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# Emergence of evolutionary cycles in size-structured food webs

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## HIGHLIGHTS

- Evolutionary cycles might be general phenomenon, since necessary asymmetry is naturally included.
- Food web characteristics are remarkably robust towards evolution.
- We suggest an alternative explanation of the “Endless trends to gigantism” that results from Cope's rule.
- Evolutionary cycles have similar characteristics to taxon cycles and imply that the latter might be a transitory phase of island colonisation.

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## ABSTRACT

The interplay of population dynamics and evolution within ecological communities has been of long-standing interest for ecologists and can give rise to evolutionary cycles, e.g. taxon cycles. Evolutionary cycling was intensely studied in small communities with asymmetric competition; the latter drives the evolutionary processes. Here we demonstrate that evolutionary cycling arises naturally in larger communities if trophic interactions are present, since these are intrinsically asymmetric. To investigate the evolutionary dynamics of a trophic community, we use an allometric food web model. We find that evolutionary cycles emerge naturally for a large parameter ranges. The origin of the evolutionary dynamics is an intrinsic asymmetry in the feeding kernel which creates an evolutionary ratchet, driving species towards larger bodysize. We reveal different kinds of cycles: single morph cycles, and coevolutionary and mixed cycling of complete food webs. The latter refers to the case where each trophic level can have different evolutionary dynamics. We discuss the generality of our findings and conclude that ongoing evolution in food webs may be more frequent than commonly believed.

## 1. Introduction

One of the main goals of evolutionary ecology is to gain insights into the interplay of population dynamics and evolution, shaping the structure and dynamics of communities (Fussmann et al., 2007; Brännström and Johansson, 2012). The outcome of eco-evolutionary processes is not easy to understand from first principles, but much progress has been achieved by theoretical approaches. Of particular interest are the conditions under which eco-evolutionary processes within communities give rise to dynamic patterns. Early theoretical studies of evolutionary driven community dynamics were restricted to simple community-modules of two or three species with fixed species roles and primarily focused on temporal changes in the abundance and mean trait values of different species or populations. These works studied the influence of co-evolution on the stability of predator-prey systems (Pimentel, 1961; Abrams et al., 1993; Abrams and Matsuda, 1997), the occurrence of character displacement in models of competition mediated by a quantitative trait (Slatkin, 1980; Rummel and Roughgarden, 1983, 1985; Taper and Chase, 1985; Taper and Case, 1992), as well as the dynamics of co-evolutionary arms races (Van Valen, 1973). Further theoretical analysis showed that evolution can also induce temporal changes in the composition and diversity of a community and may either increase species richness, for example via speciation events (Rosenzweig, 1978; Dieckmann and Doebeli, 1999), but may also reduce species richness, for example via self-extinction through evolutionary suicide (Matsuda and Abrams, 1994; Gyllenberg et al., 2002; Parvinen, 2005).

One major insight of these studies was that the interplay of ecological and evolutionary processes does not inevitably lead to an evolutionary equilibrium, but can lead to a situation of non-equilibrium states, characterized by sustained evolutionary

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change. One particularly intriguing case is that of evolutionary cycling, which is the emergence of ongoing periodic changes in species traits or community states (Dieckmann et al., 1995; Kisdi et al., 2002). In one of the first studies of evolutionary cycling, Rummel and Roughgarden (1983) suggested the appearance of community cycles, i.e. the occurrence of evolutionary cycles in the community composition going together with sustained species turnover. Rummel and Roughgarden (1983) simulated the buildup of island faunas based on a model of competitive interactions mediated by bodysize as the dominant phenotypic trait. Thereby, one key ingredient for the emergence of community cycles was attributed to the asymmetry of species interactions, The resulting community cycles, sometimes referred to as taxon cycles (Wilson, 1961; Roughgarden and Pacala, 1989), describe a scenario where an island (or local habitat), which is initially occupied by a single resident, is colonised by a new invading species of larger bodysize. The invading species forces the smaller resident to evolve to smaller bodysize, while following this evolutionary movement. The resulting coevolutionary arms-race towards smaller bodysizes weakens the viability of the resident which is eventually driven to extinction, leading again to a single species community. It was shown that this simple mechanism is able to describe the empirical patterns in the build-up of island faunas in the case of *Anolis* lizards in the Lesser Antilles (Roughgarden and Pacala, 1989) and was subsequently investigated in a series of further studies (e.g. Rummel and Roughgarden, 1985; Taper and Chase, 1985; Taper and Case, 1992; Matsuda and Abrams, 1994). In these studies, it was found that community cycles are a robust model outcome, but the details of the cycles depend on the specific model assumptions. In particular, it is possible that the bodysize change of the cycle operates in the reverse direction, so that species are driven towards larger bodysizes.

Despite this progress in describing generic mechanisms of evolutionary cycling, the studies mentioned above are limited in several respects. First, most demonstrations of evolutionary community cycles are restricted to small communities, consisting of very few species. Recently, there has been much interest in the evolutionary build-up of community structure in multi-species communities (Jansen and Mulder, 1999; Bonsall et al., 2004; Loeuille and Loreau, 2005; Scheffer and van Nes, 2006; Rossberg et al., 2006). However, these studies typically observed static community structures, whereas not much is known about the conditions that favour the emergence of ongoing evolutionary change and community cycling in multi-species assemblages (Takahashi et al., 2013, 2011). A second related question is whether larger communities can exhibit different coevolutionary processes that occur independently from each other in different community modules, possibly at different frequencies. Finally, even though community cycles have been studied extensively for competitive interactions, not much is known about their relevance in trophically structured communities. This is quite astonishing, given the striking structural similarity of allometric evolutionary food web models (Brännström and Johansson, 2012) to competition models on a niche axis (Rummel and Roughgarden, 1983; Taper and Case, 1992).

One of the first allometric evolutionary food web models was introduced by Loeuille and Loreau (2005) and several variants were studied in great detail (Loeuille and Loreau, 2006, 2005; Allhoff and Drossel, 2013; Brännström et al., 2011; Allhoff et al., 2015). In this model class, similar to Rummel and Roughgarden (1983, 1985), each species is characterized by its bodysize as a major phenotypic trait, the interactions between species are determined by their differences in bodysize, and allometric relations are considered explicitly. The essential new ingredient of allometric food web models is that they not only consider competition between species of similar bodysize, but also incorporate trophic interactions between species, so that a large species is able to prey upon smaller species. Given the strong similarity between these two model classes and the fact that predator–prey interactions are naturally asymmetric, one would expect that evolutionary community cycles, similar to taxon cycles in models of competition, are a typical outcome in evolutionary food web models. However, while several other studies have reported evolutionary dynamics in such models, e.g. irregular extinction cascades (Allhoff et al., 2015), trophic outbursts (Ritterskamp et al., 2016) and Red Queen dynamics in two species communities (Zhang et al., 2015), to date there has been no rigorous investigation of evolutionary cycling in this framework.

In this study, we revisit the well-studied evolutionary allometric food web model by Loeuille and Loreau (2005). We show that this model can indeed produce evolutionary cycles in a large parameter range and that the possibility of evolutionary cycles is related to the competition between species. When Loeuille and Loreau (2005) introduced this model, they found food webs that are relatively invariant over time. While these results proved to be robust to a broad range of feeding ranges and competition strength, the rest of the parameter space was relatively unexplored. In particular, the parameter governing the bodysize distance over which morphs can compete, the competition range, was limited to rather small values. While some biological justification for this range was given, we argue here that this range may be too small. If competition between species arises from niche overlap (sensu MacArthur and Levins, 1967), we should expect a competition range that is significantly broader and is of the same order as the feeding range of a species. This would allow interspecies competition to have a much stronger effect on the evolutionary dynamics.

Motivated by this observation, we numerically investigate the evolutionary behaviour in the model (Loeuille and Loreau, 2005), by systematically varying the strength and range of the competition between species. Our simulations show that evolutionary cycling, where species are driven towards larger bodysizes, is naturally present in the model considered – not only between single species but also in large trophic communities. Thereby, we observe a plethora of regimes with distinct dynamics. Besides static food webs, we observe evolutionary single morph cycles, complex community cycles where different trophic levels undergo separate coevolutionary cycles, as well as transient dynamics. Using invasion analysis and Pairwise Invasibility Plots (PIPs) we are able to support the numerical observations, which allows us to explain the mechanism underlying the evolutionary cycles. Our findings imply that ongoing evolution in food webs may be more frequent than commonly believed.

## 2. Model

We follow the evolutionary food web model by Loeuille and Loreau (2005). The model considers one basal resource, such as an inorganic nutrient, ($i=0$) and a variable number of evolving morphs ($i = 1, \ldots, N$). We use the term morph, rather than species, since we are not considering the speciation process. Each morph is described by its population biomass density $B_i$ and bodysize $z_i$. The resource has a total density $B_0$ and is associated with a non-evolving ‘bodysize’, which is fixed to the value $z_0 = 0$. The model consists of two components: population dynamics and evolutionary dynamics, each of which operate on different time scales. The population dynamics describe the trophic interactions among morphs and determine their respective growth, survival or extinction. On a longer time-scale, usually after the population dynamics have reached an attractor, new morphs are added to the community by an evolutionary algorithm.