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Adaptive foraging and the rewiring of size-structured food webs following extinctions

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Abstract

Over the past decade, attempts have been made to characterise the factors affecting the robustness of food webs. Many studies have been carried out using a "topological" approach, in which secondary extinctions in ecological networks are determined by the structure of the network alone. These studies have led to numerous insights; for example how robustness is highly dependent on the order of extinctions, the fraction of basal species, as well as the connectance of the webs. But there has been criticism of these investigations for their lack of biological realism, such as the inability of species to alter their diets when species are lost, or the reliance on the criterion that a species only suffers a secondary extinction once it loses all its resources. Here, building on past approaches, we address these issues by introducing allometric optimal foraging theory to explore the consequences of species adaptively responding (by altering feeding links) to loss of prey in size-structured food webs. We also explore the effect on robustness of a secondary extinction criterion based on a threshold of energy loss, rather than merely the absence of a connection to at least one prey. We show that both rewiring and energetic extinction criteria greatly affect the robustness of model food webs, and that these new factors interact with each other as well as with the body mass distribution of the community, to shape the complexity–robustness relationship.

Zusammenfassung

In der Vergangenheit wurden viele Versuche unternommen, Faktoren zu charakterisieren, die Einfluss auf die Robustheit von Nahrungsnetzen haben. In vielen Studien wurden topologische Ansätze gewählt, um sekundäres Aussterben über die Struktur des Netzwerkes zu bestimmen. Diese Studien haben zu zahlreichen neuen Erkenntnissen geführt, wie zum Beispiel der, dass Robustheit von der Reihenfolge in der die Arten aussterben, dem Anteil an Basalarten, sowie dem Verschaltungsgrad ("connectance") des Nahrungsnetzes abhängt. Kritisiert wird bei diesen topologischen Untersuchungen, dass sie biologisch unrealistisch sind, da Prozesse wie alternative Beutewahl nach Beute-Verlust nicht berücksichtigt werden. Außerdem basieren sie auf der Annahme, dass eine Art erst ausstirbt, wenn sie alle Beutearten verloren hat. Aufbauend auf den bisherigen Konzepten haben wir das Modell durch Anwendung der allometrischen "optimal foraging" Theorie erweitert, um zu testen, wie Arten adaptiv (durch Änderung der Räuber-Beute-Interaktionen) auf den Verlust ihrer Beuten in größenstrukturierten Nahrungsnetzen reagieren. Zudem passen wir das Modell durch die Einführung einer energetischen Minimum-Grenze an: Arten, denen zu wenig

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Energie zufließt, sterben aus, auch wenn sie noch Beuten haben. Wir zeigen, dass sowohl der Beuteaustausch als auch energetische Kriterien großen Einfluss auf die Robustheit der Nahrungsnetze haben. Weiterhin zeigen wir, dass die neuen Faktoren interagieren und zusammen mit der Körpergrößenverteilung innerhalb der Artengemeinschaft Einfluss auf die Komplexitäts-Robustheits-Beziehung haben.

Keywords: Body mass distribution; Connectance; Ecological network; Optimal foraging; Robustness; Secondary extinctions

Introduction

The extinction of a species does not solely entail the loss of a unique evolutionary entity but also the loss of the ecological linkages in which it is involved. With the loss of a species the nexus of species interactions begins to disassemble, bearing potentially serious consequences for other members of the assemblage (Montoya, Pimm, & Solé 2006; Bascompte & Stouffer 2009; Brose 2010). As Earth is currently experiencing exceptionally high rates of extinction (largely because of anthropogenic causes), ecologists have begun attempting to predict the consequences of species loss for our planet's ecosystems (Hoffman et al. 2010; Pereira et al. 2010).

We can describe ecological systems as networks, in which the nodes represent species with directed edges between them signifying a particular type of interaction, such as consumption (Dunne 2006). At the beginning of the last decade Albert, Jeong, and Barabási (2000) clearly demonstrated the relationship between the robustness of a network and its structure, inspiring ecologists to apply similar methods to data from food webs – networks in which the links represent one species feeding on another (Sole & Montoya 2001; Dunne, Williams, & Martinez 2002). The technique used in these papers was to progressively remove nodes from a network until the network collapsed to a pre-specified species richness. Nodes were disconnected either randomly or sequentially based on some topological property (e.g. the number of links a species has to others, or the species trophic level). If a species was left with no links to prey items, then it too would become extinct; therefore the loss of one species could trigger a cascade of further secondary extinctions. Robustness then is a measure of the likely occurrence of secondary extinctions following the loss of a species. It was discovered that food webs were generally more robust if species were removed at random, or if specialists (species with few links to prey) were removed first, but less so when generalists (species with many links to prey) were removed first. A more connected food web was generally a more robust food web (Dunne et al. 2002).

Many subsequent studies have expanded upon these ideas of the topological robustness of food webs (e.g. Allesina & Bondini 2004; Dunne, Williams, & Martinez 2004; Allesina & Pascual 2009; Dunne & Williams 2009; Gilbert 2009). However, concerns have been raised regarding the biological realism of the assumptions underlying such studies. Some have already been addressed, such as the use of increasingly realistic extinction orders (Srinivasan, Dunne, Harte, & Martinez 2007, Coll, Lotze, & Romanuk 2008), yet others remain largely unaddressed, such as the lack of an adaptive response by other species in the web to an extinction (Staniczenko, Lewis, Jones, & Reed-Tsochas 2010), as well as the lenient criterion that a species has to lose all its prey items before extinction occurs.

Whilst adaptive behaviour of species is increasingly recognised as important to food web structure and stability (Valdovinos, Ramos-Jiliberto, Garay-Narvaez, Urbani, & Dunne 2010), only one study to date (Staniczenko et al. 2010) has addressed the consequences of what has been termed the "structural dynamics" of food webs for their topological robustness. This is the concept that the topology of a food web is not fixed and therefore it can rewire following the loss of a node, due to the adaptive behaviour of the species that comprise the web. "Structural dynamics" in this sense is a discreteization, to allow us to more easily model change in a food web's topology, which does not include population dynamics. Of course, in nature there will be a continuous rewiring process, as species adjust their diets in response to changes in abundances of other species in the community (Kondoh 2005a).

In the study by Staniczenko and colleagues, food webs were rewired using an algorithm meant to represent a discretized mechanism of competitive release. Following the extinction of one of its competitors, a consumer might expand its diet to include a prey that it had previously been prevented from including in its diet. Another mechanism, different to competitive release, by which rewiring could occur, the consequences of which have yet to be investigated, is that of optimal foraging (Emlen 1966; McArthur & Pianka 1966; Beckerman, Petchey, & Warren 2006). In the discretized optimal foraging scenario, a consumer species forages on the subset of possible prey items that provides it with the highest net energy intake per unit effort, forgoing those prey that are less favourable for those that are. Following the loss of its preferred prey item a predator may expand its diet (its realised niche) to include novel, but energetically less favourable, prey items from the set of possible prey that comprise its fundamental niche (i.e. those prey species that the predator could physically consume). The predator can expand its diet to the point at which the newly included prey items again maximise its net intake.

Recent approaches in the mechanistic modelling of food web structure (Petchey, Beckerman, Riede, & Warren 2008; Thierry, Petchey, Beckerman, Warren, & Williams 2011), allow examination of the influence of food web rewiring following species extinctions on web robustness, using the