. The dotted line represents an example of an individual extinction sequence (web no. 125).

The type of deletion sequence explains more than a third of the total variation in robustness in the dynamical approach (Fig. 2; ANOVA, $r^2 = 0.38$). As expected, random basal removal entails the lowest robustness. Among the remaining deletion sequences three groups can be discerned. First, the sequences removing the least vulnerable, least generalist and largest species are undistinguishable from the random sequence. Second, food webs are less robust to the sequences removing the most connected, most vulnerable, most generalist and smallest species as compared to the random sequence. Third, food webs are more robust against the sequence removing the least connected species than against the random sequence.

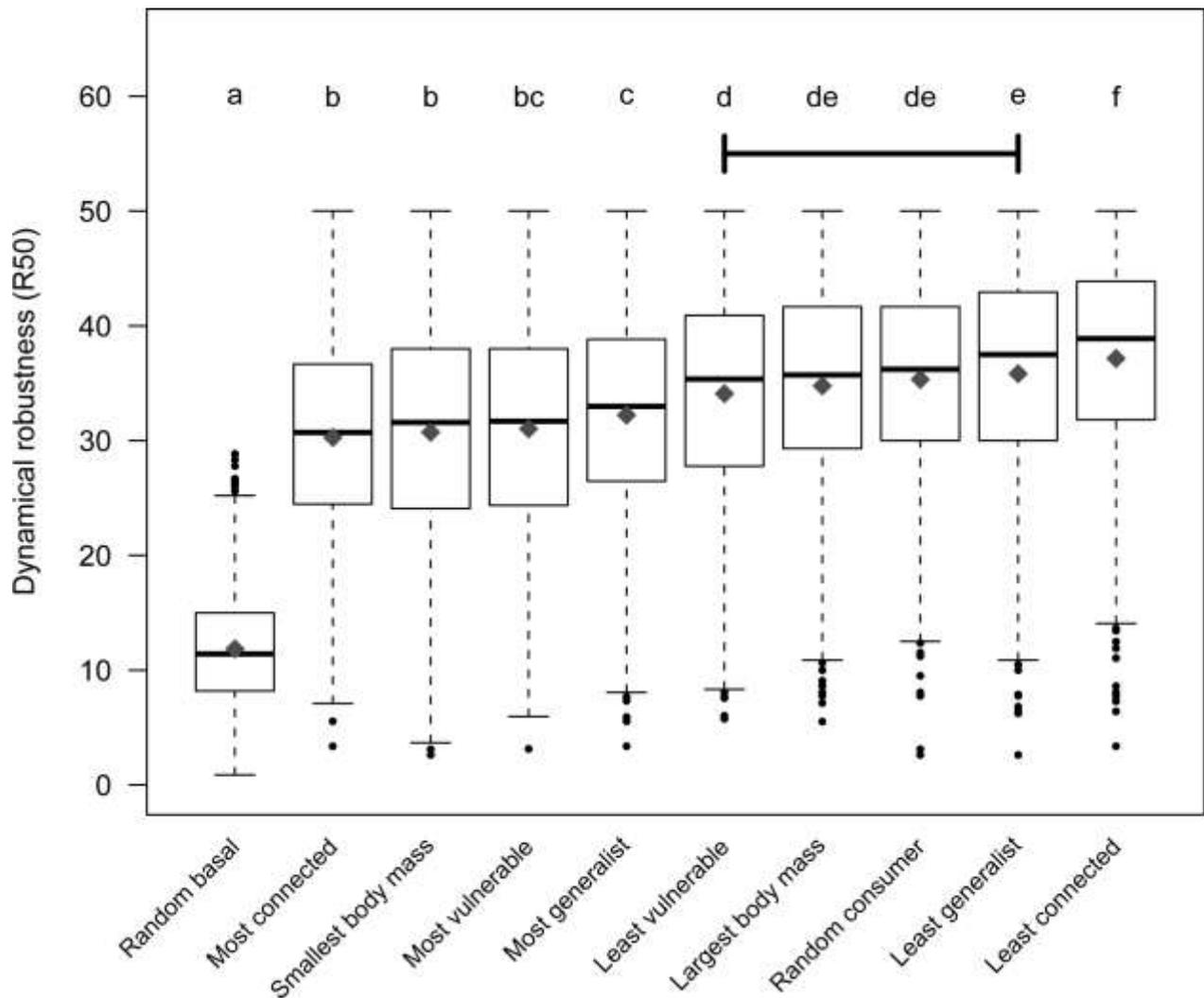


Fig. 2. The robustness to species loss in the dynamical approach. On the x-axis are the sequences, ordered by increasing robustness; on the y-axis is robustness measured as R_{50} . Each box plot contains the R_{50} values from the 997 food webs. Diamonds denote means. Lower case letters above the box plots denote significantly different sequences (different letters) in the ANOVA and Tukey HSD post hoc test at the 0.05 level. Sequences not differing from the random consumer sequence are below the bar.

In the topological approach, the deletion sequences explain almost 3/4 of the total variation (Fig. 3; ANOVA, $r^2 = 0.74$). As in the dynamical approach, the sequence removing basal species entails the lowest robustness and three groups can be discerned among the remaining sequences. However, the composition of these groups is not quite the same as in the dynamical approach. First, the sequences removing most generalist and least generalist are undistinguishable from the random sequence. Second, food webs are less robust to the sequences removing the most vulnerable, the smallest and

the most connected species as compared to the random sequence. Third, food webs are more robust against the sequences removing the least connected, the least vulnerable and the largest species than against the random sequence. It should be noted, however, that these groups neither in the topological nor in the dynamical approach are entirely homogeneous (see Fig. 2 and 3, post hoc tests).

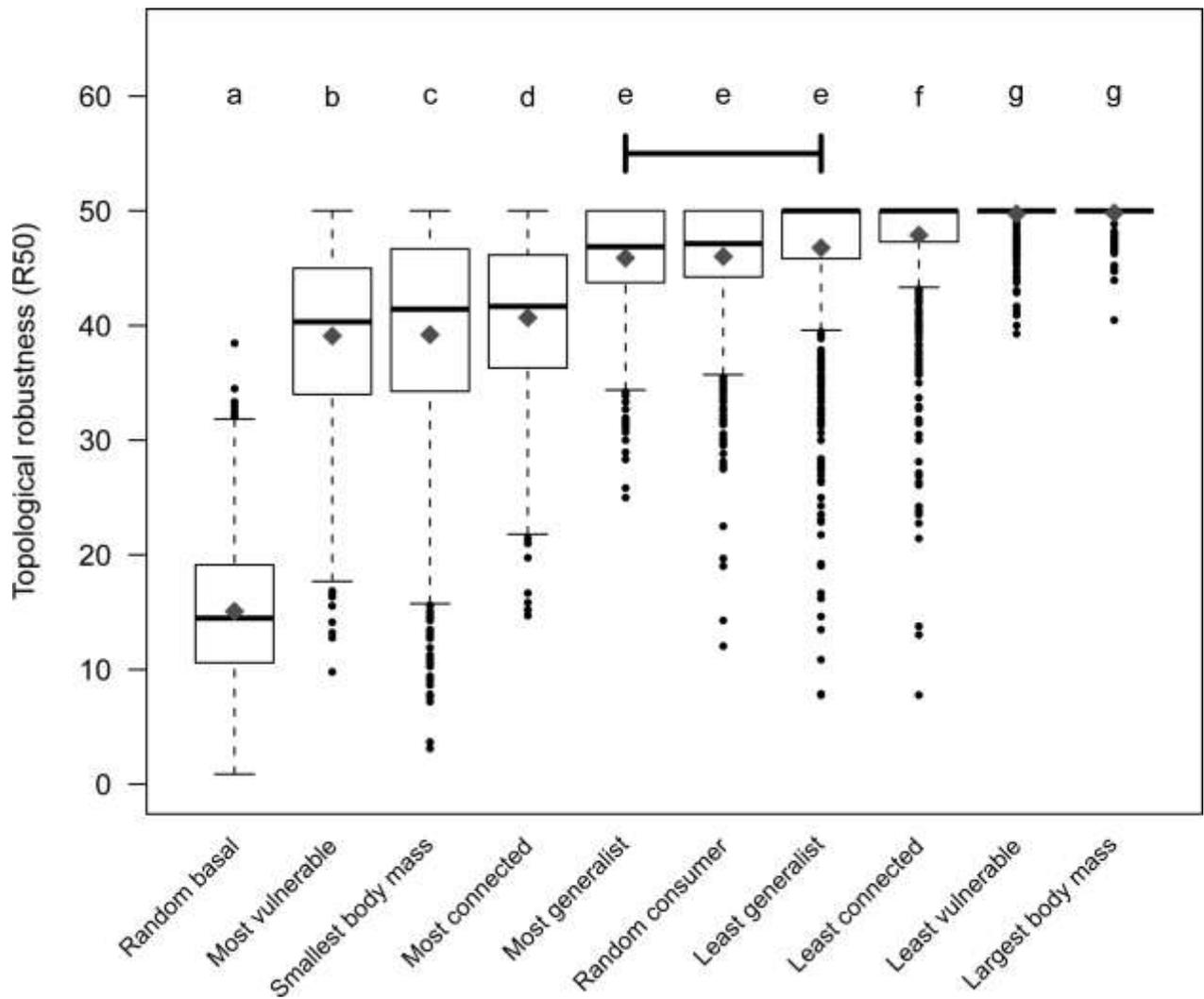


Fig. 3. The robustness to species loss in the topological approach. On the x-axis are the sequences, ordered by increasing robustness; on the y-axis is robustness measured as R_{50} . Each box plot contains the R_{50} values from the 997 food webs. Diamonds denote means. Lower case letters above the box plots denote significantly different sequences (different letters) in the ANOVA and Tukey HSD post hoc test at the 0.05 level. Sequences not differing from the random consumer sequence are below the bar.

For all sequences, robustness to species loss is generally lower in the dynamical approach than in the topological (Fig. 4; t-test, $p \leq 0.001$). The correlation between the R_{50} values from topological and dynamical approach ranges from non-significantly different from zero to 0.77. There are however a few data points (ca 3%) in Fig. 4 that lie above the diagonal, indicating a lower robustness in the topological approach than in the dynamical. This may seem quite unexpected as, following the removal of a specified set of species, the number of secondary extinctions in a topological approach can only be as high as or lower than in a dynamical approach (see *Topological vs. Dynamical – Overall patterns* in the Discussion). The explanation lies in that the set of the species removed from a certain web is not necessarily the same in the two approaches. First, as mentioned in the Methods, in case of a tie the species removed will be chosen randomly from the species with the same trait value. Second, if the extent of secondary extinctions differs between the two approaches, the resulting food web structure will be different. In the case of the interaction-based sequences, this could change the identity of the species that will be removed in the next step.

In addition to the analyses of R_{50} we performed analyses of another robustness measure, extinction area (Allesina et al. 2009), with qualitatively equivalent results (see Appendix A: Fig. 1-3).

Discussion

In this study, we addressed the risk of trait-based sequences of primary extinctions for triggering secondary extinctions in dynamic food web models. We find that communities are least robust to the loss of primary producers, species with many trophic interactions and species with a low body mass. Moreover, our comparison between the topological and dynamical approach reveals that dynamical effects contribute strongly to the vulnerability of communities to species loss and underlines the importance of including dynamics when aiming to identify the species traits crucial for food web robustness. We first compare robustness in the two approaches, and subsequently focus on results from the dynamical approach and what species traits are most important for food web robustness.

Topological vs. Dynamical – Overall patterns

Performing a sequential deletion analysis in a dynamical setting yields lower robustness than the same analysis performed in a purely topological setting. This result is quite expected, as there are several mechanisms involved in secondary extinction cascades that can only be captured using a dynamical approach.

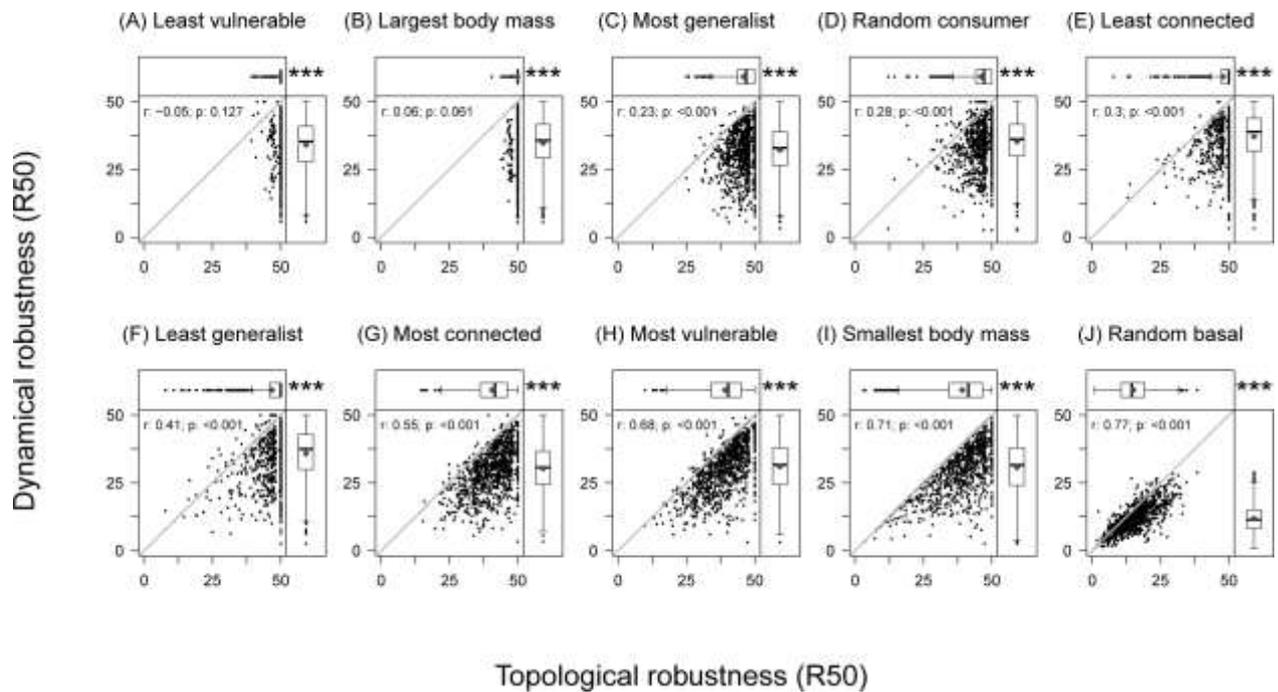


Fig. 4. Comparison of robustness between the topological and the dynamical approach. On the x-axis is robustness, measured as R_{50} , in the topological approach; on the y-axis is robustness, measured as R_{50} , in the dynamical approach. Each subplot contains the data from one of the deletion sequences and shows the same box plots as in Figs. 2 and 3, for both the topological (horizontal box plot) and the dynamical (vertical box plot) approach. T-tests were applied to test whether mean robustness in the two approaches was different. Stars designate statistical significance in this test at the 0.001 level. Each subplot further shows the correlation between the robustness of the food webs in the topological and dynamical approach and the subplots are shown in order of increasing correlation. The correlation coefficient, r , and its p value are shown in each subplot.

First, top-down effects are possible in a dynamical setting. Thus, the loss of higher level consumers may cause secondary extinctions due to overexploitation or competitive exclusion as lower level consumers are released from predation pressure. Furthermore, as both top-down and bottom-up effects are possible, the loss of a species could trigger secondary extinction cascades in both

directions. These extinction cascades may also change direction; a top-down extinction cascade may lead to the loss of a primary producer which in turn may lead to a bottom-up extinction cascade as consumers lose their resources. See Sahasrabudhe et al. (2011) for an example of such extensive secondary extinction cascades in a dynamical setting.

Second, the dynamical approach may also be more sensitive to bottom-up effects than the topological approach. As in natural ecosystems, low resource abundances can cause consumer extinctions in dynamical models, whereas topological secondary extinctions occur only when a consumer has lost all its prey species (but see Thierry et al. 2011, this special feature, for an exception).

Third, population dynamics are important for species extinction risk; the lower and the more variable the abundance of a species is, the higher the risk of extinction (Lande 1993). The configuration and strength of species interactions have a great impact on the stability of population dynamics (McCann, Hastings & Huxel 1998; Vandermeer 2006). Thus, if species extinction results in the loss of a link with crucial importance for the dynamical stability of one or more species, secondary extinctions may take place due to changes in the population dynamics. As topological approaches take into account neither species abundances nor interaction strengths secondary extinctions due to the described mechanism cannot occur.

These mechanisms can explain why robustness is lower in dynamical than in topological analyses. Moreover, this difference in robustness is greater for some sequences than others, presumably because the proportion of top-down to bottom-up cascades varies among sequences. We cannot state conclusively here what sequences trigger what cascades, as we have not looked at the relative positions of deleted and secondarily extinct species. However, the direction of the sequences themselves may provide a clue to the relative contribution of the three mechanisms discussed above to the additional secondary extinctions that occur in the dynamical approach.

Direction of deletion sequences

The direction of a sequence depends on the characteristics of the sequence-defining species trait. Removing species from a network in order of highest vulnerability is a pronouncedly bottom-up type of sequence, as it removes the topologically most important resources with most energy pathways to higher trophic levels. This bottom-up character of the sequence is further amplified by the fact that vulnerability decreases with trophic level in the model communities used in this study (see Riede et al. 2011, this special feature), in accordance with empirically observed patterns (Otto, Rall & Brose 2007; Digel, Riede & Brose 2011). On the other hand, removing species in order of highest generality is a top-down sequence as it removes the consumers with most resource interactions. Again, this is amplified as generality increases with trophic level in our model communities (see Riede et al. 2011, this special feature), as in natural ones (Otto et al. 2007; Digel et al. 2011). Accordingly, sequences removing species according to their connectivity, which is the sum of a species' generality and vulnerability, have no typical direction. Instead, in each food web the direction of a connectivity-based sequence will depend on which of the two traits (generality and vulnerability) scale most strongly with trophic level in that particular food web. Lastly, body-mass scales positively with trophic level (Riede, Brose, Ebenman, Jacob, Thompson et al. 2011). Hence, removing species in order of largest body mass is a top-down directed sequence. The species trait thus determines the direction of the sequence itself but it should be noted that this direction is not necessarily the same as that of the extinction cascade it triggers.

Topological vs. Dynamical – Sequence differences

The three sequences, showing the greatest difference in robustness between the dynamical and topological approach, are top-down directed, removing the least vulnerable species, the largest species and the most generalist species. For these sequences, the addition of secondary extinctions stemming from top-down cascades is likely to be the most important driver behind the low correlation between the robustness in the dynamical and the topological approach.

However, even though they are all top-down sequences, the sequence taking the most generalist species stands out in an unexpected manner. This sequence yields substantially lower robustness in the topological approach than the other two top-down sequences (Fig.4 A&B vs. C). We anticipate that this top-down directed sequence, removing species in order of the most generalist species, will render a food web increasingly sensitive to bottom-up extinction cascades. The longer the sequence runs, the more specialised will the average remaining consumer be, which in turn will increase the risk of secondary extinctions following the chance loss of a lower level species.

The sequences removing the most connected species, the least connected species or a random consumer do not have an intrinsic direction. Consequently, the decrease in robustness could be due to any or all of the mechanisms discussed above: top-down cascades, abundance based bottom-up cascades or destabilization of population dynamics. Removing the most connected consumer is more similar in the dynamical and topological sequences than what the other non-directional sequences are, suggesting that bottom-up effects may have a greater part in the secondary extinctions in this sequence than in the others.

The remaining four sequences, removing the least generalist species, the most vulnerable species, the species with the smallest body mass or a random basal species are all bottom-up sequences. The latter three show high correlation in robustness between the dynamical and the topological approach and additional extinctions in the dynamical analysis are likely to depend most on the increased sensitivity to bottom-up effects. Again, the generality-based sequence stands out, having surprisingly high robustness for a bottom-up sequence in a topological analysis. But while removing the most generalist species rendered the food webs more sensitive to bottom-up effects, removing the least generalist has the opposite effect. The longer the sequence runs the more generalist will the average remaining consumer be, as the specialist consumers are removed first. Surprisingly, this bottom-up deletion sequence could stabilise itself.

Species traits and food web robustness

Removing the primary producers entails the lowest robustness. This result serves as a gentle reminder that those abundant species that form the energetic base of ecosystems should not be forgotten, which they easily may be as conservation by necessity focuses on acutely threatened, rare species that quite often happen to be large consumer species (Duffy 2003; Cardillo, Mace, Jones, Bielby, Bininda-Emonds et al. 2005).

We further corroborate the importance of species connectivity found in previous topological sequential deletion studies (Dunne et al. 2002; Srinivasan et al. 2007; Dunne et al. 2009; Staniczenko et al. 2010) and dynamical studies of single species removals (Eklöf 2006). In the topological studies, the loss of the most vulnerable species has been shown to entail as low robustness (Solé et al. 2001) or lower (Srinivasan et al. 2007) than the most connected species. Hence, despite the unexpectedly low robustness caused by removing the most generalist species, it should be the vulnerability links that are the main contributors to the importance of the most connected species (see Fig. 3).

Similarly, we find in our dynamical analysis that the effect of removing the most vulnerable species cannot be statistically separated from the effect of removing the most connected one. However, removal of the most generalist species in this approach entails robustness as low as removing the most vulnerable (see Fig. 2), implying that generality can contribute strongly to the importance of the most connected species. Thus, we conclude that bottom-up as well as top-down processes are involved in the secondary extinction cascades following the loss of the most connected species and that both vulnerability and generality links contribute to the importance of this species trait.

Our results thus point to the importance of species with many interactions, whether they are interactions with prey only, with predators only or with both. Accordingly, removing the least connected species is the sequence conferring the highest robustness. Nonetheless, Dunne et al. (2002) point to a few special cases where sparsely connected species may cause extensive secondary extinctions. One such case is when the species lost is an energetic bottleneck constituting the only link to the primary resource base for many higher level consumers. Hence, even though species with

few interactions often are least important for food web robustness, such species cannot be a priori dismissed without considering their precise trophic position in the food web (see also Allesina & Bodini 2004; Dunne et al. 2009).

Removing the consumer species with the smallest body mass was associated with low robustness to secondary extinctions. As trophic level scales positively and vulnerability scales negatively with body mass, the smallest consumer species is most likely an herbivore with many predators feeding on it. Removing these species deprives the upper trophic levels, with the exception of omnivorous species, of their links to the primary production base. This suggests that the low robustness of food webs against losing small-bodied species might predominantly be driven by cutting off or reducing the energy supply to the higher trophic levels.

Contrary to expectations, food webs were not less robust to losing the species with the largest body mass than they were to losing any random consumer. This contrasts with a model study of short-term biomass changes following the loss of a single species, where the loss of a large species had the strongest impact (Berlow et al. 2009). There are two potential explanations for this difference. First, species traits important for short term biomass effects are not necessarily the same as those important for long-term secondary extinctions. Second, the short-term biomass effects of losing large-bodied species can be strong in two directions, positive or negative, but the latter case would lead to extinctions, whereas the former would prevent them. Moreover, there is an apparent contrast of our results to those of prior studies documenting the importance of large species for creating the dynamically important relationship between body masses and trophic levels (Brose, Williams & Martinez 2006; Brose 2008). The loss of large species in our simulations, however, does not disturb this relationship between body mass and trophic level of the remaining species, which renders the web's stability undisturbed.

Caveats and further directions

As with any theoretical study, our study is based on several simplifying assumptions. For instance, adding stage-structure and thus avoiding the assumption that all individuals within a species use the same resources and have the same consumers, would result in an increased risk of secondary extinctions (Rudolf & Lafferty 2011). On the other hand, including diet flexibility and thus allowing species to switch to alternative prey would result in a decreased risk of secondary extinctions (Staniczenko et al. 2010; Thierry et al. 2011, this special feature). Dynamically, not letting the system settle between species deletions could also lead to a decrease in the number of secondary extinctions, as Sahasrabudhe et al. (2011) recently showed that removing a second species, directly following a primary extinction, may actually prevent secondary extinctions that otherwise would have occurred. Also, employing more realistic allometric functional responses (Vucic-Pestic, Rall, Kalinkat & Brose 2010; Rall, Kalinkat, Ott, Vucic-Pestic & Brose 2011) and competition among basal species for limiting nutrients (Brose 2008) might have profound effects on dynamical extinctions. Finally, robustness to species loss is not only determined by the traits of the species that is lost from the community; the characteristics of the community itself matters (Riede et al. 2011, this special feature). The data from this study suggest that certain communities are sensitive to the loss of certain species: a specific food web responds quite differently depending on which deletion sequence it is subjected to. This interactive effect of species traits with community characteristics should render further investigation.

Conclusions

The comparison of robustness in the dynamical and the topological approaches reveals that excluding dynamics may lead astray in two ways. First, top-down directed sequences have no or very low impact on robustness in topological analyses, while the dynamical analysis reveals that they may be as important as high-impact bottom-up directed sequences. Second, there are no deletion sequences that result, on average, in no or very few secondary extinctions in the dynamical approach. Instead, the *least* detrimental sequence in the dynamical approach yields an average

robustness similar to the *most* detrimental (non-basal) deletion sequence in the topological approach. Hence, a topological analysis may lead to erroneous conclusions about both the relative and the absolute importance of different species traits for robustness. The dynamical sequential deletion analysis shows that food webs are least robust to the loss of species that have many trophic links or that occupy low trophic levels. In contrast to previous studies we can infer, albeit indirectly, that both bottom-up and top-down extinction cascades may contribute to the importance of these traits.

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Appendix A: Supplementary Material.

The online version of this article contains supplementary data. Please visit XXXXX.

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Appendix A

Calculation of the Extinction Area

The measure Extinction Area (EA) used here is the same as in Allesina et al. (2009). In a graph where numbers of primary extinction is on the x-axis and the number of total (primary + secondary) extinctions is on the y-axis, the EA is the area under the curve resulting from plotting the accumulative number of total extinctions, T_p , having occurred at a specific number of primary deletions, p . The EA is calculated as $A = \frac{\sum_{p=1}^S T_p}{S^2}$, where S is the number of species in the unperturbed food web. $EA = 1$ if all species go extinct directly following the first primary extinction and $EA = \frac{S+1}{2S}$, which tends to $\frac{1}{2}$ for large S , if there are no secondary extinctions.

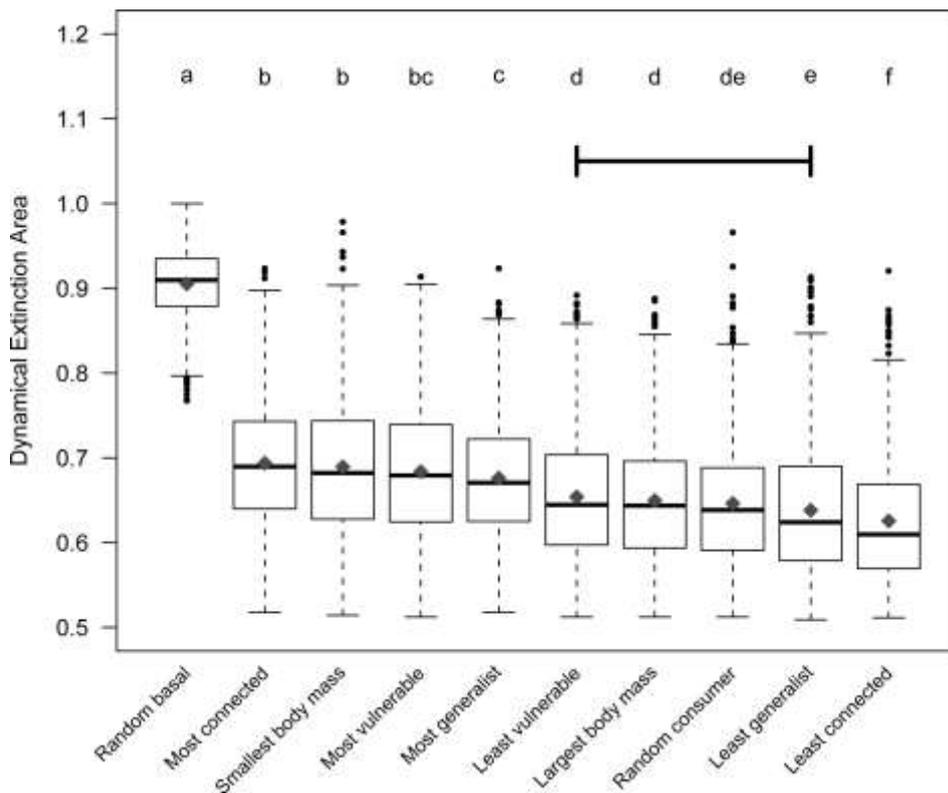


Fig. 1. The robustness to species loss in the dynamical approach. On the x-axis are the sequences, ordered by increasing robustness; on the y-axis is robustness measured as EA . Each box plot contains the EA values from the 997 food webs. Diamonds denote means. Lower case letters above the box plots denote significantly different sequences (different letters) in the ANOVA ($r^2 = 0,51$) and Tukey HSD post hoc test at the 0.05 level. Sequences not differing from the random consumer sequence are below the bar.

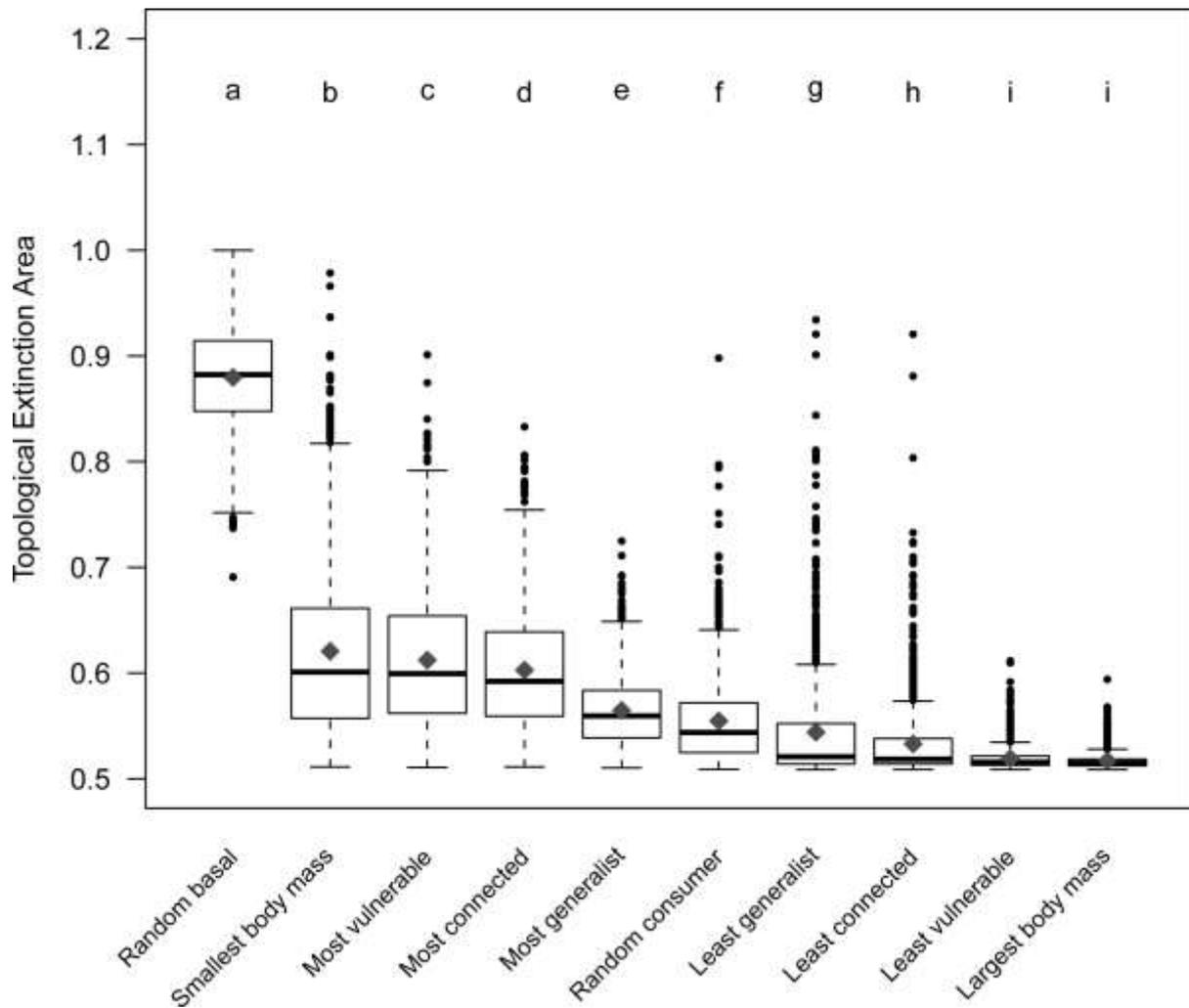


Fig. 2. The robustness to species loss in the topological approach. On the x-axis are the sequences, ordered by increasing robustness; on the y-axis is robustness measured as *EA*. Each box plot contains the *EA* values from the 997 food webs. Diamonds denote means. Lower case letters above the box plots denote significantly different sequences (different letters) in the ANOVA ($r^2 = 0,81$) and Tukey HSD post hoc test at the 0.05 level. Sequences not differing from the random consumer sequence are below the bar.

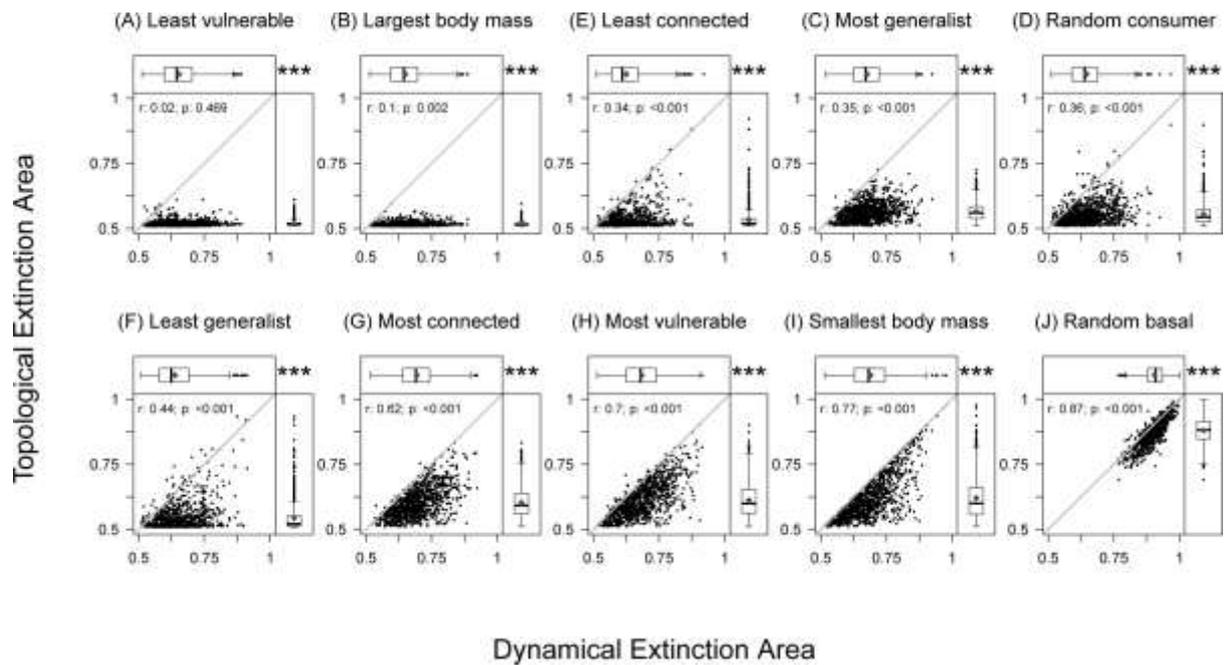


Fig. 3. Comparison of robustness between the topological and the dynamical approach. On the x-axis is robustness, measured as *EA*, in the topological approach; on the y-axis is robustness, measured as *EA* in the dynamical approach. Each subplot contains the data from one of the deletion sequences and shows the same box plots as in Figs. 1 and 2, for both the topological (horizontal box plot) and the dynamical (vertical box plot) approach. T-tests were applied to test whether mean robustness in the two approaches was different. Stars designate statistical significance in this test at the 0.001 level. Each subplot further shows the correlation between the robustness of the food webs in the topological and dynamical approach and the subplots are shown in order of increasing correlation. The correlation coefficient, *r*, and its *p* value are shown in each subplot.