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Improving nature conservancy strategies by ecological network theory

Ulrich Brose*

Department of Biology, Schnittspahnstr. 3, 64287 Darmstadt, Germany

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Abstract

Over several decades nature conservancy research has gathered increasing evidence on the processes that drive species extinctions. Nevertheless, the world's ecosystems are currently exposed to a fast wave of species extinctions, and nature conservancy research has to face the challenge of predicting the consequences of extinctions. In the context of complex food webs that compose natural ecosystems, these primary extinctions affect the biomasses and growth rates of all co-existing species, which can eventually lead to secondary extinctions and extinction cascades of multiple species. Network theory provides a tool for predicting the consequences of extinctions for other species and ecosystem functions. In this sense, ecological network theory could become the next cornerstone of nature conservancy research.

Zusammenfassung

Seit mehreren Jahrzehnten hat die Naturschutzforschung die Prozesse untersucht, die zum Aussterben von Arten führen. Dennoch überzieht derzeit eine Welle des Artensterbens die globalen Ökosysteme. Dadurch wird die Naturschutzforschung in die Lage versetzt, die Konsequenzen dieser Welle des Artensterbens vorhersagen zu müssen. Natürliche Ökosysteme sind als Netzwerke von Arten und ihren Interaktionen aufgebaut. In solchen Netzwerken bedingt das Aussterben einer Art Veränderungen der Biomassen und Wachstumsraten aller koexistierender Arten. Letztendlich können dadurch sekundäre Aussterbeereignisse und kaskadische Aussterbewellen vieler Arten in

*Tel.: +49 6151 3006; fax: +49 6151 166111.
E-mail address: brose@bio.tu-darmstadt.de

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Ökosystemen ausgelöst werden. Theoretische Modelle ökologischer Netzwerke erlauben die Vorhersage der Konsequenzen primären Artensterbens für koexistierende Arten und Ökosystemfunktion. In diesem Sinne kann die Theorie ökologischer Netzwerke zu einem weiteren Eckstein der Naturschutzforschung werden.

Keywords: Food webs; Biodiversity; Ecosystem functioning; Secondary extinctions; Cascading extinctions

Introduction

Over the last centuries, the increasing density of the human population has exposed the earth's ecosystems to a variety of external stressors such as increasing nutrient supply, decreases in habitat size and density, more frequent disturbances, global warming, acidification, and toxic substances (Vitousek et al. 1997; Tylianakis et al. 2008). These stressors have severe consequences for the structure and functioning of ecosystems, which ultimately feedback to the human population. Traditionally, nature conservancy research was focused on providing ideas about how these human effects on natural ecosystems can be attenuated to maintain the global biodiversity. In this research agenda, milestones were provided by theoretical backbones such as species-area, minimum-viable population and intermediate disturbance theories. Today, these theories are completely intermingled with natural history approaches in a comprehensive framework predicting extinction risks at the level of individual populations. Despite this detailed knowledge about individual extinction risks, biodiversity is declining rapidly at a global scale. This decline in biodiversity is referred to as the sixth wave of extinction, which is one of the largest and fastest waves of extinctions since life established on Earth (Pimm et al. 1995; Sala et al. 2000). Turning a blind eye to this extinction wave, the human population largely ignores the current nature-conservancy recommendations for preserving populations. Hence, nature conservancy research needs to face this human reluctance to take action against biodiversity loss and adopt new strategies to cope with systematic biodiversity losses. Therefore, research on responses at the ecosystem level to biodiversity losses will play a crucially important role in this new research agenda. Subsequently, I will outline how ecological network theory could help in drafting this new ecosystem conservancy by providing a theoretical backbone linking community structure and dynamics with ecosystem functions such as primary production and decomposition of organic material.

Cascading extinctions

As soon as any of the anthropogenic stressors or a combination of them leads to negative net growth rates, they result in primary extinctions of populations. Such primary extinctions can cause changes in other species' biomasses (Berlow et al. 2004), which can trigger a cascade of further species losses or secondary extinctions (Dunne et al. 2002; Srinivasan et al. 2007; Dunne and Williams 2009) and eventually alter the stability and functioning of ecosystems (Luck et al. 2003). These cascading secondary extinctions can exceed the number of primary extinctions that are directly caused by anthropogenic stressors, which accelerates extinction waves.

Most studies on consequences of anthropogenic stressors adopted laboratory approaches to determine direct effects of these stressors on isolated populations. However, natural communities are organized as complex food webs with additive and compensatory effects of species interactively regulating responses to perturbations (Ives et al. 2005; Otto et al. 2008). Any stressor effect on the density of a specific population will simultaneously have an indirect effect on the predator and prey species of that population. For instance, negative stressor effects on a population will diminish the resource availability for its consumers and reduce the top-down pressure on its prey. Most likely, this will result in indirect negative effects on the consumers and indirect positive effects on the prey. Eventually, these indirect effects will cascade through the network of interactions, and a perturbation of any species will have implications for any other species in the same network. Astonishingly, these indirect effects of stressors can be much stronger than direct effects, which renders predictions on stressor effects and extinction sequences of species in naturally complex communities impossible (Ives & Cardinale 2004). Understanding potential risks of cascading secondary extinctions thus requires knowledge of (1) the network structure (who interacts with whom) defining the pathways of cascading effects, and (2) the strength of these interactions modifying the cascades along the pathways. Hence, predicting the consequences of anthropogenic stressors and primary species' loss for ecosystems and their functioning requires adopting a network-based approach (Ives & Cardinale 2004). In this sense, ecological network theory provides a critically important tool of nature conservancy research when facing challenges of predicting extinction cascades.

Ecological network theory

Ecological networks describe the interaction structures of natural communities. Over several decades, this research agenda has been focused on food webs comprising populations and their feeding interactions. More recently, competitive interactions amongst plants for limiting nutrients and positive interactions (e.g., plant–pollinator interactions) have been added to this research agenda (Bascompte et al. 2003; Brose 2008; Ings et al. 2009). Ultimately, these and additional interaction types build complex ecological networks linking the populations of a community. Initially much emphasis has been directed towards the rules that govern the binary network structure yielding topological models that successfully predict many structural aspects of these networks (Stouffer et al. 2005; Williams and Martinez 2008). A recent approach based on optimal foraging theory has identified species' body-masses as primary determinants of feeding links (Petchey et al. 2008). Under the framework of optimal foraging theory, scaling relationships of the functional response parameters handling time and attack rate with consumer and resource body masses provide the critically important mechanistic background for understanding food-web topology. This advancement offers an important simplification of network studies: in some cases logistically demanding and time-consuming studies of individual feeding links could be replaced by body-mass based model estimates (Woodward et al. 2005; Berlow et al. 2008). Future progress in this research agenda relies on empirical studies addressing allometric scaling of handling time and attack rate across different consumer and resource categories and ecosystem types (see Aljetlawi et al. 2004; Brose et al. 2008; Rall et al. 2010; Vucic-Pestic et al. 2010 for examples).

While models of ecological network structure (identifying the binary links between species) have matured over several decades, concepts of varying interaction strengths across the links within food webs emerged later (Berlow 1999; Bersier et al. 2002; Berlow et al. 2004). This interest has been particularly stimulated by the finding that natural interaction strength distributions are responsible for the intrinsic stability of complex food webs (Neutel et al. 2002; Rooney et al. 2006; Neutel et al. 2007). This finding implies that maintaining the interaction strength structure of food webs will help maintain the biodiversity of natural ecosystems. Subsequent work demonstrated that interaction strengths between predator and prey species depend on their body masses (Emmerson & Raffaelli 2004; Brose et al. 2008) suggesting that the body mass distributions of natural communities are responsible for maintaining their stability, diversity and functioning (Brose et al. 2006; Otto et al. 2007). Together, these findings suggest that body-mass structures of natural communities may serve as an important proxy for predicting food-web structure, interaction strengths and network stability.

Consequences of extinctions

Critically, large or trophically unique species are particularly prone to extinction due to human-induced changes in their environment (Jackson et al. 2001; Petchey et al. 2004, 2008). Prior empirical studies found that loss of large-bodied species at high trophic levels may induce trophic cascades that alter the abundance of other species (Bascompte et al. 2005; Borer et al. 2005). Ultimately, these effects may further propagate through food-web networks and lead to community collapses (Roopnarine et al. 2007) and severe effects on ecosystem processes such as primary production (Otto et al. 2008). Network theory suggests that the risk of cascading secondary extinctions is driven by the species diversity of the community (Pimm, 1980; Borrvall et al. 2000; Ebenman et al. 2004; Thebault et al. 2007; Dunne & Williams 2009), and increases with the number of links between the primary extinct species and other species in the network (Sole & Montoya 2001; Dunne et al. 2002; Memmott et al. 2004) and food-web complexity (Dunne et al. 2002; Dunne & Williams 2009). More recent studies integrate the structure of large complex food webs with body-mass dependent models of population dynamics to demonstrate that consequences of keystone species loss depend on the local network structure surrounding the target species where the effect is received (Brose et al. 2005; Borer et al. 2005). Extensions of this approach demonstrated that in a complex network, the response of one species to the extinction of another can be predicted based on knowledge of only the biomasses of the two species and the body-mass of the primary extinct species (Berlow et al. 2009). These results suggest that the largest perturbations of complex, natural ecosystems will occur as a consequence of the loss of large species with a low biomass density (Berlow et al. 2009). In providing such risk profiles on the consequences of species extinctions, ecological network theory has been coming along well with providing nature conservancy new tools for predicting system level consequences of human land use.

Outlook

While coping with the challenge of predicting system-level consequences of species loss ecological network theory may also provide a wider perspective on more traditional questions in nature conservancy research. For instance, analyses of complex food webs revealed that the vulnerability of an ecosystem to instability by nutrient enrichment decreases with the complexity of the interaction network (Rall et al. 2008). This suggests that the most complex food webs in nature might be less affected by nutrient influxes than previously anticipated. Moreover, while some knowledge has been gathered on how simple predator–prey systems respond to environmental warming (Vasseur & McCann 2005), the question of how more complex networks are affected remains to be answered. This research agenda on system-level responses to anthropogenic stressors is readily extendable to other perturbations such as effects of invasive species (Romanuk et al. 2009).

While integration of ecological network theory can boost nature conservancy strategies, it can also profit a great deal from this link to applications. Most importantly, re-designing network theory to cope with applied questions will provide a critically important feedback on the success or failure of predictions. Under this new perspective, ecological network theory will also need widen it current focus on trophic interactions to also include more information on important non-trophic interactions such as mutualism and competition (Okuyama & Holland 2008; Melian et al. 2009) that can be equally important in driving consequences of extinctions. In the same vein, recent advances in our understanding of ecosystem engineers (Eisenhauer et al. 2007; Straube et al. 2009) need to be incorporated in network theory (Cuddington et al. 2009). Adopting this more general research agenda will strengthen the conceptual strength and applicability of network theory.

Certainly, applications of network theory for applied questions in nature conservancy are only beginning to emerge. Nevertheless, by bridging the gap between laboratory research on simplified systems and applied empirical studies in complex natural communities, they indicate a promising area of future research. Importantly, they also allow linking anthropogenic stressors and species' extinctions to changes in ecosystem functions with potentially strong economic consequences, which enables more efficient communication to policy makers and the general public. In the long run, ecological network theory may thus become an important cornerstone of nature conservancy research.

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