



Color and degree of interspecific synchrony of environmental noise affect the variability of complex ecological networks



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ABSTRACT

The fundamental debate on complexity–stability relationships in ecosystems is becoming more important in the face of dramatic contemporary changes. Most research using network approaches to address this challenge has focused on predator–prey interactions and static networks. We describe a stochastic ecological network simulation model that combines predator–prey interactions with mutualism, parasitism and basal species competition. Network topology is based on a generalized niche model, while temporal dynamics are specified using bioenergetic models with noise terms. We use the model to explore the effects of non-predator–prey interactions, color of environmental noise, and the degree of synchronization of environmental noise across species on the coefficients of variation of total ecosystem energy content and Shannon entropy over time. In regression trees derived by binary recursive partitioning, the presence or absence of synchrony gave the greatest difference in the means of data points for both system energy and Shannon entropy, followed in turn by white versus colored noise and pink versus red and black noise. The effects are present despite the large variation in the Monte Carlo simulations reflecting the variability of real ecosystems. Non-predator–prey interactions explained relatively small proportions of the total deviance, and each had different effect signs depending on the presence of the other interaction types and on whether energy or entropy was measured. These results underscore the importance of modeling more realistic colors of environmental noise in understanding and predicting the dynamics of food webs and ecological communities.

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1. Introduction

The complexity–stability relationship has been of central interest in ecology since the pioneering work of May (1972, 1974). Despite significant advancements (Pimm, 1984; Polis, 1998; McCann, 2000), the issue of when and how ecological complexity stabilizes or destabilizes an ecosystem remains a hot topic of research and debate (Rooney and McCann, 2012). At the same time, deeper understanding of this relationship has become ever more relevant to those scientists and policy makers hoping to mitigate potentially debilitating effects of anthropogenic pressures on ecosystems (Lewis, 2009; Rooney and McCann, 2012).

Any attempt to dissect the complexity–stability relationship in an ecosystem has to examine the variety of interactions among its constituent species (Green and Sadedin, 2005), but theory relating to this topic has traditionally been dominated by research into antagonistic interactions (Bruno et al., 2003). Although the co-occurrence of negative and positive interactions was recognized

by Burkholder (1952), only in recent years have researchers begun to more widely acknowledge the importance of accounting for the facilitative species interactions that pervade real ecological communities (Gross, 2008). Facilitation is not only of theoretical interest but has also been shown to enhance sustainability in systems exploited by man (e.g. Xie et al., 2011) and to become more prevalent under increasing environmental stress (He et al., 2013). Integration of antagonistic and facilitative components will thus enhance our understanding and prediction of ecological systems.

Ecological network research has correspondingly been dominated by networks of single interaction types (Bascompte, 2010), especially predator–prey networks or food webs. The relative neglect of non-predator–prey species interactions can have profound ramifications for our understanding of ecosystem function (Goudard and Loreau, 2008). For example, non-predator–prey interactions may exacerbate human impact on ecosystems (de Visser et al., 2011); not accounting for such interactions in fisheries models has reduced the capacity of these models to predict stock collapse (Olf et al., 2009). Food webs implicitly include some non-predator–prey interaction in the form of indirect competition, but competition among basal species and, more strikingly, facilitation are absent. Conversely, studying non-predator–prey interactions in isolation can also compromise our ability to make useful

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predictions. For example, the dynamics of host–parasite interactions depend not only on those interactions per se but also on predators and alternative hosts, with implications for infectious disease control (Orlofske et al., 2012).

Recent studies have investigated the properties of networks of various non-predator–prey interaction types. For example, species coexistence has been reported to depend on the mean and variance of interaction strengths in competitive networks (Kokkoris et al., 2002). Competitive networks constructed on game theory principles have been found to promote diversity (Allesina and Levine, 2011), which implies that this enables more species to coexist in equilibrium. In networks of competing species that cannot be ranked in a strict hierarchy of competitive ability, negative frequency dependence arises that promotes diversity (Rojas-Echenique and Allesina, 2011). Okuyama and Holland (2008) found that the structural attributes of dynamic mutualistic networks give rise to positive complexity–resilience relationships, while Ramos-Jiliberto et al. (2012) reported that incorporating adaptivity of interactions increased robustness in dynamic mutualistic networks. A comparative study by Thébault and Fontaine (2010) revealed how dynamic food webs and mutualistic networks achieve stability via different structural mechanisms. Host–parasite interactions have predominantly been investigated in the context of food webs, since parasites bear striking similarities to, but differences from, predators. The impacts of parasites on food webs are diverse, various mechanisms having been reported for both stabilizing and destabilizing effects (Lafferty et al., 2008; Sato et al., 2012).

The aforementioned studies have greatly advanced our understanding of complexity–stability relationships in ecosystems, but one of their limitations is that interaction types were considered in isolation (Ings et al., 2009; Bascompte, 2010; Thébault and Fontaine, 2010). Furthermore, many studies have been of static networks, and most dynamical studies to date have dealt exclusively with food webs (e.g. Brose, 2008; Alcántara and Rey, 2012; Boit et al., 2012; Heckmann et al., 2012). The relationships thus found may not necessarily hold true in a real ecosystem, where multiple non-predator–prey interaction types co-occur and interact with one another and with trophic interactions (Golubski and Abrams, 2011) in ways that are time-sensitive. To address these issues, researchers have developed strategies that encompass different interaction types from a non-dynamical network topology perspective (Olesen et al., 2010; Fontaine et al., 2011; Poccock et al., 2012), a system dynamics perspective (Fath and Patten, 1998; Fath, 2007; Fath et al., 2007; Olff et al., 2009) as well as a bioenergetic perspective (Kéfi et al., 2012).

Several researchers have advanced the design of dynamic models containing multiple interaction types. The analytical models of Gross (2008), involving multiple consumer species feeding on a single resource, revealed that intraguild mutualism could be an important ingredient for species coexistence in otherwise competitive environments. Goudard and Loreau (2008) studied the effects of different interactions on biodiversity and ecosystem function in a tritrophic model based on Arditi et al. (2005). Filotas et al. (2010) simulated how spatial processes affect the structure and stability of multiple-interaction networks created with random topology and link strengths. Some of the most general results so far emerging from networks of multiple interaction types come from Allesina and Tang (2012), whose analytical models suggested that the addition of mutualistic and competitive interactions reduce the probability of stability of predator–prey networks. Stability of equilibrium points, however, is just one part of the story; the response in nature of a system to perturbations and its manner and rate of recovery constitute another important line of inquiry. Indeed, some researchers have advocated that the maintenance of resilience, rather than avoidance of disturbance, should be the

focus for conservation efforts (Scheffer et al., 2001; Folke et al., 2004).

The system dynamics strategy reviewed by Fath et al. (2007) and Olff et al. (2009) is a well-established ecosystem modeling approach hitherto used mostly in the realm of marine ecology (Raffaelli et al., 2005), where parameter values and empirical flows of energy and nutrients between trophic and functional compartments in a particular system are specified (e.g. Dame and Patten, 1981; Baird and Ulanowicz, 1989; Patten, 1992; Fath and Patten, 1998; Ulanowicz, 2004; Bascompte et al., 2005; Fath, 2007). This can be a powerful predictive tool and has been used extensively for marine ecosystems (aforementioned references). The multitude of biotic and abiotic compartments and flows, however, is perhaps not the most optimal design for studying the effects of species–species transactions. Moreover, the positive effects sometimes dealt with in this research area mainly refer to negative local interactions having net positive effects on network-level energetics (Patten, 1992; Fath and Patten, 1998; Fath, 2007), rather than the effect of positive interspecific interactions on the network. This is where the community–ecology approach of bioenergetic modeling (Yodzis and Innes, 1992), which uses ecological principles to specify which species interact with which species, could complement ecosystem ecology.

In addition to having a variety of interaction types, real ecosystems are ‘buffeted by a more or less continual series of perturbations, and transient behavior may be the norm rather than the exception in nature’ (Neubert et al., 2004). In the face of increasing environmental change, it is important to understand the impact of different types of environmental variation on populations and communities (Ruokolainen et al., 2009). Sutherland et al. (2013) identified the question of how environmental stochasticity interacts with density dependence to influence population dynamics as one of the most important contemporary questions in ecology. Furthermore, the complexity–stability relationship can be of even more relevance to the real world when the effects of stochasticity are taken into consideration. Stochasticity cannot be understood adequately by linear analysis, because the stochastic system is never in equilibrium (Solé et al., 2002). Indeed, Ruokolainen and Fowler (2008) reported that analytical solutions did not capture many of the features of the simulation outputs of stochastic Lotka–Volterra models.

The impacts of stochasticity on the dynamics of populations and communities have attracted increasing attention in recent years. Stochasticity has been found to magnify extinction risk and reduce invasion risk (Dennis, 2002; Greenman and Benton, 2005), and has been highlighted as an area for further research in community viability analysis (Ebenman and Jonsson, 2005). With respect to species interactions, Ripa et al. (1998) first presented a theory of the population-level effects of environmental noise in two-species ‘food webs’. Subsequently, Ripa and Ives (2003) took an analytical approach to understanding the effects of environmental synchrony on the dynamics of populations in a two-species Lotka–Volterra competition model, and showed that the effects can be large and unexpected and can either amplify or dampen cyclic behavior. Vasseur and Fox (2007), using a theoretical four-species ‘diamond’ food web, reported that noise can stabilize food webs by synchronizing population dynamics. More recently, Gravel et al. (2011) investigated population–dynamical criteria for species coexistence in a stochastic environment, while Gjata et al. (2012) used stochastic simulations to study the effect sizes of indirect interactions resulting from trophic interactions.

Pink noise is experienced by most natural populations (Steele, 1985; Pimm and Redfearn, 1988; Morales, 1999; Vasseur and Yodzis, 2004), yet most stochastic studies have assumed white noise. The color of noise has been shown to have significant impacts on the dynamics of single populations or simple systems with a

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