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The impact of initial evenness on biodiversity maintenance for a four-species *in silico* bacterial community

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HIGHLIGHTS

- We model a four species bacterial community with fully connected competition.
- The model allows initial community evenness to be varied, unlike previous studies.
- Simulation outcomes depend strongly on initial evenness and competition scheme.
- The system is generally unstable; extinction events are frequent.
- Initial evenness has a small stabilizing effect on system dynamics.

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ABSTRACT

Initial community evenness has been shown to be a key factor in preserving the functional stability of an ecosystem, but has not been accounted for in previous modelling studies. We formulate a model that allows the initial evenness of the community to be varied in order to investigate the consequent impact on system diversity. We consider a community of four interacting bacterial species, and present a stochastic, spatial individual-based model simulating the ecosystem dynamics. Interactions take place on a two-dimensional lattice. The model incorporates three processes: reproduction, competition and mobility. In addition to variable initial evenness, multiple competition schemes are implemented, modelling various possible communities, which results in diverse coexistence and extinction scenarios. Simulations show that long-term system behaviour is strongly dependent on initial evenness and competition structure. The system is generally unstable; higher initial evenness has a small stabilizing effect on ecosystem dynamics by extending the time until the first extinction.

1. Introduction and background

1.1. Maintaining biodiversity

One of the most important aims in ecology is to identify and comprehend the mechanisms that sustain biodiversity, which is often critically important for the viability of ecosystems. Loss of biodiversity can hinder the proper functioning of ecosystems, in drastic cases even leading to mass extinctions and system collapse (Ebenman and Jonsson, 2005). Recently, the nearly unanimous scientific belief has formed that a significant portion of the Earth's species are currently being driven to extinction due to human actions, threatening biodiversity across a wide number of ecosystems (Wilcove et al., 1998). Thus the issue of biodiversity loss has taken on a particular urgency in recent years (Mendes et al., 2008).

Many theoretical models have shown that species in competition can coexist—and hence maintain the ecosystem's biodiversity—if ecological processes such as competition and movement take place over small spatial scales (Frey and Reichenbach, 2011). This is also true in the case of communities with non-transitive competition between species—that is, communities where a strict competitive hierarchy does not exist (Laird and Schamp, 2006). The classic example of non-transitive competition is the rock-paper-scissors configuration, also known as cyclic competition. There exist many examples of communities in nature that demonstrate this type of competition, such as invertebrates living in coral reefs (Jackson and Buss, 1975), lemmings in the Arctic tundra in Greenland (Gilg et al., 2003), side-blotched lizards in California (Sinervo and Lively, 1996), the Pacific salmon (Guill et al., 2011), certain bacterial species engaging in antibiotic production

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(Reichenbach et al., 2007), and microbial populations of colicinogenic *Escherichia coli* (Kerr et al., 2002).

From among the various ecosystems in which cyclic competition has been observed, microbial communities have become model systems for studying the complex interplay between the nonlinear dynamics of evolutionary games, stochastic fluctuations arising from the probabilistic nature of interactions, and spatial organization (Frey and Reichenbach, 2011). Much effort has been dedicated to advancing the qualitative and quantitative understanding of mechanisms that sustain biodiversity and ensure the viability of microbial colonies, by allowing for species diversity and social behaviours such as cooperation.

Recent work in this area has focused on microscopic models describing the interactions at the individual rather than the population level—see for example Frey and Reichenbach (2011), Adamson and Morozov (2012), Berec (2002), Nadell et al. (2010) and reviews (Hellweger and Bucci, 2009; Ferrer et al., 2008). One study which has attracted particular attention in the field is due to Reichenbach et al.; these authors used a stochastic lattice-based model to demonstrate that coexistence of three species is mediated by their dispersal. Thus once species' mobility exceeds a critical rate, biodiversity is lost, independent of spatial environment and details of cyclic competition (Reichenbach et al., 2007). Empirical evidence for this assertion can be found in a study that employed a non-transitive model community containing three populations of *E. coli* (Kerr et al., 2002). The study found that diversity was rapidly lost in the experimental community when dispersal and interaction occurred over relatively large spatial scales, whereas all populations could coexist when the same ecological processes were localized (Kerr et al., 2002).

Much recent effort has been spent on studying the mechanisms that promote the maintenance of biodiversity, one of which is increased species diversity (Frey and Reichenbach, 2011). Species diversity is generally understood to be composed of two components: species richness and species evenness (Magurran, 2004). Species richness refers to the absolute number of species present in the population of interest, while species evenness refers to the relative abundances of the different species—if a population is completely even, all species are equally abundant (Heip, 1974). Richness and evenness play different roles in community functioning and have therefore often been treated separately. For example, species richness is responsible for the number of functional traits in a community, while evenness may influence the richness effect by controlling the variation of traits present in the community (Lemieux and Cusson, 2014).

1.2. *Species evenness*

Species evenness has been shown to be a key factor in preserving the functional stability of ecosystems (Hillebrand et al., 2008; Wittebolle et al., 2009; De Roy et al., 2013). Evenness is also known to have a positive impact on productivity by increasing the representation of each species' functional traits (Lemieux and Cusson, 2014). Despite this recognition, studies and conservation efforts often focus on restoring or maintaining richness, since the impact of richness on many ecological processes has been well described (see e.g. Crowder et al., 2010; Hooper et al., 2005; Isbell et al., 2009b). In contrast, much less attention has been paid to the ecological effects of disrupted evenness (Hillebrand et al., 2008), an unfortunate oversight since environmental degradation and damage due to human actions can skew the relative abundance of species, and because uneven communities are often more susceptible to invasion and less resilient to stresses and disturbances (Wittebolle et al., 2009).

Declining evenness has also been shown in field studies to be an important early warning sign of diversity decline, specifically in response to species invasion (Wilsey et al., 2009). The authors noted that if they had taken species richness as the only index of diversity, they would have falsely concluded that diversity had not changed over the first year of study. Initial drops in evenness preceded the drops in richness that occurred in the second year, an effect the authors singled out as interesting for future study (Wilsey et al., 2009).

In general, the development of theory has outpaced experimental studies concerning evenness as a mechanism promoting maintenance of biodiversity (Isbell et al., 2009b). Empirical evidence was provided by one study showing that maintenance of biodiversity can be promoted by a rare species advantage (Wills et al., 2006) or a common species disadvantage (Harpole and Suding, 2007), both of which are mechanisms leading to a more even community.

As a further example, one experimental study set in a field in Canada varied species evenness and the identity of the dominant plant species in order to test whether plant productivity would increase with increasing evenness, and whether such a relationship would be dependent on species identity (Wilsey and Potvin, 2000). Results showed that biomass production increased linearly with increasing evenness, and was invariant of the identity of the dominant species. These results support the view that a decrease in plant diversity due to human actions would lead to an indirect decrease in productivity (Hillebrand et al., 2008).

Further evidence for the importance of evenness can be found in a global meta-analysis of 54 studies regarding the diversity–productivity relationship in forest ecosystems (Zhang et al., 2012). The authors concluded that the strong positive effects on productivity due to increased evenness provide strong empirical evidence to support the theoretical assertion that evenness affects the relative strength of interspecific and intraspecific interactions within communities, therefore causing an appreciable shift in the diversity–productivity relationship (Zhang et al., 2012). Futhermore, the authors suggest that the neglect of evenness in previous empirical studies can be attributed to the limited levels of evenness found in those experiments, where typically only high and "realistically low" levels of evenness were included (Polley et al., 2003; Isbell et al., 2009a).

Although ecological studies have only just begun to examine the mechanisms underlying such evenness effects, studies so far suggest that many of the same processes underlying the impacts of species richness may be at work (Hillebrand et al., 2008). For instance, evenness in bacterial communities promotes resilience to disturbance by ensuring sufficient densities of species in key functional roles (Wittebolle et al., 2009). This is akin to the "insurance effect" described in the species richness literature (Lemieux and Cusson, 2014). One possibility is that decreasing evenness leads to increasingly underused niches that become fully vacant once species are lost, to the detriment of the ecosystem's proper functioning (Crowder et al., 2010).

1.3. *Motivation and scope*

We are motivated to investigate variable evenness in microbial ecosystems for all these reasons, and because it has not yet been investigated in computational studies concerning non-transitive competition (see for example Case et al., 2010; Cheng et al., 2014; Frachebourg et al., 1996). Additionally, there is substantial evidence to suggest that perfectly even communities are rarely found in nature (Wilsey and Polley, 2004; Huston, 1997; Grime, 1998; Smith and Knapp, 2003). Thus it may well be dangerous to assume, as previous studies have done, that community evenness is always maximal.

The remainder of this paper is structured as follows. In Section 2, we introduce the fundamental processes that underpin ecosystem functioning, and discuss how they are typically modelled.