









































417 well. Furthermore, previous topological studies (Allesina and Bodini 2004, Dunne et al. 2002)  
418 have found ecological networks to be “error resistant” (Albert et al. 2000) in the sense that  
419 random primary deletions of species are unlikely to cause many secondary extinctions), but  
420 vulnerable to the primary extinction of highly connected species (Allesina and Bodini 2004,  
421 Jordán et al. 2002). In contrast, our results, based on a dynamical analysis, suggest that food  
422 webs are not particularly error resistant, because random removals cause a considerable  
423 amount of secondary extinctions.

424 One property of food web structure that has been argued to correlate with food web  
425 robustness is connectance. Using a topological approach, Dunne et al. (2002) found that the  
426 robustness of food webs (against sequential removals of the most connected species)  
427 increased with connectance. Analysing our food webs that were subjected to the same type of  
428 deletion sequences as in Dunne et al., we find support for this relationship in the simulations  
429 that use a topological approach. However, in the dynamical simulations, we find little or no  
430 support for this relationship (Table 2). Only one out of six dynamical sequences show the  
431 suggested significant positive relationship between robustness and food web connectance,  
432 while four sequences instead showed a negative relationship (two of which are statistically  
433 significant). In the study of Dunne et al. (2002) (as well as in the food webs analysed here  
434 using a topological approach) a high connectance in the food webs delayed the onset of  
435 secondary extinctions following primary loss of a highly connected species. This effect may  
436 not be very surprising, as in topological studies, species go secondarily extinct only when they  
437 have lost all their prey species. Hence, a high connectance in the food web can buffer against  
438 secondary topological (structural) extinctions, as the probability of having at least one feeding  
439 interaction intact after the removal of a highly connected species increases in a well-  
440 connected system. Consequently, many studies that used topological approaches for assessing  
441 the robustness of communities against sequential extinctions have identified the importance of

442 highly connected species (de Visser et al. 2011, Dunne and Williams 2009, Memmott et al.  
443 2004, Sole and Montoya 2001, Srinivasan et al. 2007). Regardless of whether the system is  
444 well-connected or not, the removal of a highly connected species will always mean that a  
445 higher proportion of all feeding links are eliminated, compared to the removal of a species  
446 with low connectance, thus increasing the likelihood of secondary topological (structural)  
447 extinctions.

448 When species go locally extinct from a community, this affects more than just the species  
449 composition and link structure of the food web; to compensate for lost prey consumers may  
450 (i) adjust feeding efforts on their remaining resources and/or (ii) start to feed on entirely new  
451 prey species. The first mechanism involves switching (Murdoch 1969), while the second  
452 involves trophic rewiring (and requires that the fundamental niche of the consumer is wider  
453 than the realized). In reality, it can be difficult to distinguish between them (since it is difficult  
454 to know if a “new” prey really is new, or was just a very rare part of a consumer’s diet  
455 earlier). Nevertheless, a real-world example of prey-induced changes in resource use is some  
456 killer whale populations, who switched to pinnipeds and sea otters when their original prey,  
457 great whales, were severely diminished by whaling (Springer et al. 2003). To analyse the  
458 consequences for food web robustness of induced prey switching theoretically, would require  
459 the use of type 3 functional responses of consumers, in combination with some rule for how  
460 to rewire a system after every species loss. Here, we have only used linear functional  
461 responses of consumers and include no opportunity for trophic rewiring. This means that our  
462 study could represent a worst-case scenario under the dynamical approach, since switching  
463 and trophic rewiring can be expected to lower the risk of bottom-up extinctions (because  
464 consumers can compensate for lost prey). At the same time trophic rewiring might increase  
465 the risk of some top-down extinctions (because predation pressure on some prey might  
466 increase), making the net effect of switching and trophic rewiring uncertain. However, the

467 importance of considering these mechanisms is debatable since the actual extent of switching  
468 in real systems is unclear (Hassell 2000), making the incidence of trophic rewiring even more  
469 vague. Furthermore, switching and trophic rewiring could in theory be the result of either  
470 changing diet preferences of individual consumers (individual response), or changing  
471 proportion of individuals with different fixed preferences (population level response). To  
472 distinguish between these two possibilities could be important since they can be expected to  
473 occur on different time scales (with a behavioural response of individuals being faster than a  
474 population level response). If it can be established how and under what circumstances  
475 switching and trophic rewiring occur in real systems (e.g., using high resolution food web  
476 data, with diet information on individual consumers and how it varies with prey availability),  
477 future studies should analyse the consequences of this for the robustness of food webs.

478       Curtsdotter et al. (2011) evaluated the impact of extinction sequences based on the  
479 following species traits: connectivity, generality, vulnerability and body size. So far, this and  
480 our study are the only studies incorporating species dynamics when assessing the response of  
481 ecological communities to sequential species deletions. In the deterministic deletion  
482 sequences analysed by Curtsdotter et al., basal species were not allowed to go primarily  
483 extinct. Despite this, they found sequences based on traits resulting in a bottom-up direction  
484 of extinctions to be the most destructive. We instead identify traits resulting in a top-down  
485 oriented removal of species to be most destructive (provided that basal species are not  
486 allowed to go primarily extinct) and traits resulting in a bottom-up oriented deletion of species  
487 only to be important when basal species could go primarily extinct. Since the functional  
488 response of consumers affects dynamical properties of food web models and the structure of  
489 food webs has been shown to influence the response of communities when subjected to  
490 perturbations (Dunne and Williams 2009, Riede et al. 2011) as well as the extinction risk of  
491 species (Jonsson et al. 2006, Karlsson et al. 2007), differences in the results between our

492 study and the study by Curtsdotter et al. (2011) could potentially be due to differences in the  
493 dynamical model and/or the food web structures used. The studies differ in that (i) species  
494 dynamics in our study (as in Saharashuhde & Motter 2011) are described by Lotka-Volterra  
495 predator-prey interactions with a linear functional response, whereas Curtsdotter et al. used a  
496 bioenergetic predator-prey model with functional responses of type II and type III, (ii) our  
497 model systems started from a state where all species coexist in a deterministic environment  
498 before species loss took place, while Curtsdotter et al. started from a non-stable state (making  
499 it difficult to separate between secondary extinctions caused by a primary species deletion and  
500 extinctions that are taking place as a result of the non-stable model), and (iii) the study of  
501 Curtsdotter et al. (2011) used food webs created using the niche model (Williams and  
502 Martinez 2000) while our webs were generated using a sequential assembly algorithm. Thus,  
503 differences in the modelling approach and results between our study and the study by  
504 Curtsdotter et al. (2011) highlights the need to explore in more detail how network structure  
505 and functional responses of consumers interact and affect the vulnerability of food webs to  
506 repeated species extinctions. More specifically, real food webs differ in number of species,  
507 species composition as well as trophic structure and there is probably a continuum of  
508 functional responses of different consumers, from almost linear (type 1) to sigmoid (type 3),  
509 with different types of communities being dominated by different types of consumers. To  
510 address this complexity and provide a more stable ground for any general conclusions to be  
511 drawn on what affects the robustness of food webs to species loss (and how), future  
512 theoretical studies should use a gradient of web sizes and connectance values, in combination  
513 with different distributions of functional responses of consumers, and different web structures  
514 (generated using several different web algorithms). This is not a trivial problem since a large  
515 number of combinations will need to be analysed and functional responses of type 2 and 3  
516 require several additional parameters (attack rates, handling times, interference exponents

517 etc.) for which it is not obvious how to obtain realistic values (although successful attempts  
518 have been made to relate these parameters to body size in a mesocosm experiment; Schneider  
519 et al. 2012). However, if these problems can be overcome, a comprehensive theoretical  
520 analysis of the effect of trophic structure and consumer functional responses on the robustness  
521 of food webs to species loss will generate many testable hypotheses. Our study for example,  
522 predicts that removing consumers at the top of food chains could lead to as many secondary  
523 extinctions in communities as removing primary producers and, in principle, this and similar  
524 hypotheses can be tested experimentally, using micro- or mesocosm experiments (see e.g.,  
525 Sanders et al. 2013). Such future combination of theoretical prediction and experimental  
526 testing of hypothesis has the potential to significantly advance our understanding of key  
527 factors that affect the response of food webs to species loss.

528 Here, we based the rank of the robustness of food webs to different extinction sequences,  
529 as in many other studies, on  $R_{50}$ . However, focusing on  $R_{50}$  is a subjective decision and the  
530 importance of different extinction sequences could in theory differ between different collapse  
531 thresholds. However, for the network structures, deletion sequences and dynamical model  
532 used here the rank of robustness changed only marginally if other collapse thresholds were  
533 used (e.g.  $R_{20}$  or  $R_{80}$ , Jonsson et al. 2014), suggesting that  $R_{50}$  is a robust and useful measure.  
534 Furthermore we found that  $R_{50}$  tends to be highly correlated with the alternative measure of  
535 food web robustness  $1.A_E$  (Fig. S2).

## 536 **Conclusions**

537 Although earlier studies (e.g., Cardillo et al. 2005, Lande 1993, Petchey et al. 1999) have  
538 indicated that certain groups of species, including top predators and large-bodied species, are  
539 very sensitive to human induced perturbations and have a high extinction risk, few studies  
540 have actually evaluated the risk of secondary extinctions in ecological communities due to  
541 realistic extinction scenarios. The few exceptions (e.g., de Visser et al. 2011, Srinivasan et al.

2007 using a topological approach, and Curtsdotter et al. 2011 using a dynamical approach) have, however, all found such extinctions to have a relatively low impact on community structure. We show here instead that, when species dynamics are considered, removing large-bodied species at the top of food chains can be as destructive as removing only primary producers, suggesting that the consequences of losing extinction prone species may be highly underrated. In other words, our study suggests that large-bodied species with a high trophic position and low numerical abundance may play an important role in upholding the structure of ecological communities. This is supported by several studies that have revealed the importance of top predators in real systems (where the loss of these species resulted in dramatic effects, e.g., Beschta and Ripple 2009, Estes and Palmisano 1974, Myers et al. 2007). Furthermore, recent theoretical studies have shown that large-bodied (Berg et al. 2011) and rare (Berg et al. in prep.) consumer species also have disproportionately large effects on dynamical and structural properties of a community (resilience and distribution of equilibrium abundances) when exposed to small perturbations. Taken together, these results suggest that the response of communities to small and large perturbations may be consistent so that the same kinds of species are important in both situations. If correct, this has important implications: the same kinds of species that have been found to be keystone species (in the sense of causing disproportional effects if exposed to small as well as large perturbations) are also the ones most prone to extinctions (e.g., Lande 1993). To conclude, our results indicate that the ongoing species loss worldwide, which disproportionately targets large-bodied species with a high trophic position and low numerical abundance, may, contrary to the findings of many previous studies (e.g., Curtsdotter et al. 2011, de Visser et al. 2011, Dunne et al. 2002, Jacob et al. 2011, Srinivasan et al. 2007), cause severe degradation of community structure and ecosystem functioning and suggests, in line with the results of Saavedra et al. (2011), that a positive correlation between a node's vulnerable to extinction and its' effect on network



567 persistence could be general property of ecological networks. Thus, in addition to ethical  
568 arguments, there may indeed be important ecological reasons for focusing much conservation  
569 efforts on rare, extinction-prone species.

570

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680 **Table 1.** Proportion of species going secondary extinct with a lower ( $Th_{low}$ ), higher ( $Th_{high}$ ) or  
681 equal ( $Th_{equal}$ ) trophic position, respectively, than the primarily removed species. Proportions  
682 are shown for extinction sequences with the lowest  $R_{50}$  (when basal species are not included in  
683 the extinction sequence).

<b>Extinction sequence</b>	<b><math>Th_{low}</math></b>	<b><math>Th_{high}</math></b>	<b><math>Th_{equal}</math></b>
largest body size	0.828	0.102	0.07
highest biomass abundance	0.154	0.587	0.259
highest net effect	0.75	0.143	0.107
lowest numerical abundance	0.948	0.039	0.013
least vulnerable	0.778	0.13	0.092
highest trophic position	0.995	0	0.005

684

685

686 **Table 2.** Regression statistics for the relationship between connectance ( $C = L/S^2$ ), and  
 687 topological and dynamical robustness ( $R_{50}$ ) respectively, in 100 model communities exposed  
 688 to primary species extinctions, for the deletion sequences studied by Dunne et al. (2002).

Deletion sequence	$b$	$P$	$R^2$
<i>Topological approach</i>			
Most connected All	0.284	0.000	0.475
Most connected NB	0.249	0.005	0.077
Least connected All	0.138	0.628	0.002
Least connected NB	NA	NA	NA
Random All	0.510	0	0.184
Random NB	0.668	0.076	0.032
<i>Dynamical approach</i>			
Most connected All	0.262	0.000	0.230
Most connected NB	-0.015	0.529	0.004
Least connected All	-0.105	0.000	0.140
Least connected NB	-0.096	0.001	0.110
Random All	0.023	0.682	0.002
Random NB	-0.054	0.223	0.020

689 Note:

690  $b$ : the estimated slope of the linear regression ( $R_{50} = a + bC$ ),

691  $P$ : the significance of the relationship

692  $R^2$ : the coefficient of determination.

693 NA: Regression statistics not available due to no variation in  $R_{50}$  between food webs



694 All: Deletion sequences where all species (including basal) could be deleted.

695 NB: Deletion sequences where basal species were protected from deletion.

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696 **LEGENDS**

697 **Figure 1.** Food web collapse down to 50% remaining species in model food webs as a result  
698 of different deletion sequences based on species characteristics (see Methods), where basal  
699 species were (A) allowed to and (B) could not go primarily extinct. Dashed diagonal in (A)  
700 and (B) represent the hypothetical case where primary species deletions cause no secondary  
701 extinctions. Pairs of deletion sequences that are primarily top-down and bottom-up oriented  
702 respectively are coded by red and green colour, while pairs of deletion sequences with no  
703 clear direction, with respect to trophic position, are coded by blue and orange colour.

704 **Figure 2.**

705 Average dynamical and topological robustness ( $R_{50}$ ) of 100 ecological communities subjected  
706 to deletion sequences based on eight species traits. Each subplot shows the robustness for a  
707 given sequence where species are deleted in order from the maximum (= max) or minimum  
708 value (= min) of the trait, with basal species either being allowed to be deleted (= All) or  
709 being protected from deletion (= NB). Letters above bars group dynamical sequences within  
710 subplots that are not significantly different (at a significance level of 0.05). Error bars show  
711 the 95% CI. Different shades of bars signify the proportion of deleted (primarily extinct)  
712 species in dynamical simulations that come from one of four trophic groups (see legend)  
713 where Tg 1 includes all basal (producer) species (defined as having a trophic position,  $tp$ , =  
714 1). Tg 2 includes all herbivore species (i.e. species with  $tp$ , = 2, where  $tp$  of a consumer is one  
715 plus the average trophic position of its prey), Tg 3 corresponds to species with  $2 < tp \leq 3$  and Tg  
716 4 to species with  $3 < tp \leq 4$ . Topological sequences (dotted bars) without error bars produced no  
717 secondary extinctions and thus show no variation in  $R_{50}$  among food webs (i.e. all  $R_{50}$ 's =  
718 0.5).  $r^2$  values give the amount of variation in dynamical  $R_{50}$  values of individual webs that  
719 can be explained by the corresponding topological  $R_{50}$  value. For sequences without any  
720 variation in topological  $R_{50}$  values  $r^2$ =NA.

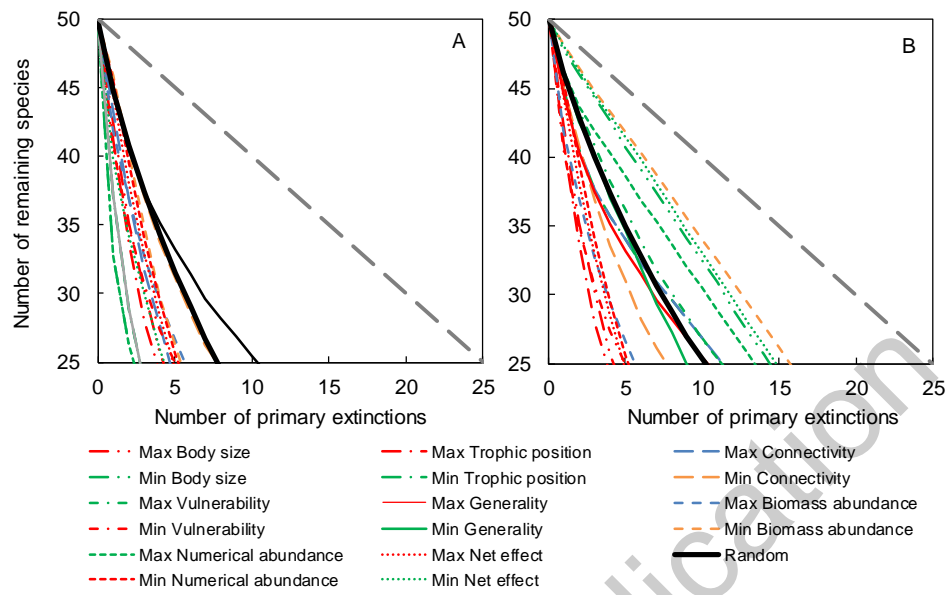
721 **Figure 3.** The relationship between mean dynamical robustness and mean topological robustness  
722 (averaged across all model webs) for deletion sequences where basal species could (A) and could not  
723 (B) be deleted. Dashed lines are least linear square regression lines.

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Figure 1



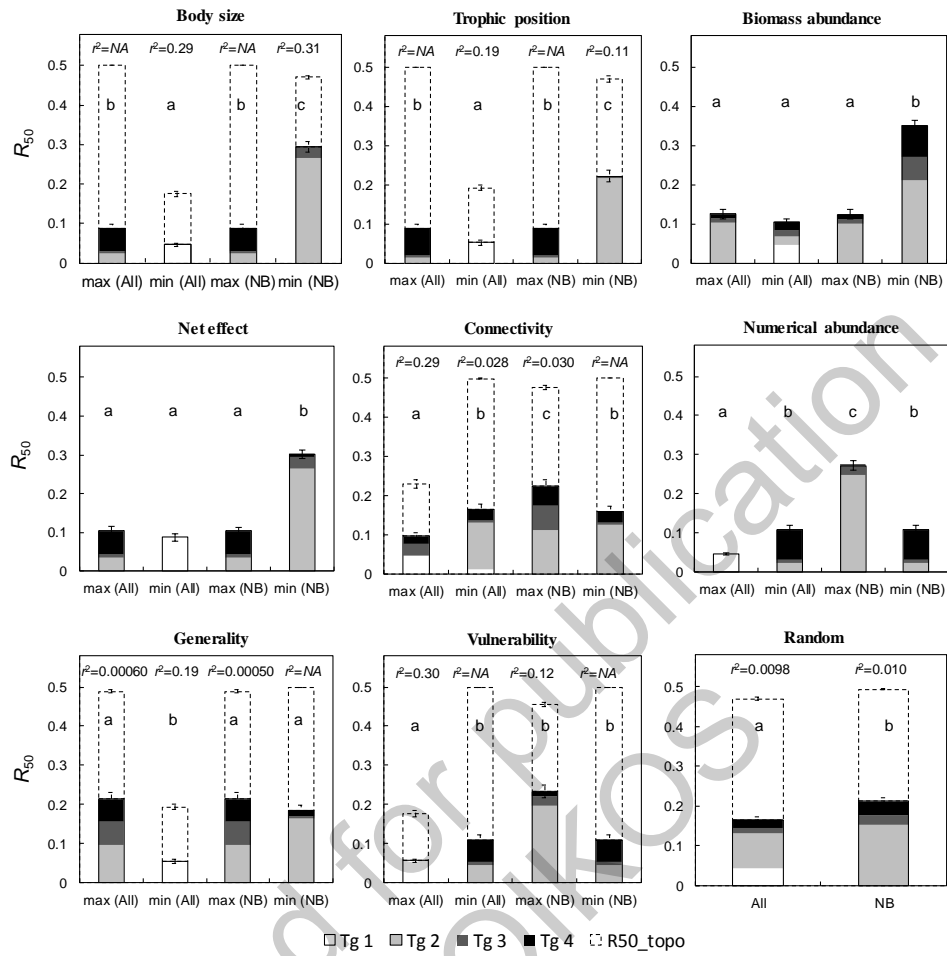
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Figure 2

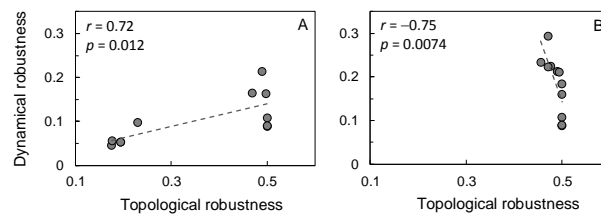


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**Figure 3**



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