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SPECIAL FEATURE

## Extinctions in complex, size-structured communities

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### Assessing species extinction risks

Over the next decades, the continuing growth of the human population will increase the demand for agricultural, forest and marine resources, the area occupied by urban settlements and the magnitude of traffic. This will inevitably lead to an accelerating pressure on natural ecosystems that compete for space with human land-use systems. Additionally, anthropogenic land-use modifies the physical and chemical environment with effects ranging from global warming to local pollution. Together, these effects lead to biodiversity declines in natural ecosystems (Tylianakis, Didham, Bascompte, & Wardle 2008), which has triggered an intensive debate whether we are facing a sixth wave of mass extinctions with an expected loss of more than 80 percent of the global biodiversity within a million years (Barnosky et al. 2011). This degradation of biodiversity will inevitably lead to deprivation or even complete loss of important functions in the ecosystems. Irrespective of extinction magnitude, the debate

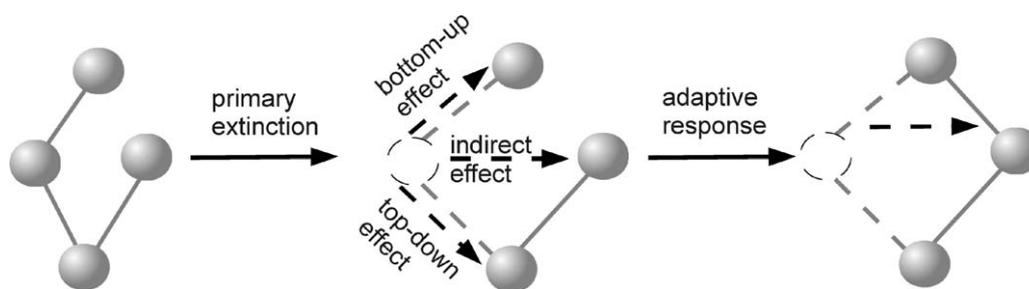
highlights some urgent questions on how this extinction wave is progressing: (1) Which species are most vulnerable to extinction? (2) Which primary extinctions will be triggering avalanches of secondary extinctions? (3) Which types of ecosystems face the highest rates of extinction? (4) Are certain food web structures more vulnerable to collapse than others? This special feature combines studies applying recent modeling advances to address these questions.

Most empirical studies on extinctions and their consequences remained specific to some species or ecosystems and often provided a-posteriori explanations for instead of a priori predictions of extinctions. Some meta-approaches identified recurrent patterns in extinctions: large-bodied species of high trophic levels with low densities have the highest extinction risk (McKinney 1997; Pauly, Christensen, Dalsgaard, Froese, & Torres 1998; Purvis, Gittleman, Cowlshaw, & Mace 2000). However, these studies were limited by their dominant focus on vertebrates, whereas natural ecosystems are almost exclusively composed of invertebrates. While general progress has been hampered by the iron claw of taxonomic specificity in individual studies, model approaches on extinction risks across ecosystems have remained scarce. However, natural species are embedded in complex interaction networks, which implies that changes in any species' loss can have severe indirect effects on any other species in the same interaction network (Ives & Cardinale 2004; Berlow et al. 2009). Network studies may thus serve as a conservation biology tool elucidating the relative importance of direct and indirect effects of species loss (Brose 2010a; Tylianakis, Laliberté, Nielsen, & Bascompte 2010).

Much of this recent progress in our understanding of a general size structure of communities across ecosystems has been fostered by the establishment of a European Science

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**Fig. 1.** The consequences of a primary extinction include the loss of links to other species. Traditional topological models assume secondary extinctions if a species loses all of its links by bottom-up effects. Dynamic models also include top-down and indirect effects. Adaptive models allow for rewiring of links after species loss. Both approaches can severely modify predictions on the consequences of extinctions.

Foundation research network in 2007: SIZEMIC, “Body size and ecosystem dynamics integrating pure and applied approaches from aquatic and terrestrial ecology to support an ecosystem approach” (Blanchard 2011). Within this research network, the working group on food-web dynamics has addressed extinction risks in size-structured communities. Based on universal scaling relationships relating characteristics of species and their interactions to their body masses, these models equally apply to aquatic and terrestrial ecosystems. This special feature combines four model studies addressing different aspects of extinction risks in these complex, size-structured networks. Here, I will first briefly introduce how size structure is included in network models and subsequently discuss topological and dynamic approaches to analyzing extinction risks in complex networks.

### Size structure of natural communities

Recent empirical advances in our understanding of community structure have unraveled some body-mass patterns that are consistent across ecosystems. Generally, predator and prey body masses are positively correlated with predators being on average one to two orders of magnitude larger than their prey (Brose, Jonsson, et al. 2006). This results in an increase in species’ body masses with their trophic level, whereas the predator–prey body-mass ratios decrease the higher up the species are in the food webs (Riede et al. 2011). Moreover, across lakes, streams, marine and terrestrial ecosystems predator generality (the number of prey species) increases with body mass, whereas vulnerability (the number of consumer species) decreases (Otto, Rall, & Brose 2007; Digel, Riede, & Brose 2011; Yvon-Durocher et al. 2011). This striking generality in the size structure of natural communities is related to body-mass constraints on individual feeding interactions (Brose et al. 2008; Rall, Vucic-Pestic, Ehnes, Emmerson, & Brose 2010; Vucic-Pestic, Rall, Kalinkat, & Brose 2010; Rall, Kalinkat, Ott, Vucic-Pestic, & Brose 2011; Vucic-Pestic, Ehnes, Rall, & Brose 2011) and metabolism (Ehnes, Rall, & Brose 2011).

Feeding efforts of predators yield sufficiently effective consumption rates only within specific ranges of prey masses, whereas attacks on smaller or larger prey remain ineffective in balancing metabolic demands (Brose 2010b). This “Goldilock factor” of food webs (Berlow, Brose, & Martinez 2008) has been used to successfully predict individual feeding links in a variety of natural food webs (Petchey, Beckerman, Riede, & Warren 2008). While taxonomic identities of predator and prey species partially drive food-web structure (Ives & Godfray 2006; Rohr, Scherer, Kehrl, Mazza, & Bersier 2010; Williams, Anandanadesan, & Purves 2010) and interaction strengths (Rall et al. 2011), species body masses have been identified as a major determinant of feeding niche structure (Williams et al. 2010; Stouffer, Rezende, & Amaral 2011; Zook, Eklof, Jacob, & Allesina 2011). Together, these empirical advances allow employing species’ body sizes as a general proxy for many species traits (e.g., respiration, growth, handling time and attack rate) in size-structured models of complex communities (Brose, Williams, & Martinez 2006; Brose 2008; Rall, Guill, & Brose 2008).

### Topological approaches

Over the last decade, modeling approaches predicting extinctions and the risk of secondary extinctions have been emerging (Sole & Montoya 2001; Dunne, Williams, & Martinez 2002; Montoya, Pimm, & Sole 2006; Bascompte & Stouffer 2009; Staniczenko, Lewis, Jones, & Reed-Tsochas 2010). They have been based on models of complex natural food webs describing species and the resource flow between them. In these energetic structures, species extinctions also remove links to other species thereby affecting their rates of growth and mortality. Topological approaches have determined secondary extinction risks in these complex food webs by progressively removing species to simulate extinction sequences. In these sequences, some species lose all of their links to resource species and thus become secondarily extinct (see Fig. 1, bottom-up effect). Consequently, the loss of some species can trigger avalanches of secondary extinctions that can severely exceed the number

of primary extinctions. Interestingly, these pioneering studies identified that the loss of the most linked or most vulnerable species causes more secondary extinctions than random species losses (Sole & Montoya 2001; Dunne et al. 2002). While subsequent studies have employed different extinction sequences (Allesina & Bodini 2004; Dunne, Williams, & Martinez 2004; Srinivasan, Dunne, Harte, & Martinez 2007; Allesina, Bodini, & Pascual 2009; Gilbert 2009), they all shared some limiting assumptions of the topological approach including (1) the lack of an adaptive response of species to compensate for resource loss (Fig. 1 – adaptive response), (2) extinctions being restricted to complete resource loss, and (3) exclusion of top-down and indirect effects (Fig. 1).

The first two of these limitations are addressed by an adaptive network study in this Special Feature based on models of allometric optimal foraging theory (Thierry et al. this Special Feature): species are allowed to adaptively change their links to resources in response to the loss of other species, and extinctions can occur prior to the loss of all resources if the resource supply falls below critical thresholds. Interestingly, both factors, adaptive rewiring and the application of an energetic extinction threshold, as well as the body-size structure of the community have severe implications for predicting the risk of secondary extinctions (Thierry et al. this Special Feature).

## Dynamic approaches

While topological studies provide a baseline giving the minimum impact an extinction can have in a food web, one centrally important question remaining is whether top-down cascades (Fig. 1 – top down effects) and other indirect effects will modify the consequences of primary extinctions. These effects are driven by dynamic changes of lower trophic level biomasses after species loss, and three of the studies of this Special Feature employ dynamic models of complex food webs to account for potential top-down cascades. One of these studies specifically compares the secondary extinctions amongst topological and dynamical simulations of extinction sequences (Curtsdotter et al. this Special Feature). As expected, the topological approach causes less secondary extinctions, and all sequences that have predominantly top-down directed effects have a severely lower impact on secondary extinctions than under the dynamic approach. This suggests that purely topological approaches may lead to inaccurately low estimates of secondary extinctions and omission of certain species traits affecting robustness (Curtsdotter et al. this Special Feature).

Another study in this special feature addressed which communities are most susceptible to secondary extinctions (Riede et al. this Special Feature). The results indicate that multiple community characteristics simultaneously determine

secondary extinction risks. In contrast to prior studies, this study demonstrated that food-web connectance does not affect secondary extinction risk, which might be caused by the interplay of positive and negative effects of connectance in dynamic models (Thierry et al. this Special Feature). Interestingly, the body mass–abundance relationship of the community was strongly correlated with secondary extinction risk suggesting it might be used as an indicator at the community level (Riede et al. this Special Feature).

While these approaches identified the risk of secondary extinctions after actively triggering one or a sequence of primary extinctions, one study looked at the primary extinction risk of species in complex food webs (Binzer et al. this Special Feature). Clearly, different aspects contribute to primary extinction risks amongst which low energy input, specialism and factors contributing to unstable population dynamics are most important. These results provide critically important information which extinction scenarios in the other approaches of the other studies in this Special Feature are generally most likely and a general risk assessment for species in complex communities (Binzer et al. this Special Feature).

## Modeling extinctions in complex food webs

Extinctions or local extirpations in natural ecosystems inevitably occur in complex food webs with potentially profound effects on all other species of the same community. Together, the studies in this special feature have demonstrated the potential of size-structured models to provide a theoretical perspective on extinctions and extinction risk. Ultimately, food-web theory may provide a more mechanistic and efficient approach towards conservation risk assessment (Gilbert 2009; Brose 2010a; Tylisanakis et al. 2010), but crucial to this goal is the ability to suitably inform practitioners as to the variability associated with any prediction. Future progress in this research area will continue to provide a deeper understanding of extinctions and the associated processes.

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