A new dimension: Evolutionary food web dynamics in two dimensional trait space

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HIGHLIGHTS

- Higher dimensional space increases spectrum of network structures and evolutionary dynamics.
- Dynamics arise from interactions between small groups (e.g. red-queen dynamics).
- Ratio between predation and competition determines structure and evolutionary dynamic.
- Variation of trophic and spatial food web structure appears to be interdependent.
- Food web assembly in space (horizontal) faster than in the trophic dimension (vertical).

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ABSTRACT

Species within a habitat are not uniformly distributed. However this aspect of community structure, which is fundamental to many conservation activities, is neglected in the majority of models of food web assembly. To address this issue, we introduce a model which incorporates a second dimension, which can be interpreted as space, into the trait space used in evolutionary food web models. Our results show that the additional trait axis allows the emergence of communities with a much greater range of network structures, similar to the diversity observed in real ecological communities. Moreover, the network properties of the food webs obtained are in good agreement with those of empirical food webs. Community emergence follows a consistent pattern with spread along the second trait axis occurring before the assembly of higher trophic levels. Communities can reach either a static final structure, or constantly evolve. We observe that the relative importance of competition and predation is a key determinant of the network structure and the evolutionary dynamics. The latter are driven by the interaction—competition and predation—between small groups of species. The model remains sufficiently simple that we are able to identify the factors, and mechanisms, which determine the final community state.

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1. Introduction

Ecologists have long been interested in the complex structures exhibited by empirical food webs, the first studies dating back at least to the seventeenth century (see Egerton, 2007; Dunne and Meyers, 2009). Food webs describe the structure of 'who-eats-whom' in a community and constitute one of the most fundamental levels of biological organisation. This structural richness has inspired theoretical approaches to capture food web topology and dynamics in terms of mathematical models. Most theoretical food web studies can be separated into two categories: generating food web structures and describing population dynamics.

On the one hand, narrative statistical models have been put forward that combine stochastic elements with simple link assignment rules and allow networks of trophic interactions between species that closely resemble empirical food webs to be synthesised (Dunne and Meyers, 2009). The most prominent examples are the cascade model (Cohen and Newman, 1985), the niche model (Williams and Martinez, 2000) and the random model (Heckmann et al., 2012). Models of this type are able to provide a detailed understanding of the structural complexity of food webs (Stouffer et al., 2006; Williams and Martinez, 2008; Stouffer et al., 2007) and, with certain refinements, produce ecologically reasonable food web structures (Rossberg et al., 2006; Allesina et al., 2008; Rohr et al., 2010). However, the population

dynamics of the resultant community are not addressed within this framework and must be modelled separately.

Thus, a separate stream of research has focused on dynamical models, describing the temporal change of populations within a food web structure. These models have proven to be able to capture a huge range of dynamic complexities, such as population cycles, multi-stability and chaotic dynamics. However, they contain a large number of free parameters that have to be carefully chosen to fit to empirical food webs, without over fitting the model (Fussmann and Heber, 2002; Turchin, 2003). This problem is elegantly solved in allometric food web models, which were introduced by Yodzis and Innes (1992) and extensively studied since (Brose et al., 2006; Binzer et al., 2011). These models automatically determine the model parametrisation using allometric scaling to determine how species dynamics vary with body size. Where the food web structure can be determined a priori such models can accurately predict the dynamics of ecological communities (Boit et al., 2012; Fung et al., 2015). However, just as statistical models cannot describe population dynamics, dynamical models cannot be used to generate food web structure, since the food web topology is required to initialise the model.

These two approaches are combined in population based, evolutionary food web models (Caldarelli et al., 1998; Drossel et al., 2001; Tokita and Yasutomi, 2003; Rossberg et al., 2008; Takahashi, 2011; Takahashi et al., 2013). One prominent class of such models are niche based evolutionary food web models, which were introduced by Loeuille and Loreau (2005). In these models each species is characterised by a position, related to its body size, on a continuous niche axis. The strengths of interactions between species are then simply determined by their pairwise distances along the niche axis and allometric scaling with body size. New species can be added to the community simply by assigning them a trait value, with the change in food web topology being determined automatically. As such they provide a simple means to capture the combinatorial increase in possible food web structures that occurs as community size increases.

Niche based coevolutionary food web models were examined in great detail. Refinements of the original model (Loeuille and Loreau, 2005) studied, for example: the influence of trade-offs in resource consumption on the network structure (Ingram et al., 2009); the emergence of diversification by incorporating gradual evolution (Brännström et al., 2011); and evolvable shapes of the feeding interaction kernels to produce more realistic food webs (Allhoff et al., 2015). However these studies also revealed that niche based evolutionary models do not generate the degree of variety in food web structure (Allhoff and Drossel, 2013) that is observed in empirical food webs. Additionally, where such models typically generate a single dynamic regime (Loeuille and Loreau, 2005; Brännström et al., 2011; Allhoff et al., 2015), it is assumed that empirical food webs display a range of dynamical states (Wilson, 1961; Ricklefs and Bermingham, 2002).

This limited variety could be related to the fact that these niche based evolutionary models consider only a single evolutionary trait—body size. Several studies have raised the question whether a larger number of traits may be necessary to realistically describe species interactions or food web intervality (Allesina et al., 2008; Petchey et al., 2008; Stouffer et al., 2011; Eklöf et al., 2013). In this case, trophic niche space would be spanned by other factors or phenotypic traits, apart from body size. Subsequent studies showed that the dimensionality of trophic niche space has strong implications for food web structure and the adequate dimensionality of trophic niche space remains an ongoing debate in the food web literature (Cohen, 1977; Rohr et al., 2010; Rossberg et al., 2010; Allesina, 2011; Nagelkerke and Rossberg, 2014).

Thus, a higher dimensional trait space could resolve the aforementioned limitations in the structural and dynamical variety of niche based evolutionary food web models. Zhang et al. (2014)

constructed one example of such a model by incorporating spatial dimension into the evolutionary food web framework. In this model each species is characterised by two traits: body size and a spatial habitat preference, used to characterise a population's distribution in space. The strength of feeding interactions was modelled as a function of the pairwise distance between predator and prey species in the two-dimensional niche space. The analysis by Zhang et al. (2014) showed that the second trait dimension had significant influence on the emerging size spectra and maximal trophic levels. However, this study did not investigate how the interaction parameters in the two dimensional niche space influence the variety of food web structures and dynamics which can emerge.

In this study, we propose a conceptual evolutionary food web model that describes the population dynamics of a community of species in a two-dimensional niche space, characterised by body size and a second abstract trait. Our model is similar to that of Zhang et al. (2014) although we follow closely Loeuille and Loreau (2005) when determining interactions along the body size axis and introduce new species via an evolutionary algorithm. Most notably, we model competitive interaction between species along the second trait dimension. Thus, our model unifies the seminal MacArthur–Levin's model of competition on a niche axis with an evolutionary food web model on a body size axis. In our model, species are described by their trait values in a two dimensional space and their interactions—feeding and competition—by the niche overlap in this space. The second trait can be interpreted in a variety of ways, for example, as a vertical position in a water column, day time of activity, habitat preference, phylogeny, a hidden gradient (e.g. temperature, salinity, rainfall, day length) or it may simply be regarded as a spatial coordinate.

Our primary goal in this study is to investigate the diversity of food web structure and dynamics that emerges when such a second trait axis is introduced to the evolutionary food web framework. Note that using a conceptual model that remains sufficiently simple, within the evolutionary food web framework, it is possible to obtain insights into the factors and mechanisms underlying particular phenomena. Thus a secondary aim of this study will be to identify possible ecological processes that are responsible for greater food web diversity. Using intensive numerical simulations we show that the additional trait axis allows the emergence of communities with a much greater range of network structures, similar to the diversity observed in real ecological communities. Thereby, the combined interplay of evolutionary and population dynamics gives rise to a plethora of community structures and dynamical outcomes, such as evolutionary outbursts where a top-layer of morphs at high body size spontaneously emerges and collapses, or directed evolutionary motion, where species are co-evolutionarily driven towards smaller body sizes. Community emergence follows a consistent pattern with spread along the second trait axis occurring before the assembly of higher trophic levels. Communities can reach either a static final structure, or constantly evolve. We observe that the relative importance of competition and predation is a key determinant of the network structure and the evolutionary dynamics. Finally, we will show that the model produces ecologically reasonable results by undertaking a limited comparison to empirical food webs.

2. Model

We develop an evolutionary food web model, describing the dynamics of one resource and a variable number of evolving morphs $(i = 1, …, N)$. We use the term morph instead of species, since we neglect reproductive isolation and the underlying isolation mechanism that leads to speciation. Each morph is characterised by two evolutionary traits, logarithmic body size z_i, and an abstract