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Omnivory and stability of food webs

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ARTICLE INFO

Article history:

Received 18 January 2007

Received in revised form

24 April 2007

Accepted 26 June 2007

Published on line 2 April 2008

Keywords:

Food web

Omnivory

Intraguild predation

Lotka-Volterra model

Chaos

Risk

ABSTRACT

The role and prevalence of omnivory, defined as feeding on more than one trophic level, are critical to understand food web structure and dynamics. Whether omnivory stabilizes or destabilizes food webs depends on the assumptions of theoretical models. Recently, Tanabe and Namba [Tanabe, K., Namba, T., 2005. Omnivory creates chaos in simple food web models. *Ecology* 86, 3411–3414] found that omnivory can create chaos in a simple food web model with linear functional responses and 12 model parameters. In this paper, first we numerically examined bifurcation diagrams with all the parameters as bifurcation parameters, including self-limitation of the intermediate consumer and predator. Chaos spontaneously appears when the intraguild predator's consumption rates are low for nutrient-rich intraguild prey and high for nutrient-poor basal resource and the intraguild prey reproduces efficiently feeding on the basal resource. Second, we investigated effects of the addition of a species into the basic model food web which exhibits chaos. The additional species is assumed to consume only one of the basal resource, intermediate consumer, or omnivorous predator. Consequences of the addition greatly depend on the trophic level on which the additional species feeds. While the increased diversity of predators feeding on the intermediate consumer stabilizes the web, the increased diversity of prey feeding on the basal resource induces collapse of the food web through exploitative competition for the basal resource. The food chain with the top predator feeding on the omnivorous predator is highly unstable unless the mortality of the top predator is extremely low. We discuss the possibility of real-world chaos and the reason why stability of food webs strongly depends on the topological structure of the webs. Finally, we consider the implications of our results for food web theory and resource management.

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1. Introduction

Food webs are complex networks of trophic interactions among diverse species (Jordán and Scheuring, 2004; Dunne, 2005; Rossberg et al., 2006). The trophic interactions shape patterns in food webs, and the food web architecture and strengths of interactions in turn influence patterns of trophic dynamics in food webs with particular architecture (Lawler and Morin, 1993; Morin and Lawler, 1995). The prevalence of

omnivory is one of the important topological indices which characterize properties of trophic networks (Dunne et al., 2002; Jordán and Scheuring, 2004). Omnivory, defined as feeding on more than one trophic level (Pimm and Lawton, 1978), complicates trophic structures and influences expressions of the trophic cascades, or indirect effects of predators on basal resources via intermediate consumers (Finke and Denno, 2004, 2005; Bascompte et al., 2005; Bruno and O'Connor, 2005; Shurin et al., 2006). Although omnivory is

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doi:10.1016/j.ecocom.2008.02.001

found to be common in recent detailed descriptions of food webs (Sprules and Bowerman, 1988; Winemiller, 1990; Polis, 1991; Arim and Marquet, 2004), the role of omnivory in food webs is not yet fully resolved. Communities including omnivorous insects and protists are sometimes more stable than those without omnivores (Lawler and Morin, 1993; Morin and Lawler, 1996; Fagan, 1997; Holyoak and Sachdev, 1998; Morin, 1999). However, bacterivore populations temporally vary more in webs with an omnivore than in webs with a non-omnivorous predator (Lawler and Morin, 1993; Morin and Lawler, 1996). Enrichment increases the amplitudes of population fluctuations and unpredicted extinctions of an omnivorous predator may occur (Diehl and Feißel, 2000), although it might be attributed to demographic stochasticity (Diehl and Feißel, 2001).

Intraguild predation is the simplest form of omnivory in which a predator and a prey share a common resource (Polis et al., 1989; Polis and Holt, 1992). Models of intraguild predation can potentially produce complex population dynamics, since the resource, intraguild prey, and intraguild predator interact indirectly through trophic cascade, exploitative competition and apparent competition (Polis et al., 1989; Diehl, 1993). However, stability of food webs with intraguild predation depends on types and strengths of interactions (Jordán and Scheuring, 2004). On the one hand, McCann and Hastings (1997) used the Holling type II functional responses for the intermediate consumer and the top predator and showed that the intraguild predation stabilizes food chains which may exhibit chaos in the absence of omnivory. In similar models of four species, it was shown that weak apparent competition and intraguild predation can stabilize the food webs dynamically (McCann et al., 1998). However, whether intraguild predation stabilizes or destabilizes food webs may depend on where omnivory is placed among three gradients between two of three baseline food web configurations, tritrophic food chain, two exploitative competitors sharing a common resource, or two apparent competitors sharing a common enemy (Vandermeer, 2006).

In the Lotka-Volterra models, intraguild predation may destabilize otherwise stable equilibrium (Holt and Polis, 1997; Nakazawa and Yamamura, 2006) and produce limit cycles (Holt, 1997). Furthermore, it was recently found that omnivory can create chaos (Tanabe and Namba, 2005). Pimm and Lawton's classic works (1977, 1978) of omnivory in Lotka-Volterra models of food chains with four species are famous for arguing that omnivory is rare in nature since the systems with higher degree of omnivory tend to be unstable. However, Emmerson and Yearsley (2004) recently analyzed the same models and showed that a skew in interaction-strength distributions towards weaker interactions increases the probability of omnivory occurring, although it decreases stability of communities that do not contain omnivores. Therefore, careful examinations are still necessary to reveal which factors are essential in stabilizing or destabilizing food chains with omnivory.

Chaos often appears in mathematical models of food chains both without omnivory (Hastings and Powell, 1991) and with omnivory (Tanabe and Namba, 2005). However, chaos has been considered rare in natural populations (Berryman and Milstein, 1989; Hastings et al., 1993; Ellner and Turchin,

1995; Perry et al., 2000) although excellent demonstrations of chaos in experimental populations have appeared recently (Cushing et al., 2003; Becks et al., 2005). Fussmann and Heber (2002) investigated twenty eight simple food web models of up to eight species and five trophic levels with the Holling type II functional responses and examined the probability of chaos in permanent food webs. Their conclusions were that the frequency of chaotic behavior among persistent webs decreases as omnivory or complexity increases, although it also depends on other properties of food webs. This means that the probability of chaotic dynamics depends on the topological properties of food webs in models with nonlinear functional responses. Types of functional responses and interaction strengths also influence food web dynamics. Therefore, it may be necessary to investigate effects of food web structures in the Lotka-Volterra models of food webs.

The aim of the present article is two-fold. First, we consider a similar Lotka-Volterra model of intraguild predation to Holt and Polis (1997) and Tanabe and Namba (2005), but we incorporate self-limitation in the consumer and predator populations. We use all the 12 model parameters successively as bifurcation parameters and perform numerical bifurcation analyses to reveal which interactions among the resource, the intermediate consumer and the omnivorous predator are responsible for creating chaos in this model. Second, we introduce an additional species into the basic model with a set of fixed parameter values at which it exhibits chaos. The fourth species consumes only one of the basal resource, the intermediate consumer, or the omnivorous predator. Thus, we increase either prey diversity, predator diversity or the number of trophic levels and investigate whether the increased complexity stabilizes chaotic model food webs or not. We will show that the results highly depend on the trophic level on which the additional species feeds.

In the next section, we introduce our basic model. In the third section, results of numerical bifurcation analyses of the basic model will be explained. In the fourth section, we introduce an additional species either into the second, the third, or the fourth trophic level, and examine effects of the increased complexity in the food webs. Finally, we discuss the possibility of real-world chaos and the reason why stability of food webs strongly depends on the topological structure of the webs, and consider the implications of our results on food web theory and resource management.

2. Basic model

Let N_1 , N_2 and N_3 denote the densities of basal resource, intermediate consumer (intraguild prey) and omnivorous predator (intraguild predator), respectively. We assume interactions of the Lotka-Volterra type among the resource, consumer and predator. Then, our model is described as

$$\begin{aligned} \frac{dN_1}{dt} &= (r_1 - a_{11}N_1 - a_{12}N_2 - a_{13}N_3)N_1, \\ \frac{dN_2}{dt} &= (-r_2 + a_{21}N_1 - a_{22}N_2 - a_{23}N_3)N_2, \\ \frac{dN_3}{dt} &= (-r_3 + a_{31}N_1 + a_{32}N_2 - a_{33}N_3)N_3, \end{aligned} \quad (1)$$

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