Multiple dimensions of biodiversity and ecosystem processes: Exploring the joint influence of intraspecific, specific and interspecific diversity

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HIGHLIGHTS

- Biodiversity affects ecosystem processes.
- Currently, biodiversity is extensively explored as a unidimensional measure.
- A model was used to simulate species, genotypic, and functional richness jointly.
- The biodiversity components affect differentially the ecosystems.
- Research on multiple dimensions of biodiversity is relevant in ecosystem research.

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ABSTRACT

The positive influence of biodiversity on ecosystem processes was the focus of intense debate in ecology throughout the recent decades, becoming accepted and treated as a new paradigm in contemporary ecology. However, the available literature in this research field extensively explores species richness as an unidimensional measure for biodiversity. The present study explores how different components of biological diversity (number of genotypes, species, and functional groups) can influence an ecosystem process (biomass fixation). A mathematical model was employed and the simulation results showed that species richness *per se* does not affect the ecosystem productivity. Genotypic richness affected positively the ecosystem, but only if the genotypes are functionally complementary. The functional groups richness always affected positively the simulated ecosystem process. When together, richness at the different components of biological diversity showed stronger effect on ecosystem, and the scenarios with high species, genotypes and functional groups richness were the most productive ones. The results also allowed to observe that the ecosystems which are diverse in terms of functional groups and genotypes can be less susceptible to species loss. Finally, it is argued that a multiple dimension approach to biodiversity is relevant to advance the current knowledge on the relation between biodiversity and ecosystem functioning.

1. Introduction

A robust empirical and theoretical effort in ecological research has shown that biological diversity has a major influence on the dynamics of ecosystem processes (biodiversity and ecosystem functioning research program, or BEF) (Isbell et al., 2011; Loreau, 2010; Naeem, 2002; Pasari et al., 2013; Wang and Loreau, 2014). The first hypotheses were developed in the early 1990s decade (Loreau 2001; Tilman et al., 1997) and proposed that, in general, the number of species positively influences a particular process.

Speculation about the nature of this relationship generated three main hypotheses: linear relationship, asymptotic relationship, or an idiosyncratic relationship (Loreau, 2010, 2001). The first one is based on the intuitive idea that, if each species is unique, so ecosystem process should decrease linearly with species losses. The asymptotic relationship is based on the theoretical expectation that many species are in fact ecologically similar, working redundantly in the ecosystem. In a diverse ecological system, this would prevent the substantial reduction in ecosystem process due to loss of species. The idiosyncratic relationship is expected if the biotic and abiotic interactions in the ecosystems are so complex that the addition or loss of species would cause unpredictable effects.

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Throughout the 1990s decade, considerable empirical efforts was expended in the evaluation of these hypotheses (Hooper et al., 2005; McCann, 2000) and the positive asymptotic influence of species richness was gradually confirmed. But that was just the beginning of a great discussion in the ecological literature (Hooper et al., 2005; Loreau 2001; Naeem, 2002; Naeem et al., 2002). For example, Bengtsson (1998) outlined several critical points in BEF research. He draws attention for what was being claimed an "effect" of biodiversity, arguing that it could be, in fact, an effect of species attributes. Researchers in BEF should be able to distinguish among the effects of species richness, functional groups diversity, and of interactions in the community, as well as the effects of the identity of each species making up the ecosystem (since different species probably stand out differently in the maintenance of different ecosystem process). Indeed, some of the problems identified by Bengtsson (1998) had been discussed in the literature at that time, such as the effect of species composition versus the effect of species richness (i.e., the identity of the species) (Lambers et al., 2004; Loreau, 2010; Tilman et al., 1997). The skepticism of Bengtsson (1998) seems to reflect the discomfort of many biologists on the simplified and phenomenological treatment given to biodiversity in the initial research on BEF.

Maclaurin and Sterelny (2008) provide a deeper discussion for the current concept of biodiversity, drawing attention to its complexity. In addition to the species richness and the distribution of species abundance, there is also biological variability among different populations of the same species (Luck, 2003) and within one unique population (Hughes et al., 2008), among the interactions of species that make up an ecosystem (Goudard and Loreau, 2008; Thébault and Loreau, 2005), and also there is biological variability in the interaction among communities and ecosystems along the landscapes (Loreau., 1996; Marleau et al., 2014). Purvis and Hector (2000) pointed biodiversity as a multidimensional ecological quantity, whose approach through proxy measures (e.g., species diversity indexes) should be used with caution. In fact, some of its dimensions can be correlated, such as functional diversity and species richness, but this is not a general rule (Díaz and Cabido, 2001).

Despite this, most of the currently available literature regarding the influence of biodiversity on ecosystem processes extensively employs species richness as a surrogate measure of biological diversity, neglecting the investigation of the consequences of possible interactions among its different dimensions (Caliman et al. 2010). Only among recent studies, a broader approach to biological diversity began to appear in the literature (e.g., Jousset et al., 2011;. Luck, 2003; Münzbergová et al., 2009). In general, the two main attributes of biodiversity focused in these studies are genetic diversity and functional diversity (Bailey et al., 2009; Caliman et al., 2010). An important feature of the most of this new generation of BEF studies is that they are limited to use another one-dimensional surrogate measure of biological diversity to draw conclusions. Thus, the potential interactions among the different dimensions of biodiversity stills poorly explored (for some of the few exceptions, see: Fridley and Grime, 2010; Goudard and Loreau, 2008; Reiss et al., 2011; Thébault and Loreau, 2003).

Using the formalism of mathematical modeling, Thébault and Loreau (2003) explored how trophic structure and species richness could affect an ecosystem process. These authors concluded that the trophic interactions have a marked effect on ecosystem productivity, causing the conversion of an asymptotic relationship between species richness and productivity (observable in a community with only plants) into a more complex, not asymptotic relationship (observable in a community with herbivores and carnivores, interacting in a more elaborate trophic structure, with generalist and specialist species). Particularly, Thébault and Loreau (2003) found that the strength of the trophic interactions in the food web was important to their results. Moreover, Goudard and Loreau (2008) employed a variation of the same model of Thébault and Loreau (2003) to explore the effects of trophic and not trophic interactions (e.g., mutualisms) on the ecosystem productivity. Their conclusion was that we should not expect a critical interference of non-trophic interactions, being trophic relationships the most important.

Such works represent the first and few theoretical studies focusing on the influence of other aspects of biological diversity on ecosystem functioning, moving beyond species richness. In addition to the advance in basic knowledge in ecology, the production of theoretical studies to clarify how the different components of biological diversity can affect ecosystems has the potential to contribute with the optimization of efforts in biodiversity conservation (Barnosky et al., 2011; Ebenman, 2011; Naeem et al., 2012). In this context, only a deeper understanding of how biodiversity components work together for the maintenance of ecosystem processes would drive the conservation efforts to the most critical and/or feasible ones.

The present study aimed to investigate how different components of biological diversity influence a hypothetical ecosystem process and to evaluate potential interactions among these components. It was employed a model based on the work of Thébault and Loreau (2003) and Goudard and Loreau (2008). The intraspecific variability (assumed in this study as the number of genotypes), interspecific (number of species) and functional (functional complementarity among species) are the components (or dimensions of biodiversity) investigated. These dimensions were selected to be modeled because of the consistent theoretical literature available to model them. Different scenarios were employed to explore the isolated and jointly effects of the components. Such approach provides complementary projections to theoretical work so far available, contributing to BEF research with an explicit analysis of biodiversity as a multidimensional predictor variable.

2. Methods

The model used in the present study is based on the work developed by Loreau (1998) and Thébault and Loreau (2003). It simulates an ecosystem with a limiting resource (or nutrient) and with an arbitrary number of plant species distributed in different functional groups and genotypes.

One limiting nutrient is considered, being represented by the variable R. Plants depends critically on R, and are distributed in S_G genotypes, S_S species, and S_F functional groups. The variable $P_{(ij)}$ represents the plant biomass in the i-th species, j-th genotype. Through physical processes (represented by the rate k), the nutrient in the soil reaches the absorption zone of the plant roots ($L_{(ij)}$). The absorption zone occupies a volume ($V_{P(ij)}$) in the soil and this represents the physical space occupied by the roots system of the genotype j, species i, in the ecosystem (Thébault and Loreau, 2003). This means an equivalent situation where, for example, different functional groups of plants exploit nutrients at different soil depths (Navas and Violle, 2009; Zobel and Zobel, 2002). Loreau (1998) used a similar approach to investigate species redundancy employing a simpler version of the model used in the present study.

The nutrient is incorporated in the plant biomass through a rate $a_{(ij)}$, and returns to the soil through biological processes (e.g., death of organisms), which is modeled by the rate $m_{(ij)}$. A fraction of the nutrient contained in the biomass lost by the plants (represented by λ_P) become available again in the soil at a rate $(1 - \lambda_P)$. The nutrient concentration available in neighboring ecosystems is represented by the parameter R_0 and λ_R is the rate at which this