

LETTER

Stage structure alters how complexity affects stability of ecological networks

V. H. W. Rudolf¹* and Kevin D. Lafferty²

¹Department of Ecology and Evolutionary Biology, Rice University, Houston, TX, USA

²Western Ecological Research Center, U.S. Geological Survey, c/o Marine Science Institute, UC, Santa Barbara, CA 93106, USA

*Correspondence: E-mail:

volker.rudolf@rice.edu

Abstract

Resolving how complexity affects stability of natural communities is of key importance for predicting the consequences of biodiversity loss. Central to previous stability analysis has been the assumption that the resources of a consumer are substitutable. However, during their development, most species change diets; for instance, adults often use different resources than larvae or juveniles. Here, we show that such ontogenetic niche shifts are common in real ecological networks and that consideration of these shifts can alter which species are predicted to be at risk of extinction. Furthermore, niche shifts reduce and can even reverse the otherwise stabilizing effect of complexity. This pattern arises because species with several specialized life stages appear to be generalists at the species level but act as sequential specialists that are hypersensitive to resource loss. These results suggest that natural communities are more vulnerable to biodiversity loss than indicated by previous analyses.

Keywords

Body size, complex life cycle, diversity–stability, extinction, food web, host–parasite, ontogenetic niche shift, predator–prey, species richness.

Ecology Letters (2011) 14: 75–79

INTRODUCTION

Destruction and fragmentation of habitats, invasive species, pollution and climate change are leading to unparalleled and increasing rates of species extinction (Chapin *et al.* 2000; McCann 2000; Sala *et al.* 2000; Loreau *et al.* 2001). How the complexity of natural ecosystems affects their robustness to this biodiversity loss is a long-standing debate (May 1973; McCann 2000; Loreau *et al.* 2001; Montoya *et al.* 2006). A key assumption of robustness analysis is that consumers go extinct if they cannot obtain essential resources within their foraging range (implying that resource loss occurs across large spatial scales) (Dunne *et al.* 2002). A recent review (Fowler 2010) indicates considerable observational and experimental evidence for such secondary extinctions. For instance, loss of an estuarine snail led to the secondary extinction of several parasites that used the snail as intermediate host (Torchin *et al.* 2005). Secondary extinction cascades can dramatically reorganize entire communities. Most notably, community disassemblies occurred after Pleistocene sea-level rise formed the archipelagoes of Indonesia and Malaysia (Okie & Brown 2009) and after a hydroelectric dam in Venezuela created islands of forest fragments in 1986 (Terborgh *et al.* 2001).

Studies investigating how complexity affects stability have been criticized for their simplistic representation of ecological networks (Cohen *et al.* 1993; Polis & Strong 1996; Woodward & Hildrew 2002). In particular, food-web data rarely include information at the ontogenetic stage, requiring researchers to assume resources are substitutable through all life stages (e.g. McCann *et al.* 1998; Williams & Martinez 2000; Dunne *et al.* 2002; Montoya *et al.* 2006; Petchey *et al.* 2008; Gross *et al.* 2009). This may be a reasonable approach for some mammals and birds, clonal invertebrates, filter feeders, scavengers, detritivores, hemi-metabolous herbivorous insects and parasites with direct life cycles. However, ecological interactions change during the ontogeny of individuals in the large majority of species (Werner & Gilliam 1984; Polis & Strong 1996; Woodward & Hildrew 2002). For instance, ontogenetic niche shifts are a major mode of life in 25 of 33 phyla, or 80% of animal taxa (Werner 1988), which could have important consequences for the structure and dynamics of ecological networks (Persson 1999; Persson *et al.* 2003; Lafferty *et al.* 2006; Rudolf 2007b; Schreiber & Rudolf 2008). Species with feeding larvae (marine fishes, marine invertebrates and amphibians), holometabolous insects (terrestrial and aquatic ecosystems), species with gape-limited predation (particularly fishes, amphibians and reptiles) and parasites with complex life cycles (all ecosystems), have ontogenetic diet shifts (Werner & Gilliam 1984). In addition, many herbivores and predators require complimentary plant or animal species to meet stoichiometric balances (Pennings *et al.* 1993), and some species have sex-specific diets (e.g. mosquitoes) suggesting that resources are unlikely to be all substitutable even in the absence of ontogenetic niche shifts.

The key prediction we evaluate is that species with broad diets should be less vulnerable to secondary extinction because they will be able to persist on alternative resources as biodiversity declines. Broad diets (i.e. 'generalist' species; Fig. 1) also increase the complexity of ecological networks, suggesting that complexity may stabilize ecological networks (McCann 2000; Dunne *et al.* 2002; Montoya *et al.* 2006). However, a species with a broad diet could be an *ontogenetic specialist* (with several stages, each of which consumes a different resource; Fig. 1). Ontogenetic specialists should face a dramatically higher risk of secondary extinction at the species level because their resources are not all substitutable (Fig. 1). The distinction between a generalist and an ontogenetic specialist could have important implications for the robustness of networks. For instance, trematode parasites reduce the robustness of an estuary food

web to secondary extinction, in large part due to their complex life cycles (Lafferty & Kuris 2009). It is otherwise unknown how ontogenetic shifts affect the extinction risk of species, the stability of complex communities or the relation between complexity and stability of natural ecosystems. We analysed model and empirical networks to investigate when and how these ontogenetic changes in resource use impact network stability and whether these conditions are likely to be met in nature.

METHODS

Modelling stage-structured food webs

Current disagreement in the literature on the relationship between stability and complexity is partly due to different methodologies. For this reason, we relied on robustness analysis (Dunne *et al.* 2002; Dunne & Williams 2009). Following previous studies (e.g. Brose *et al.* 2006; Dunne & Williams 2009; Gross *et al.* 2009), we simulated theoretical network structures using the 'niche model' where the nodes were randomly assigned a niche value based on the beta distribution (Williams & Martinez 2000). Randomly dividing species into distinct stages that have an overlap p ($0 \leq p \leq 1$) in their resource use allowed us to impart additional structure to the model at the species level. In particular, we generated a range of networks with different numbers of species (N) and connectance (C) and restricted variation in connectance to $< 5\%$ of the specified value. After all links in a network were established this way, we calculated the stage-specific link matrix for each consumer within a given network by randomly drawing the number of stages (S) for each species from a uniform distribution in the interval $1 - M$, where M is the total number of resources of a species (R). M never exceeded the maximum number of prey per species as this would result in functionally redundant stages without dynamical consequences. To test how robust models were to the value of M , we constrained M to a range of maximum levels $< R$ (see Appendix S1 in Supporting Information). Primary producers were not divided into stages as this would have no dynamical consequences. Each stage within a species was allowed to consume each species' resource with the probability p ($0 \leq p \leq 1$), and we assured that each stage consumed at least one resource. Extensive simulations showed that p directly corresponded to the empirically estimate of the average niche overlap, p within a network. Thus, varying p allowed us to examine how changes in the average niche overlap among stages within species impacts network robustness. Note that p is the niche overlap among stages averaged across species in a network. Species varied in the extent that their stages overlapped. Our analyses do not require knowing the ontogenetic ordering of life stages and their diets; our models inherently consider different types of resource overlap, ranging from no nestedness to complete nestedness. Additional simulations indicate that networks with stages and $p = 1$ show identical robustness to networks without stages, indicating that introducing stages itself does not alter the properties of the network. Comparisons to our empirical networks indicated that simulated stability estimates obtained from these models were well within the 95% CI of empirical estimates.

Robustness analysis

We analysed network stability by examining the potential for secondary extinctions after species loss. Secondary extinctions occurred when a single stage of a consumer lost all its resources. This assumes that each stage has to have at least one resource for the whole species to persist, and primary producers are only vulnerable to primary

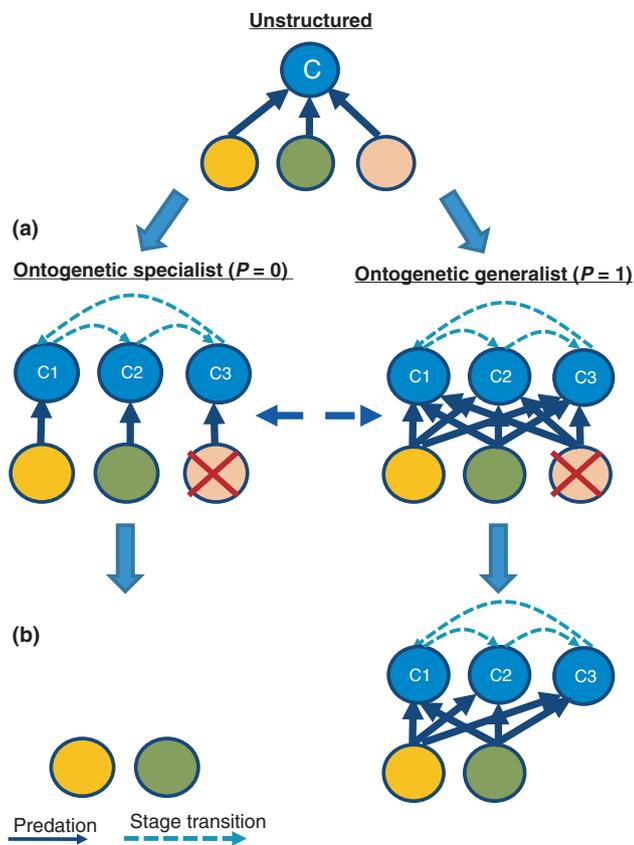


Figure 1 Biodiversity loss in stage-structured networks compared with non-structured networks. (a) Examples of the information lost by pooling feeding relationships of different stages (C1–C3) of a generalist predator (C) with multiple prey species. Unstructured networks make no differentiation between *ontogenetic specialists* with no overlap in resource use among stages ($p = 0$) or *true generalists* where all stages consume all resources, or other scenarios between both extremes. (b) Loss of a resource can have very different consequences for the extinction risk of species depending on the degree of diet overlap among stages ($p = 1$ vs. $p = 0$), but this cannot be predicted from unstructured networks. Solid arrows indicate resource–consumer relationships and dashed arrows indicate transitions (development/reproduction) between ontogenetic stages.

removals, not secondary extinctions. Primary species loss was simulated by sequentially removing a random species from the web and adjusting the network for any subsequent secondary extinction before the next primary removal. The structural ‘robustness’ of networks (Dunne & Williams 2009) was calculated as the fraction of species that needed to be removed from a given network to result in $\geq 50\%$ extinctions (including primary removals plus secondary extinctions). Thus, robustness is at maximum at 0.5 indicating no secondary extinctions, and the minimum is $1/N$.

Relative importance of ontogenetic niche shifts

To evaluate the importance of ontogenetic specialization relative to other factors that are known to influence network stability, we analysed the robustness of 4500 simulated networks that varied in species richness (N), connectance (C) and overlap in resource use among stages (p) (see Methods; Table 2). We examined the effects of N , C and p using a multifactorial design with three levels of connectance (0.1, 0.2, 0.3), three levels of species richness (15, 35, 55) and five levels of p (0, 0.25, 0.5, 0.75, 1) using a general linear model. Each of the 45 combinations was replicated 100 times. While it is important to keep in mind that the relative change within a parameter differs, the parameter ranges represent that observed in natural networks and are comparable to previous studies. Comparisons of effect sizes were based on F statistics.

Species extinction risks

We calculated the extinction risk of individual species by randomly removing 30% of the species from the network and then determined which of the remaining species went extinct. Additional simulations indicated that altering the % of species removed did not alter the general results. As above, species were considered extinct if they lost all their

resources, or when one of their stages lost all its resources. Extinction risk was calculated as the proportion of extinctions for a given consumer type (i.e. based on the number of resources per species) following random species removals in 50 000 simulated webs. Note, that this analysis only focused on primary extinctions and did not include secondary extinction cascades as those were already included in the robustness analysis of networks.

Empirical

We calculated the average overlap among stages in eight empirical networks as follows. For species with metamorphic stages or stage-specific information on resource use, $p = [\sum_{i,j=1}^S (\kappa_{i,j}/w_{i,j})]/S$, for $i \neq j$, where S is the number of stages within a species, $\kappa_{i,j}$ is the total number of resources shared between stages i and j and $w_{i,j}$ is the total number of unique resources used across both stages. Some species, like predatory fishes and invertebrates, grow substantially during development and have gape-limited ontogenetic diet shifts. For these species we assumed $p = 0.4$, after Woodward & Hildrew (2002). All other species were conservatively assumed to be ontogenetic generalists ($p = 1$). We estimated connectance in the webs according to the first method recommended by Lafferty *et al.* (2006) for parasite webs (i.e. eliminating predator–parasite and parasite–parasite links from the denominator, though this approach did not alter the qualitative nature of the results).

We used a general linear model to test the effect of connectance and stages on robustness, using webs as replicates. We then used a general linear model to test how stages and parasites affected the robustness of empirical webs. The webs used included one arctic lake (Takvatn) (Amundsen *et al.* 2009) and four intertidal estuary webs [Carpinteria Salt Marsh, Bahia San Quintin, Estero de Punta Banda (Kuris *et al.* 2008; Hechinger *et al.* in preparation) and Ythan Estuary (Huxham & Raffaelli 1995)], an intertidal mudflat [Company Bay (Thompson *et al.* 2005)], and one stream web [Muskingham Brook (Hernandez & Sukhdeo 2008)], for which parasites and their various stages are carefully quantified. Three of the webs (Muskingham Brook, Ythan Estuary and Company Bay) did not separate species by stages, hence we used information on natural history to determine species that clearly had distinct larval feeding stages. Additional analysis indicated that removing these three networks did not alter the general results. Robustness was estimated as the median of 5000 random disassemblies. Note, that robustness analysis was performed on the actual stage-specific feeding links in each network and not on network average estimates of p . As for other robustness analyses, we included only feeding links that would entirely support the persistence of a consumer (discounting, for instance, most predator–parasite links).

RESULTS

We examined how ontogenetic niche shifts impacted the stability of complex ecological networks by focusing on structural robustness (Dunne *et al.* 2002), that is, the potential for secondary extinctions after simulation of primary species loss (see Methods). Under the classical assumption of $p = 1$, increasing network complexity via increased connectance (i.e. the proportion of possible interactions) increased the robustness of networks to biodiversity loss as predicted by classical theory (Borrvall *et al.* 2000; Dunne *et al.* 2002; Eklof & Ebenman 2006). Although previous studies suggest that many species shift their resources during ontogeny (Werner & Gilliam 1984; Werner 1988; Polis & Strong 1996; Woodward & Hildrew 2002; Lafferty *et al.* 2006; Rudolf & Armstrong 2008; Schreiber & Rudolf 2008), p has not been quantified across ecological networks. We estimated the average overlap in resource use among stages (p) in seven diverse empirical networks that have sufficient detailed information on stage-specific resource use for a variety of species (Table 1). Resource overlap is least ambiguous for species with metamorphosis; on average, only 0–7.6% (p range: 0–0.076) of resources were shared among ontogenetic stages (Table 1). However, empirical estimates suggest that even predatory species without metamorphosis may share only 40% on average between size classes (p range: 0.32–0.55) (Woodward & Hildrew 2002). We assumed this applied to species like predatory fishes that show diet shifts as they grow due to gape limitation. For species without clear diet shifts due to growth or metamorphic stages, we conservatively estimated that all resources were substitutable ($p = 1$). These estimates, when applied to complete networks (see Methods), suggested average resource overlap among stages ranged from 35 to 80% ($p = 0.35$ –0.8; Table 1). Thus, the classical assumption of uniformity of resource use within species is highly unlikely in natural communities, especially in systems dominated by species with metamorphic stages.

Figure 2 shows that the magnitude of ontogenetic shifts in resource use seen in nature (Table 1) strongly decreases the stability of ecological networks. In addition, the relationship between robustness and connectance (i.e. complexity) switches from positive to negative below a critical level of resource overlap among stages (Fig. 2a). This shift and negative relationship cannot be predicted by current unstructured models. The specific critical level of this reversal depends on some other factors (i.e. the number of ontogenetic stages within species and on the decline in p with increased resource use, see Methods; Appendix S1) and could even occur at relatively high levels of resource overlap for moderate to high levels of connectance. For the many species

Table 1 Average overlap in resource use among stages (p) in empirical networks

Network	Average overlap among stages (p) (\pm SD)		n_s	N	C
	Metamorphic species network	Full consumer network			
TAK	0.00 (\pm 0.000)	0.790 (\pm 0.39)	7	43	0.149
CSM	0.073 (\pm 0.221)	0.627 (\pm 0.456)	53	154	0.120
BSQ	0.039 (\pm 0.159)	0.571 (\pm 0.469)	60	155	0.106
EPB	0.031 (\pm 0.141)	0.569 (\pm 0.466)	76	201	0.113
MUS	0.061 (\pm 0.184)	0.370 (\pm 0.413)	30	58	0.104
YTH	0.076 (\pm 0.246)	0.790 (\pm 0.462)	52	128	0.096
COM	0.073 (\pm 0.213)	0.619 (\pm 0.465)	27	73	0.170

TAK, Takvatn; CSM, Carpinteria Salt Marsh; BSQ, Bahia San Quintin; EPB, Estero de Punta Banda; MUS, Muskingham Brook; YTH, Ythan Estuary; COM, Company Bay.

n_s , number of species with information on stage-specific resource use within a food web; N , total number of species; C , connectance. Network estimates of p for metamorphic species are based on species with stage-specific information (n_s). Full consumer network estimates of p include metamorphic species and extrapolated p values for all other species ($N - n_s$) based on natural history information (Methods). The webs used included one arctic lake (Takvatn) (Amundsen *et al.* 2009), four intertidal estuary webs [Carpinteria Salt Marsh, Bahia San Quintin, Estero de Punta Banda (Kuris *et al.* 2008; Hechinger *et al.* in preparation) and Ythan Estuary (Huxham & Raffaelli 1995)], an intertidal mudflat [Company Bay (Thompson *et al.* 2005)], and one stream web [Muskingham Brook (Hernandez & Sukhdeo 2008)], for which parasites and their various stages are carefully quantified.

in our empirical webs with high levels of ontogenetic niche shifts (16–51% of species within our webs; Table 1), extinction risk increased with resource links per species, leading to a negative relationship between complexity and robustness (Fig. 2b). This calls into question the generality of many current models (e.g. Dunne *et al.* 2002; Ebenman *et al.* 2004; Eklöf & Ebenman 2006; Gross *et al.* 2009). In summary, low resource overlap among stages, as seen in nature, strongly reduces network robustness and can reverse the previously observed positive relationship between network stability (i.e. robustness) and complexity, particularly for certain groups. This indicates that the complexity–stability relationship is not uniform across and within communities but depends on the degree of ontogenetic niche overlap within communities.

To evaluate the importance of ontogenetic specialization relative to other factors that are known to influence network stability, we analysed the robustness of 4500 simulated networks that varied in species richness (N), connectance (C) and overlap in resource use among stages (p) (see Methods; Table 2). Overall, changes in resource overlap among stages (p) had by far the strongest effect ($F = 11\,239.1$, $P < 0.0001$), which was 15-fold higher than that of increasing the number of species ($F = 772.5$, $P < 0.0001$), and sixfold higher than the effect of connectance ($F = 1919.2$, $P < 0.0001$; Table 2). This indicates that the destabilizing effect of ontogenetic niche shifts can override the effects of other factors known to stabilize ecological networks.

For parasites with complex life cycles, stages are unambiguous and the resource needs of each stage are also possible to document. This makes them ideal for investigating how the consideration of stages affects network stability. For seven large empirical networks (Table 1) for which stage-specific resource use was available for

parasites and some other species, we calculated robustness by either including or not including parasites crossed with keeping or pooling stages. In agreement with our model predictions (Fig. 2a; Appendix S1), p was high enough for there to be a positive association between connectance and robustness ($F_1 = 9.16$, $P = 0.012$), independent of the destabilizing effect of stages ($F_1 = 35.1$, $P < 0.0001$). However, the stability of the networks was strongly reduced compared with predictions from unstructured models. Stages (nested within web; $F_7 = 15.2$, $P = 0.002$) and inclusion of parasites (nested within web; $F_7 = 4.5$, $P = 0.044$) reduced the robustness of empirical networks. The interaction between the two variables indicated that the effect of parasites was mostly driven by stages (parasite \times stage, $F_1 = 21.9$, $P = 0.003$; Fig. 3), indicating it was the ontogenetic niche shifts of parasites, not parasites *per se*, that strongly reduced robustness. The reduction in robustness associated with the presence of stages seems highly conservative given that parasite richness and stage specificity in free-living species (e.g. predators) were strongly underestimated in these networks, and the number of stages within parasites is typically lower ($M = 3$) than expected in many predatory species (see Supporting information). This destabilizing effect of ontogenetic niche shifts confirms the results from our models and indicates that robustness in empirical networks is indeed strongly reduced by ontogenetic niche shifts. The implication is that past studies of robustness have over-estimated the stability of natural communities and, in some cases, may have reversed the association between complexity and stability.

DISCUSSION

Resolving whether complexity imparts stability has been a perennial challenge in ecology (May 1973; McCann 2000; Montoya *et al.* 2006). Past network analyses have typically assumed that all members of a species are identical, or at least that any variation below the species level is irrelevant for the stability of complex ecological networks (May 1973; McCann *et al.* 1998; Dunne *et al.* 2002; Ebenman *et al.* 2004; Brose *et al.* 2006). Here, we show that this assumption of uniformity of resource use within species is highly unlikely both, for theoretical networks structured to mimic natural communities where ontogenetic niche shifts in diets are ubiquitous and for empirical networks that contain parasites [which may differ in structure from networks created by the niche model (Warren *et al.* 2010)]. Our results suggest that these ontogenetic niche shifts can fundamentally alter the complexity–stability relationship, the stability of complex communities and species’ extinction risks. Specifically, in our model and empirical networks, the robustness of ecological networks to secondary extinctions strongly decreased with increasing differences in resource use among ontogenetic stages within species. Although our analyses of empirical networks were restricted to aquatic systems, empirical data suggests that ontogenetic niche shifts are also ubiquitous and often strong in terrestrial systems (Polis 1991), but more empirical data are needed to test how general our results are across ecosystems. In light of our simulations, this suggests that natural communities might be more vulnerable to biodiversity loss than previous analyses indicated and argues for resolving interactions below the species level. If differences among life stages are sufficiently large, then stability decreases with increasing complexity, counter to the always-positive relationship predicted by classical unstructured models (Borrvall *et al.* 2000; Dunne *et al.* 2002; Ebenman *et al.* 2004; Eklöf & Ebenman 2006). Furthermore, consideration of ontogeny can reverse the perception of which species face the highest risks of extinction. In general, these findings suggest that the complexity–stability relationship is not consistently positive across and within communities but instead depends on the degree of ontogenetic niche shifts.

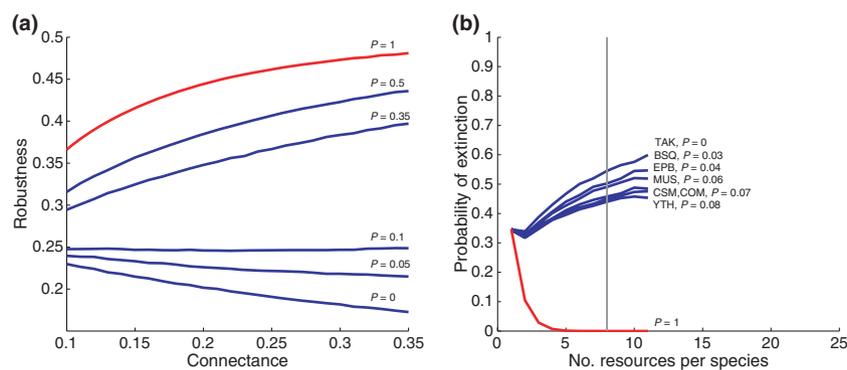


Figure 2 Effects of ontogenetic niche shifts on the stability and extinction risk in ecological networks. (a) Robustness of networks as a function of connectance for unstructured networks ($p = 1$, red line) and different levels of resource overlap among stages (blue lines), with $N = 25$. (b) The individual extinction risk of a species with a given number of resources in 50 000 networks after removing 30% (dashed line) in each network at classical ($p = 1$, red line) and natural levels ($p = 0.8-0$, blue lines) of p . $N = 25$, $C = 0.15$. Letters indicate natural networks of species with metamorphic stages (see Table 1 for details).

Table 2 Effects on network stability

Dependent variable	Effect on stability	SS	d.f.	<i>F</i>	<i>P</i> -value
Species richness ($N = 15, 35, 55$)	↑	1.26	2	772.5	<0.0001
Connectance ($C = 0.1, 0.2, 0.3$)	↑	3.13	2	1919.2	<0.0001
Average overlap among stages ($p = 0, 0.25, 0.5, 0.75, 1$)	↓	36.66	4	11 239.1	<0.0001
$N \times C$	↑	0.14	4	43.7	<0.0001
$N \times p$	↓	3.82	8	586.1	<0.0001
$C \times p$	↓	2.42	8	371.6	<0.0001
$N \times C \times p$	↓	0.24	16	18.4	<0.0001
Error		3.63	4455		

Analyses were performed using a general linear model. Each of the 45 combinations was replicated 100 times resulting in 4500 simulated networks. While it is important to keep in mind that the relative change within a parameter differs, the parameter ranges represent the range observed in natural networks and are comparable to previous studies. Due to the large number of replicates, even the smallest effects have statistically significant *P*-values. For this reason, the relative value of the *F* and SS statistic are the most appropriate measures of the importance of a particular factor. Arrows of main effects indicate stabilizing (↑) or destabilizing effects (↓); for interaction terms, arrows indicate whether effects are enhanced (↑) or decreased (↓).

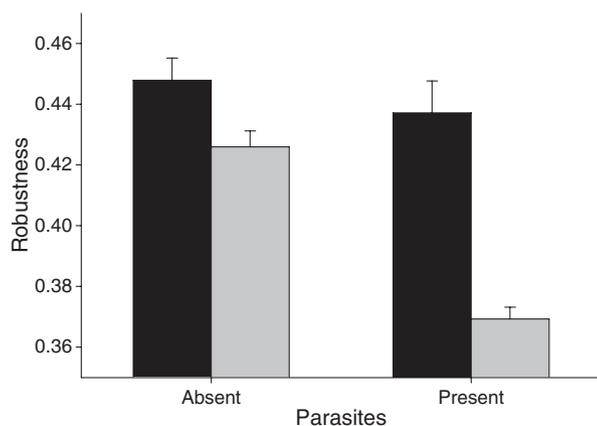


Figure 3 Stability of empirical networks. Comparing the mean (\pm SE) robustness of seven empirical networks (Table 2) indicates that accounting for stage-specific resource use (light grey bars) significantly ($P = 0.002$) decreased robustness of networks relative to networks that do not account for these ontogenetic niche shifts (dark grey bars), particularly when parasitic species are included.

The simplest explanation for our model results is that we distinguished between ‘substitutable’ resources (i.e. resources in a species’ diet are interchangeable) and ‘non-substitutable’ resources (i.e. a resource that is unique and cannot be substituted by another resource in a species’ diet) (Fig. 1), while with the exception of Lafferty & Kuris (2009), past analyses have assumed all resources are substitutable. Generalists that can use many substitutable resources ($p = 1$) are more resilient to secondary extinction than specialists (Fig. 2b). These generalists add complexity to networks and this creates the positive association between complexity and stability observed in previous studies. However, species that require many non-substitutable resources (e.g. due to ontogenetic shifts in resource needs, complementary dietary requirements or seasonal changes in resource availability) can be even more susceptible to resource loss than species that use a single resource (Fig. 2b). At low p , such species might appear to be generalists at the species level, yet each ontogenetic stage is specialized on a different set of resources (Fig. 1). Species with such ontogenetic niche shifts also add complexity to networks, but because they face a much higher risk of secondary extinction (Fig. 2b) they reduce network stability. As p partly determines the extinction risk of a species (Fig. 2b), the net effect of complexity on stability, therefore, depends on the relative degree of ontogenetic specialization within networks. This implies that we need to revise how we define ‘generalism’ and at what level (e.g. species vs. stage) to adequately predict the dynamic and functioning of natural communities.

It is important to consider the extent to which the assumptions in our model might alter the interpretation of our results. First, we note that extinction due to a lack of resources is an extreme outcome common to robustness analyses and our results could change for other measures of stability. Second, while structural robustness is the first crucial step towards understanding how ontogenetic shifts impact complex ecological networks, individual population dynamics and feedbacks could also influence network stability (e.g. Yodzis & Innes 1992; McCann *et al.* 1998; Brose *et al.* 2006; Bagdassarian *et al.* 2007). Previous studies suggest that ontogenetic niche shifts can reduce stability, resulting in alternative stable states (Schreiber & Rudolf 2008). Our simulations of simple consumer–resource food webs also indicate less stable population dynamics in systems with ontogenetic niche shifts than in systems where resources are shared (see Appendix S2). Interestingly, these simulations suggest that the addition of growth rates, another potential factor that could influence stability, did not change the general effects of ontogenetic niche shifts. In general, the results are consistent with previous studies indicating that structural robustness typically represents a conservative estimate that, if anything, overestimates the stability of networks (Eklöf & Ebenman 2006). Increasing evidence suggests that ontogenetic niche shifts have important implications for population and community dynamics (Mittelbach & Osenberg 1993; Persson *et al.* 2003; Rudolf 2007a,b; De Roos *et al.* 2008; Schreiber & Rudolf 2008) and the inclusion of population dynamics in stage-structured networks represents a future challenge in network theory.

Finally, because it is unclear whether nested diets are typical or rare in natural systems, we let the degree of nestedness vary among species in our models. While most of the effect of nestedness on robustness was captured by p , we note that increasing nestedness while keeping p constant can somewhat alter the extinction risks (V.H.W. Rudolf and K.D. Lafferty, unpublished data), and this could influence the robustness of networks. An important next step will be to determine whether there are systematic patterns in the nestedness of diet use within species, and how this might influence the stability of complex communities.

A fundamental challenge in the analysis of ecological networks is to choose the appropriate level of organization. In almost all published ecological networks, interactions are analysed at the species level and represent sums (or averages) across all individuals within a species (reviewed in Ings *et al.* 2009). Recent alternatives to classical food webs use partial differential equations or individual-based models to examine the dynamics and structure of size-structured food webs that account for diet shifts with the size of individuals (Law *et al.* 2009; Blanchard *et al.* in press). However, the later approach typically only models the dynamics of size classes (size-spectra) and does not keep track of individual species. While these studies on classical networks and size-spectra have provided important insights into different aspects of natural networks, they also lose potentially important biological details. Our results indicate that ontogenetic niche shifts reduce the stability of ecological networks and alter the complexity–stability relationship in a manner that cannot be predicted from classical unstructured models. This argues for stage-specific approaches that resolve ecological interactions below the species level to reliably predict how natural communities respond to biodiversity loss and other natural or anthropogenic disturbances.

ACKNOWLEDGEMENTS

We thank D. Queller, J. N. Holland, T. X. Miller and A. Dunham for comments on earlier version of the manuscript. Funding was provided by NSF DEB-0841686 to V.H.W.R. Hechinger, M. Sukhdeo, R. Poulin and P. Amundsen provided raw data. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

REFERENCES

- Amundsen, P.A., Lafferty, K.D., Knudsen, R., Primicerio, R., Klemetsen, A. & Kuris, A.M. (2009). Food web topology and parasites in the pelagic zone of a subarctic lake. *J. Anim. Ecol.*, **78**, 563–572.
- Bagdassarian, C.K., Dunham, A.E., Brown, C.G. & Rauscher, D. (2007). Biodiversity maintenance in food webs with regulatory environmental feedbacks. *J. Theor. Biol.*, **245**, 705–714.
- Blanchard, J., Law, R., Castle, M. & Jennings, S. (in press). Coupled energy pathways and the resilience of size-structured food webs. *Theor. Ecol.* DOI: 10.1007/s12080-010-0078-9.
- Borrvall, C., Ebenman, B. & Jonsson, T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecol. Lett.*, **3**, 131–136.
- Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food webs. *Ecol. Lett.*, **9**, 1228–1236.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L. *et al.* (2000). Consequences of changing biodiversity. *Nature*, **405**, 234–242.
- Cohen, J.E., Beaver, R.A., Cousins, S.H., DeAngelis, D.L., Goldwasser, L., Heong, K.L. *et al.* (1993). Improving food webs. *Ecology*, **74**, 252–258.
- De Roos, A.M., Schellekens, T., Van Kooten, T. & Persson, L. (2008). Stage-specific predator species help each other to persist while competing for a single prey. *Proc. Natl. Acad. Sci. USA*, **105**, 13930–13935.
- Dunne, J.A. & Williams, R.J. (2009). Cascading extinctions and community collapse in model food webs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, **364**, 1711–1723.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, **5**, 558–567.

- Ebenman, B., Law, R. & Borrvall, C. (2004). Community viability analysis: the response of ecological communities to species loss. *Ecology*, 85, 2591–2600.
- Eklof, A. & Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *J. Anim. Ecol.*, 75, 239–246.
- Fowler, M.S. (2010). Extinction cascades and the distribution of species interactions. *Oikos*, 119, 864–873.
- Gross, T., Rudolf, L., Levin, S.A. & Dieckmann, U. (2009). Generalized models reveal stabilizing factors in food webs. *Science*, 325, 747–750.
- Hechinger, R.F., Lafferty, K.D., McLaughlin, J.P., Fredensborg, B.L., Huspeni, T.C. *et al.* (in press). Food webs including parasites, biomass, body sizes, and life stages, for three California/Baja California estuaries. *Ecology* (accepted).
- Hernandez, A.D. & Sukhdeo, M.V.K. (2008). Parasites alter the topology of a stream food web across seasons. *Oecologia*, 156, 613–624.
- Huxham, M. & Raffaelli, D. (1995). Parasites and food-web patterns. *J. Anim. Ecol.*, 64, 168–176.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F. *et al.* (2009). Ecological networks – beyond food webs. *J. Anim. Ecol.*, 78, 253–269.
- Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A. *et al.* (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454, 515–518.
- Lafferty, K.D. & Kuris, A.M. (2009). Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 1659–1663.
- Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006). Parasites dominate food web links. *Proc. Natl. Acad. Sci. USA*, 103, 11211–11216.
- Law, R., Plank, M.J., James, A. & Blanchard, J.L. (2009). Size-spectra dynamics from stochastic predation and growth of individuals. *Ecology*, 90, 802–811.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- May, R.M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton Univ. Press, NJ, USA.
- McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.
- McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Mittelbach, G.G. & Osenberg, C.W. (1993). Stage-structured interactions in bluegill: consequences of adult resource variation. *Ecology*, 74, 2381–2394.
- Montoya, J.M., Pimm, S.L. & Sole, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.
- Okie, J.G. & Brown, J.H. (2009). Niches, body sizes, and the disassembly of mammal communities on the Sunda Shelf islands. *Proc. Natl. Acad. Sci. USA*, 106, 19679–19684.
- Pennings, S.C., Nadeau, M.T. & Paul, V.J. (1993). Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. *Ecology*, 74, 879–890.
- Persson, L. (1999). Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos*, 85, 385–397.
- Persson, L., De Roos, A.M., Claessen, D., Byström, P., Lovgren, J., Sjögren, S. *et al.* (2003). Gigantic cannibals driving a whole-lake trophic cascade. *Proc. Natl. Acad. Sci. USA*, 100, 4035–4039.
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl. Acad. Sci. USA*, 105, 4191–4196.
- Polis, G.A. (1991). Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.*, 138, 123–155.
- Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Nat.*, 147, 813–846.
- Rudolf, V.H.W. (2007a). Consequences of stage-structured predators: cannibalism, behavioral effects and trophic cascades. *Ecology*, 88, 2991–3003.
- Rudolf, V.H.W. (2007b). The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology*, 88, 2697–2705.
- Rudolf, V.H.W. & Armstrong, J. (2008). Emergent impacts of cannibalism and size refuges in the prey on intraguild predation systems. *Oecologia*, 157, 675–686.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000). Biodiversity – global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- Schreiber, S.J. & Rudolf, V.H.W. (2008). Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecol. Lett.*, 11, 576–587.
- Terborgh, J., Lopez, L., Nunez, P., Rao, V.M., Shahabuddin, G., Orihuela, G. *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926.
- Thompson, R.M., Mouritsen, K.N. & Poulin, R. (2005). Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J. Anim. Ecol.*, 74, 77–85.
- Torchin, M.E., Byers, J.E. & Huspeni, T.C. (2005). Differential parasitism of native and introduced snails: replacement of a parasite fauna. *Biol. Invasions*, 7, 885–894.
- Warren, C., Pascual, M., Lafferty, K.D. & Kuris, A.M. (2010). Parasitic networks in food webs: clustering, nestedness, and the inverted niche model. *Theor. Ecol.*, 3, 285–294.
- Werner, E.E. (1988). Size, scaling and the evolution of complex life cycles. In: *Size-Structured Populations* (eds Ebenman, B. & Persson, L.). Springer, New York, pp. 60–81.
- Werner, E.E. & Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size structured populations. *Annu. Rev. Ecol. Syst.*, 15, 393–425.
- Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.
- Woodward, G. & Hildrew, A.G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.*, 71, 1063–1074.
- Yodzis, P. & Innes, S. (1992). Body size and consumer-resource dynamics. *Am. Nat.*, 139, 1151–1175.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Complexity and stability.

Appendix S2 Population stability in consumer systems with and without ontogenetic niche.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Ferenc Jordan

Manuscript received 13 July 2010

First decision made 15 August 2010

Second decision made 26 September 2010

Manuscript accepted 11 October 2010