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Climatic seasonality may affect ecological network structure: Food webs and mutualistic networks

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ABSTRACT

Ecological networks exhibit non-random structural patterns, such as modularity and nestedness, which determine ecosystem stability with species diversity and connectance. Such structure–stability relationships are well known. However, another important perspective is less well understood: the relationship between the environment and structure. Inspired by theoretical studies that suggest that network structure can change due to environmental variability, we collected data on a number of empirical food webs and mutualistic networks and evaluated the effect of climatic seasonality on ecological network structure. As expected, we found that climatic seasonality affects ecological network structure. In particular, an increase in modularity due to climatic seasonality was observed in food webs; however, it is debatable whether this occurs in mutualistic networks. Interestingly, the type of climatic seasonality that affects network structure differs with ecosystem type. Rainfall and temperature seasonality influence freshwater food webs and mutualistic networks, respectively; food webs are smaller, and more modular, with increasing rainfall seasonality. Mutualistic networks exhibit a higher diversity (particularly of animals) with increasing temperature seasonality. These results confirm the theoretical prediction that the stability increases with greater perturbation. Although these results are still debatable because of several limitations in the data analysis, they may enhance our understanding of environment–structure relationships.

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1. Introduction

Ecological communities consist of a number of species that are connected via inter-specific interactions, such as trophic and mutualistic relationships. Their structure and dynamics are significant in ecology, because they are important not only in the context of basic scientific research, such as structure–stability relationships (Allesina and Tang, 2012; Bascompte, 2010; Mougi and Kondoh, 2012; Thébault and Fontaine, 2010), as typified by May's paradox (May, 1972), but also in the context of applied ecology, such as biodiversity maintenance and environmental sustainability (Allesina and Tang, 2012; Bascompte, 2010; Mougi and Kondoh, 2012).

The development of field observation technology, and the improvement of infrastructures such as databases, have increased the availability of ecological data on inter-specific interactions and have enabled large-scale data analysis of real-world ecosystems. Because of the importance of network science (Barabási, 2013), ecological communities are often represented as networks (Bascompte, 2010; Proulx et al., 2005) (so called ecological networks, in which nodes and edges correspond to species and inter-specific interactions, respectively), and have been actively investigated recently using complex network analysis techniques (Takemoto and Oosawa, 2012).

Previous network analytical studies have revealed that ecological networks (plant–animal mutualistic networks in particular) exhibit two representative non-random structural patterns: a modular structure (Olesen et al., 2007), and nested architecture (Bascompte et al., 2003). Despite the correlation between them, these two structural patterns can provide complementary information on how interactions are organised in communities (Fortuna et al., 2010). The modular or compartmentalised structure describes the deconstruction of a network into dense, and yet, weakly interconnected subnetworks (subgroups), and indeed, modular organisation is an important feature of biological systems (Hartwell et al., 1999). A nested structure indicates that the interaction pairs of a certain (specialist) species form a subset of those of another (generalist) species, in a hierarchical fashion.

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However, the degree of modular and nested architectures (generally called modularity and nestedness, respectively) differ with the ecosystem type: antagonistic (or trophic) networks (e.g. food webs) and mutualistic networks (e.g. plant-pollinator networks). In general, the modularity of antagonistic networks is higher than that of mutualistic networks, and the nestedness of antagonistic (i.e. resource–consumer) networks is lower than that of mutualistic networks (Bascompte et al., 2003; Thébault and Fontaine, 2010); however, food web subnetworks are significantly nested (Kondoh et al., 2010).

These non-random structural patterns are believed to influence ecological dynamics. For example, nestedness may minimise competition and increase biodiversity in mutualistic networks (Bastolla et al., 2009) (but see (James et al., 2012; Staniczenko et al., 2013)), and emerges as a result of an optimisation principle aimed at maximising species abundance in mutualistic networks (Suweis et al., 2013). Modularity is a particularly important property, because it is related to robustness (Hintze and Adami, 2008) and evolvability (Yang, 2001). In addition to species diversity (the number of organisms) and connectance (the relative number of interactions), both modular and nested architectures are also related to ecosystem stability (i.e. persistence and resilience) (Thébault and Fontaine, 2010). However, the relative contributions of nestedness and modularity, in addition to the effects of diversity and connectance, to ecosystem stability differs between mutualistic and antagonistic networks.

Although the structure and stability of ecological networks are highly significant in ecology, the impact of the environment (e.g. geography and climate) on ecological communities is equally significant, because it is important when discussing the effect of climate change on ecosystems. In particular, the environment is expected to influence ecological networks according to latitudinal gradients in species diversity (Araújo and Costa-Pereira, 2013; Condamine et al., 2012). In fact, several studies (e.g. Baiser et al., 2012; Marczak et al., 2011) have focused on latitudinal and geographic variations in ecological networks, although these studies do not mention large-scale structural patterns such as modularity and nestedness.

Because of the importance of modularity and nestedness, the association between these structural patterns and the environment is a key area for active investigation. Trøjelsgaard and Olesen (2013) found that the mean annual precipitation affects both nestedness and modularity in pollination networks, independent of the sampling effort. Dalsgaard et al. (2013) demonstrated that historical climate change (i.e. the quaternary rate of temperature change) was negatively associated with modularity and positively associated with nestedness in pollination networks. However, temperature seasonality, unrelated to historical climate change, exhibits a positive correlation with modularity in seed dispersal networks, using a more realistic definition of modularity (Schleuning et al., 2014), whereas temperature change rate and phylogenetic signals are only weakly associated with modularity.

The positive correlation observed between climatic seasonality and modularity is consistent with several theoretical studies (Friedlander et al., 2013; Kashtan and Alon, 2005), which demonstrate that modular networks spontaneously evolve under changing environments, using an evolutionary optimisation algorithm based on edge rewiring (mutation). Lipson et al. (2002) suggested that environmental variability can lead to modularity. Several data analytical studies have found a positive correlation between environmental variability and network modularity in several types of biological system (e.g. metabolic networks (Parter et al., 2007) and cancer signalling networks (Takemoto and Kihara, 2013)). Nevertheless, scepticism still exists regarding the impact of environmental variability on modularity in intracellular networks (Clune et al., 2013; Hansen, 2003; Holme, 2011; Takemoto, 2013, 2012).

Because of the generality of this theory, changes in network structure due to environmental variability (increases in modularity, in particular) such as climatic seasonality should also be investigated in different types of ecological networks. However, the relationship between the environment and ecological network structure is not well understood. This hypothesis has only been partially supported in plant–seed dispersal networks, and environment–structure relationships have only been investigated in plant–animal mutualistic networks (i.e. pollination and seed dispersal networks). Therefore, in this study, we conducted a detailed investigation on the relationship between the environment and ecological network structure by using the data on a number of empirical ecological networks collected from the literature and from databases. In particular, the climatic seasonality effects on (plant-pollinator) mutualistic networks, in addition to environment–structure relationships in food webs and mutualistic networks were evaluated, because they are still poorly understood. In addition, we compared the environment–structure relationships between food webs and mutualistic networks, and discussed the contribution of such relationships to ecosystem stability.

2. Materials and methods

2.1. Construction of ecological networks

Food web data were downloaded from the GlobalWeb database (Thompson et al., 2012) (www.globalwebdb.com). Plant-pollinator mutualistic network data were obtained from the supporting online material (database S1) in (Bascompte et al., 2006), and the interaction web database (www.nceas.ucsb.edu/interactionweb/). After removing duplications, we selected ecological networks, the locations (i.e. latitude and longitude) of which could be identified in the literature: 305 food webs and 50 plant-pollinator networks were found.

We constructed ecological networks according to adjacency matrices or lists of species interactions provided by the databases. Food webs are represented as networks, in which nodes and edges correspond to organisms and trophic links (Baiser et al., 2012; Kondoh et al., 2010; Thompson et al., 2012). It is to be noted that food webs are represented as unipartite directed networks, because predator–prey relationships are direction-oriented. However, plant-pollinator networks are represented as bipartite networks, because mutualistic links are only found between two types of organisms (i.e. plants and animals) (Bascompte et al., 2003; Olesen et al., 2007; Trøjelsgaard and Olesen, 2013). Both types of ecological network were represented as binary networks (i.e. presence 1, or absence 0, of a given link), because the databases partially included binary data, and the software programs needed for calculating modularity and nestedness require binary networks.

2.2. Climatic parameters and elevation

We manually extracted the information on the latitudes and longitudes of the ecological networks from the literature. Consequently, we obtained the following climate data, with a spatial resolution of 0.5 min of a degree (i.e. $0.93 \times 0.93 = 0.86\ \text{km}^2$), from the WorldClim database (version 1.4, release 3) (Hijmans et al., 2005) (www.worldclim.org) using R version 3.0.2 (www.R-project.org) and an R-package raster version 2.2-12 (cran.r-project.org/web/packages/raster): annual mean temperature (T_{mean}) ($\times 10\,^{\circ}$C), temperature seasonality (standard deviation) (T_{var}), annual precipitation (P_{ann}) (mm), and precipitation, or rainfall seasonality (coefficient of variation) (P_{var}). The WorldClim database defines temperature seasonality as a standard deviation, because the coefficient of variation is nonsensical at temperatures between -1 and +1. Elevations or altitudes (m) were estimated

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