International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report IR-12-025

Modeling the ecology and evolution of communities: A review of past achievements, current efforts, and future promises

Åke Brännström
Jacob Johansson
Nicolas Loeuille
Nadiah Kristensen
Tineke Troost
Reinier HilleRisLambers
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Pavel Kabat
Director General and Chief Executive Officer

February 2015

Modeling the ecology and evolution of communities: a review of past achievements, current efforts, and future promises

Åke Brännström[1,2], Jacob Johansson[2,3], Nicolas Loeuille[4,5], Nadiah Kristensen[6]
Tineke Troost[7], Reinier HilleRisLambers[8] and Ulf Dieckmann[2]

[1]Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187 Umeå, Sweden
[2]Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), A-2361 Laxenburg, Austria
[3]Theoretical Population Ecology and Evolution Group, Department of Biology, Lund University, SE-22362 Lund, Sweden
[4]Laboratoire Ecologie et Evolution, UMR 7625, Université Pierre et Marie Curie, CNRS, 7 quai St Bernard, F-75005 Paris, France
[5]Institut National de la Recherche Agronomique (INRA), USC 2031, Ecologie des populations et des communautés, F-75005 Paris, France
[6]Commonwealth Scientific and Industrial Research Organisation (CSIRO) Entomology, G.P.O. Box 1700, Canberra, Australian Capital Territory 2601, Australia
[7]Deltares, P.O. Box 85467, NL-3508 AL Utrecht, The Netherlands
[8]Oceans and Coasts Program, World Wildlife Fund, P.O. Box 7, NL-3700 AA Zeist, The Netherlands

ABSTRACT

Background: The complexity and dynamical nature of community interactions make modeling a useful tool for understanding how communities develop over time and how they respond to external perturbations. Large community-evolution models (LCEMs) are particularly promising, since they can address both ecological and evolutionary questions, and can give rise to richly structured and diverse model communities.

Questions: Which types of models have been used to study community structure and what are their key features and limitations? How do adaptations and/or invasions affect community formation? Which mechanisms promote diverse and stable communities? What are the implications of LCEMs for management and conservation? What are the key challenges for future research?

Models considered: Static models of community structure, demographic community models, and small and large community-evolution models.

Conclusions: LCEMs encompass a variety of modeled traits and interactions, demographic dynamics, and evolutionary dynamics. They are able to reproduce empirical community structures. Already, they have generated new insights, such as the dual role of competition, which limits diversity through competitive exclusion, yet facilitates diversity through speciation. Other critical factors determining eventual community structure are the shape of trade-off functions, inclusion of adaptive foraging, and energy availability. A particularly interesting feature of LCEMs is that these models not only help to contrast outcomes of community formation via species assembly with those of community formation via gradual evolution and speciation, but that they can furthermore unify the underlying invasion processes and evolutionary processes into a single framework.

Keywords: coexistence, community ecology, community evolution, niche theory, trait-based models

INTRODUCTION

Understanding how evolution shapes ecological communities is of key importance for the successful conservation of species and ecosystems, for predicting impacts of environmental perturbations, and for understanding the origin and loss of biodiversity in general. The complexity and dynamical nature of community interactions make modeling a useful tool for deriving insights about community dynamics. This is, for example, shown by the increasing number of hypotheses derived from theoretical models that have been tested in community and meta-community experiments (Naeem *et al.*, 1994; Hector *et al,*. 1999; Morris *et al.*, 2004; Dickie *et al.*, 2011; Steiner *et al.*, 2011). Models have also shed light on how the fundamental types of ecological interactions differentially affect the dynamics of communities, and they have been used to understand the role complex interactions play in determining community structure (Pimm & Lawton, 1978; McCann *et al.*, 1998; Krause *et al.*, 2003).

Even though the first models of ecological communities were relatively simple, in that they considered the interaction between several given species with externally prescribed and unchanging ecological niches, those models nevertheless already produced powerful results that prompted new insights and generated new hypotheses (e.g., Rosenzweig, 1971, Oksanen *et al.*, 1981, Oksanen & Oksanen, 2000). Since then, researchers have strived to achieve a more realistic amount of complexity in models that incorporate population dynamics. This has been no trivial task. One way to increase community complexity in fixed-niche models is by means of community assembly (Post & Pimm, 1983; Drake, 1990b; Morton & Law, 1997), which typically involves exposing a model community to a series of invasions by species from an external predefined species pool.

While models of species with fixed ecological niches provide interesting clues about the organization of natural communities (e.g., Tilman, 1982; Peterson *et al.*, 2002; Cottenie, 2005), recent works have underscored that ecological dynamics alone may not suffice for understanding community structure. Ample evidence for rapid or contemporary evolution (Coltman *et al.*, 2003; Yoshida *et al.*, 2003; Olsen *et al.*, 2004; Hairston *et al.*, 2005; Phillips *et al.*, 2006) suggests that it is instructive, and probably essential, to include evolutionary elements in models of community structure. The ecological dynamics of large communities have been studied extensively (e.g., Post & Pimm, 1983; Moton, 1997; Thébault, 2010), and there is a growing body of work on the evolutionary dynamics of small communities (Pimentel, 1961; Rosenzweig, 1978; Slatkin, 1980; Dieckmann *et al.*, 1995; Dieckmann & Doebeli, 1999; Gaba & Ebert, 2009). Recent increases in computational power have allowed for the simultaneous incorporation of ecological complexity and evolutionary dynamics in theoretical models. Such an integrative approach is a promising direction of research since the resulting models can address both ecological and evolutionary consequences emerging from different scenarios, and the modeled communities may more accurately represent the structural organization of natural ecological communities.

The goal of the present review is to give an overview of large community-evolution models, in which both the abundances and the niches of species can change over time. For comparison, we contrast the features of these innovative models with those of static community models, large dynamic community models, and small evolutionary models that preceded them. Several existing reviews have already covered the influence of evolution on food-web structure (Yoshida, 2006; Fussman *et al.*, 2007; Loeuille & Loreau, 2009; Loeuille, 2010b). The present work therefore aims to go beyond food-web aspects, by accounting also for communities involving non-trophic interactions. In addition, as community-evolution models are related to community assembly models, yet differ in important ways, we consider how the two processes of assembly and evolution interact to forge communities. Finally, we suggest applications of the community-evolution models in several areas of community and conservation ecology.

The article has been structured according to the key elements of the different modeling traditions (Fig. 1) that precede the burgeoning study of large community-evolution models. We start by reviewing ecological community models without any evolutionary components. Such models may or may not include population dynamics, may or may not include changes in species number by invasion and extinction, and also differ in whether the modeled interactions are trait-based or not. We then move on to review models in which interactions depend on underlying traits that undergo evolutionary changes. We review models that consist of one, two, or at most a few species with fixed ecological roles, which we refer to as small community-evolution models, before we review large community-evolution models, which crucially extend small community-evolution models by allowing for changes in species number. We discuss the main assumptions and compare the building blocks of the aforementioned three types of community models. Finally, we discuss applications of these models, point out open challenges, and identify promising new directions for future research.

STATIC AND DYNAMIC COMMUNITY MODELS WITHOUT EVOLUTION

Static community models (Cohen *et al.*, 1990a; Williams and Martinez, 2000; Cattin *et al.*, 2004) and dynamic community models (e.g. Post & Pimm, 1983; Taylor, 1988; Drake, 1990b; Law & Morton, 1996; Bastolla *et al.*, 2005), both without evolution, represent two important but contrasting modeling approaches in community ecology. Static community models consist of simple rules that generate binary community networks with properties comparable to those found in empirical food-web data, whereas dynamic community models describe the demographic change of populations as a function of the current state of the community. The differences in model formulation and historical motivation between these two approaches, and the areas in which they succeed and fail, are discussed below.

It was recognized early on that food webs differ from random networks (Cohen & Newman, 1985; Proulx *et al.*, 2005; Montoya *et al.*, 2006). Static community models are motivated by structure rather than dynamics, and arose in an effort to find the most minimal rules that would predict the empirically observed properties of real food webs (Cohen & Newman 1985). They were refined (Williams & Martinez, 2000; Cattin *et al.*, 2004) after major improvements were made to the catalogue of empirical food webs (Paine, 1988; Sugihara *et al.*, 1997; Martinez, 1991; Polis, 1991; Hall & Raffaelli, 1993; Winemiller & Polis, 1996). A common element in these models is a hierarchy of niche values, often suggested to be linked to body sizes (Warren and Lawton, 1987; Williams & Martinez, 2000), such that species largely prey on species of lower niche value (Stouffer, 2005). While such a hierarchy is strict in the cascade model (Cohen *et al.*, 1990), later models such as the niche model

(Williams & Martinez, 2000) allow species also to feed on species with higher niche values. Phylogenetic origin is believed to be important for structuring communities (Cattin *et al.*, 2004) and it has been demonstrated that phylogenetic correlations can give rise to food-web intervality or near-intervality (Rossberg *et al.*, 2010; Brännström *et al.*, 2011a), a pattern widely observed in empirical food webs (Williams & Martinez, 2000). These findings indicate that trait-based and evolutionary mechanisms are likely underlying trophic relationships, and that these mechanisms thus are a primary organizing principle of food-web structure.

Dynamic models of interacting communities have been an important tool in ecology since the pioneering work by Alfred Lotka and Vito Volterra almost one century ago, and range from two-species models to large community models with physiological detail (Rosenzweig, 1978; Armstrong & Mcgehee, 1980; Yodzis, 2000; Abrams, 2003; Hartvig *et al.*, 2011). Dynamical community models have made predictions about food-web structure, including the roles of weak interactions (McCann *et al.*,1998), omnivory (Pimm & Lawton ,1978; McCann & Hastings, 1997), compartmentalization (May, 1973), and the number of trophic levels (Pimm & Lawton, 1977), in stabilizing large webs. Some predictions, such as those concerning compartmentalization, find empirical support (Krause *et al.*, 2003), whereas others, like those concerning low levels of omnivory, are not consistent with later and more detailed empirical findings about natural food webs (Martinez, 1991; Polis 1991).

Some models reconcile the aforementioned static and dynamic modeling approaches by superimposing dynamical equations onto a community structured by an underlying static model, such as in the Lotka-Volterra Cascade Model (Cohen *et al.*,1990b) or a variety of models investigated by Williams and Martinez (2006). However, while this approach has shed light on the interaction between dynamics and structure (Williams & Martinez, 2006), the question of what causes the underlying food-web structures to emerge remains unclear (Williams & Martinez, 2000; Dunne, 2006).

Many dynamic community models have been developed in the context of the complexity-stability debate (McCann, 2000). This debate ignited after Robert May (1973) used local stability analysis of random community matrices to challenge the popular notion that complexity implied stability (Odum, 1953, MacArthur, 1955; Elton, 1958). An important critique of May’s result was that natural systems are not random, but may arise through community-level selection for stability (Pimm & Lawton, 1977, 1978). This has inspired the development of community-assembly models, which are capable of building up large and stable communities (Taylor, 1988; Post & Pimm, 1983; Drake 1990a,b; Law & Blackford 1992; Law & Morton 1996). These models incorporate explicit population dynamics and emulate naturally occurring processes of invasion and colonization. The interaction strength between two species is usually determined randomly or can be derived from individual-level traits (e.g. Law & Morton, 1996). Studies based on community-assembly models have shed light on community-ecology processes such as extinction cascades (Borrvall *et al.*, 2000; Lundberg *et al.*, 2000) and succession dynamics (Law & Morton, 1996).

Community-assembly models are able to address questions about both the structure and the dynamics of communities. However, these models need to justify assumptions about the invading species that are made *a priori* through the specification of an external species pool from which these invading species are randomly drawn. Moreover, as the considered structuring principle is invasion, these models do not account for phylogenetic correlations and often lack trade-offs among species’ traits. Evolutionary models of community assembly may help to overcome these limitations, since in such models – which we will now consider for the remainder of this review – the invading morphs endogenously arise from an already present community, phylogenetic correlations naturally emerge, and trade-offs among traits are readily incorporated.

SMALL COMMUNITY-EVOLUTION MODELS

Models accounting for evolutionary dynamics are numerous and have been around for quite a while (e.g., Pimentel, 1961). They represent the interactions between species as functions of heritable individual-level traits subject to evolutionary change. The determination of demographic coefficients from heritable traits gives rise to eco-evolutionary feedback: the change of a trait depends on the selection pressures arising from the ecology, which in turn leads to changes in the ecological environment (e.g. Geritz *et al.*, 1998; Fussmann *et al.*, 2007; McGill & Brown, 2007).

In the literature, a large variety of ecologically important traits has been explored in evolutionary models. Some models investigate the dynamics of general traits such as body size (Troost *et al.*, 2008), degree of specialization (Egas *et al.*, 2004), and degree of cooperation (Doebeli *et al.*, 2004; Brännström & Dieckmann, 2006; Brännström *et al.*, 2011b). Other models investigate more systems-specific traits like cannibalism (Dercole, 2003), tree height (Iwasa *et al.*, 1985), root mass (O’Brien & Brown, 2008), plant defenses (de Mazancourt *et al.*, 2001; Loeuille *et al.*, 2002), or crypsis (Nilsson & Ripa, 2010). The traits themselves can be scalar-valued (or univariate, as in the references above), vector-valued (or multivariate), or even function-valued (Dieckmann *et al.*, 2006; *Parvinen* et al., 2006). In the last case, the expressed phenotype is specified as a function of a state variable, e.g., individual size, or of an external environmental factor, e.g., ambient temperature. Also, evolutionary changes in many kinds of ecological interactions have been analyzed, including competition (Dieckmann & Doebeli, 1999), mutualism (Bronstein *et al.*, 2004), and predation (Krivan & Diehl, 2005).

In all of the studies above, the evolving traits are subject to trade-offs and constraints: change in a trait value will improve one aspect relevant for survival and/or reproduction, while worsening another such aspect. For example, in Iwasa's (1985) tree-height model, increasing a tree's height increases its competitive ability, but also requires it to invest higher maintenance costs. Such trade-offs are fundamental aspects of evolutionary ecology and remove the possibility that 'Darwinian demons' (Law, 1979) arise in evolutionary models. It is interesting to note, however, that trade-offs are often surprisingly difficult to reveal in empirical studies (e.g. Reznick *et al*., 2000).

Evolutionary models of small communities have been used to address several general questions in evolutionary ecology. First, the earliest evolutionary model in ecology (Pimentel, 1961) was designed to examine whether coevolution may stabilize population dynamics. Since then, a large number of other models have been analyzed to elucidate the general influence of evolution on stability: while many studies have identified mechanisms through which coevolution stabilizes population dynamics (Saloniemi, 1993; van Baalen & Sabelis, 1993; Hochberg & Holt, 1995; Schreiber & Vejdani 2006), others have shown that destabilization is also possible (Abrams & Matsuda, 1997). Second, character displacement (evidenced by competing species exhibiting larger niche differences in sympatry than in allopatry) has been investigated using models in which the niche positions and niche widths or two or more species are subject to evolutionary change (Slatkin, 1980; Taper & Case, 1985; Drossel & McKane, 1999). A third classical focus is to study coevolutionary dynamics, to scrutinize the Red Queen hypothesis (Van Valen, 1973), to investigate evolutionary arms races, and to illuminate recurrent coevolutionary dynamics arising from a process known as evolutionary cycling (Dieckmann *et al*., 1995; Gaba & Ebert, 2009). Fourth, processes that change a community's diversity have been studied using small community-evolution models. Evolution may have a positive effect on total diversity, either by speciation (Rosenzweig, 1978; Dieckmann & Doebeli, 1999), in particular through a process known as evolutionary branching (Metz *et al*., 1992), or by adaptive evolution allowing a population to survive while its environment is changing, through a process known as evolutionary rescue (Gomulkiewicz & Holt, 1995; Bell & Gonzalez, 2011). Such positive effects of evolution on diversity are not guaranteed, however, as evolution under other circumstances may weaken a population's viability and even lead to its extinction, through a process known as evolutionary suicide (Gyllenberg *et al*., 2002; Parvinen, 2005); likewise, evolution of one species may lead to another species' extinction, through a process known as evolutionary murder (Dieckmann *et al*., 1995; Dercole et al. 2006).

The small community-evolution models reviewed above can be used to investigate a large array of phenomena arising through eco-evolutionary feedbacks. They also include trait-based interactions and trade-offs, two aspects often neglected in static and dynamic community models without evolution. However, they suffer from two shortcomings. First, they consist of only a few species, which raises the question of the extent to which the analyzed phenomena persist in high-diversity scenarios. Second, the ecological roles of species in these models are often prescribed, and are themselves not subject to flexible evolutionary change. For example, in a recent model of the evolution of a host-parasite system (Gaba & Ebert, 2009), species could evolve their traits, but they could not evolutionarily alter their roles of being designated either a host or a parasite. These restricted ecological roles artificially constrain the evolutionary processes and the possibility of investigating important questions, such as how new trophic levels evolve and influence a food web's structure and functioning. Including such processes requires a rethinking of the definition of trait spaces used in community modeling. Should such trait spaces be unique for each species or type, or could they be more encompassing, so as to allow representing the trait combinations of all species of interest in a particular study? In the latter case, the evolutionary emergence and alteration of ecological roles becomes amenable to model-based analyses, as we will now discuss in greater detail.

LARGE COMMUNITY-EVOLUTION MODELS

The past decade has seen burgeoning growth in the evolutionary modeling of large communities and food webs, with diverse approaches to incorporating explicit population dynamics together with trait-based species descriptions. For lack of a better name, we use the term large community-evolution models or LCEM (Loeuille & Loreau, 2009) to describe models in this class. These models often incorporate shared trait spaces, in the sense that all considered species interactions are inferred from a common list of functional traits: while each considered species is characterized by specifying its list of trait values, the list's structure, and thus the total set of considered traits, is the same across all considered species. Since interactions among species are thus determined by their respective trait values, and since those trait values can evolve in response to the prevalent section pressures, species can evolve into other ecological roles. The community structure that eventually develops is then a consequence of explicit ecological and evolutionary processes. This sets LCEMs firmly apart from static community models, but also from community-assembly models in which the structuring principle is not evolution but invasion. Below we give a brief overview of some LCEM approaches. Their key features will be compared in the next section.

As an early forerunner, Roughgarden (1972) introduced a community-evolution model based on Lotka-Volterra competition. Species in this model are characterized by a continuous trait value representing their preferred resource type, and the interaction strength between two species depends on their similarity in terms of this preference, with the interaction strength being maximal when the two species' preferences coincide. The competitive ability of a species is furthermore affected by the abundance of an underlying resource with a specified distribution, often referred to as a resource landscape (Rummel & Roughgarden, 1983). Some later variants of this model incorporate two groups of species, consumers and predators (Brown & Vincent, 1987; Ripa *et al.*, 2009). In these latter models, the ecological roles of species as predator or prey are fixed, which means that they these models employ two separate trait spaces. A related model, by Ferrière *et al.* (2002), is similarly based on Lotka-Volterra dynamics, but incorporates mutualistic interactions. This model allows the build-up of large communities with two groups of mutualistic species, for example flowers and pollinators, evolving in two separate trait spaces.

Although variants of the Roughgarden (1972) model can successfully capture the adaptive radiation of large communities and food webs (e.g. Ripa *et al.*, 2009), evolution remains constrained by the separation of the underlying trait spaces; for example, a prey species cannot evolve into a predator species. An alternative approach utilizes a fully shared trait space, and this allows for fundamental changes in ecological roles through evolution, such as in the models by Loeuille & Loreau (2005), Troost *et al.* (2008), and Brännström *et al.* (2011c). In these models, the shared evolving trait defining a species is its body size. The foraging rate is defined as a unimodal function of the relative difference between two species' body sizes, such that a species has low foraging rates on individuals with much larger or much smaller body size. Using this approach, Loeuille & Loreau (2005) studied evolving food webs to identify ecological factors constraining their structure, and Brännström *et al.* (2011c) incorporated gradual evolutionary change to explore the relationship between conditions for the initial diversification and the eventual diversity of evolved food webs. This approach can be extended to investigate evolution in traits other than body size, such as degree of specialization (Ingram *et al.*, 2009) or temperature dependence (Stegen *et al.*, 2009).

Ito & Ikegami (2006) and Ito *et al.* (2009) also considered a shared trait space, but with abstract traits, such that each individual is characterized by two continuously valued traits characterizing its profile as prey and predator, respectively. Similar to the models above, the foraging rate of one species upon another depends on the distance between the two species' traits; however, in their model, the predator trait can evolve freely with respect to the prey trait. In spite of the relative simplicity of this two-dimensional trait space, complex food webs emerge through gradual evolutionary change and evolutionary branching in the predator trait, as well as in the prey trait. These models thus shed light on factors that favor community complexity, including intermediately strong predator-prey interactions, similar competitive interactions across the community, and functional responses that are close to ratio-dependent.

Another abstract, but much more complex, trait space is explored in the WebWorld model (Caldarelli *et al.* 1998; Drossel *et al.*, 2001). Here a species is described by a binary string representing the presence or absence of features that can affect interspecific interactions (e.g. 'nocturnal vs. diurnal'), defining a potentially very large, but finite, pool of possible species. The interaction strength between two species with binary strings $\boldsymbol{v}$ and $\boldsymbol{u}$, respectively, is obtained by a bilinear form, $a = \boldsymbol{v}^{\mathrm{T}} M \boldsymbol{u}$, in which the matching matrix M is antisymmetric, with random elements determined at the beginning of a model run. New species are introduced as mutants differing in one binary feature from their parental species. The antisymmetry of M ensures that a species does not interact with itself, as it requires that all diagonal elements are zero. When there are no other zeros in M (as is the case in published applications of the WebWorld model), a species interacts as predator or prey with all other species. An optimal-foraging model component then restricts which of these potential predator-prey relationships are actually realized in the modeled community's population dynamics. This latter component turns out to be important for the stability and diversity of the resulting community (Drossel *et al.* 2001, 2004; Quince *et al.*, 2005). Similarly to the WebWorld model, Yoshida (2003) assumed that species interactions are controlled by an abstract feature string. In contrast to the WebWorld model, however, Yoshida divides species into plants and animals described by two separate trait spaces, with species being prevented from traversing from one of those spaces to the other.

The matching model (Rossberg *et al.*, 2006) is another example of a model in which two binary strings determine a species' profile as predator and prey. Again, feeding relations between species are defined by their relative body sizes, but rather than using body size to inform population dynamics, the body size is directly related to the speciation rate. As a consequence, a species' speciation rate is directly correlated with its position in the resultant food web. This model does not incorporate population dynamics. Despite these simplifications, the matching model gives rise to food webs whose statistical features are in good general alignment with empirical data. Rossberg *et al.* (2008) later introduced a version of this model with explicit population dynamics and continuous trait vectors in lieu of binary strings. This model was used to study scaling relationships between body masses and species abundances in multitrophic communities.

While the above portrayal of LCEMs is not meant to be exhaustive (see, for example, the tangled nature model of Christensen *et al.* 2002), it highlights how this class of models can simultaneously account for ecological complexity and evolutionary dynamics, and it illustrates the variety of ways in which models can produce food-web structures that agree with empirical observations in important aspects.

COMPARISON OF KEY FEATURES OF LARGE COMMUNITY-EVOLUTION MODELS

As can be seen from the examples above, there are many apparent differences in how models of large community evolution are constructed. We now contrast the key features of LCEMs: Table 1 shows how characteristics of the models considered above compare in three key areas: traits and interactions, demographic dynamics, and evolutionary dynamics. In what follows, we discuss each of these areas in detail.

Traits and interactions

The models surveyed in the previous section differ in whether traits are assumed to be discrete or continuous. In the former category, we find the tangled nature model and the WebWorld model, which are both based on binary strings. In contrast, the models by Loeuille & Loreau (2005, 2006), Brännström et al. (2011c), and Ito & Ikegami (2006) are based on continuous traits. Falling in both domains, the original matching model (Rossberg *et al.*, 2006) is an example of a model that combines discrete and continuous traits: binary strings for a species' profile as prey and predator, and body size as a species property that imposes fundamental constraints on trophic interactions.

A related aspect in which LCEMs differ is the dimensionality of the considered trait space, which can be one-dimensional (Troost *et al.*, 2005; Loeuille & Loreau, 2005; Brännström *et al.*, 2011c), two-dimensional (Ito & Ikegami, 2006; Troost *et al.*, 2008; Ingram *et al.*, 2009), or have much higher dimensionality (Rossberg *et al.*, 2006; Caldarelli *et al.*, 1998; Drossel *et al.*, 2001; Christensen *et al.*, 2002).

Related to the representation of traits is the way in which individual traits give rise to interactions. To avoid the emergence of a 'Darwinian demon' (Law, 1979), all models must explicitly or implicitly incorporate trade-offs, with the precise details differing from model to model. Three fundamental groups can be discerned: the interaction strength between species pairs may depend on binary traits and a random matching matrix (tangled nature model, WebWorld model), on the similarity between continuous traits (resource-competition models, matching-model variants, and the Ito & Ikegami model), or on empirical or physiological principles associated with the considered continuous traits (Loeuille & Loreau, 2005; Brännström *et al.*, 2011c).

A further distinction comes from the types of interactions that are considered. Most models mentioned above include trophic interactions, but some models additionally include direct competitive interactions (Loeuille & Loreau 2005, 2006; Brännström *et al.*, 2011c) or mutualistic interactions (Ferrière *et al.*, 2002). Thus far, no LCEM has considered all of these interaction types together (but see Loeuille, 2010b) – an important omission, considering that all three interaction types are simultaneously present in natural communities (Fontaine *et al.*, 2011).

Demographic dynamics

LCEMs can also be classified according to the modeled type of demographic dynamics. The resource competition models and the models by Loeuille & Loreau (2005) and Brännström *et al.* (2011c) are based on the classic Lotka-Volterra equations with a linear functional response, while the other models employ nonlinear functional responses. The use of nonlinear responses and adaptive foraging may play an important role in enabling the latter models to create and sustain large and diverse communities.

Adaptive foraging means that predators allocate their efforts to more abundant and/or more profitable prey species, thus offering a dynamically emerging refuge to any prey species that moves toward the brink of extinction. Thus, adaptive foraging has a stabilizing effect on population dynamics, facilitates coexistence of different types, and is thereby conducive to the formation of larger communities (Drossel *et al.*, 2001; Kondoh, 2003). A few studies have compared the effects of different functional responses in the context of LCEMs (e.g., Drossel *et al.*, 2001; Ito *et al.*, 2009), and have found that nonlinear functional responses and adaptive foraging are often critical for the evolution of diverse communities (Loeuille, 2010a).

A few aspects that are commonly studied in ecological models are yet to be explored in LCEMs. These include age- and stage-structured populations, environmental and demographic stochasticity, as well as spatially structured populations (but see Rossberg *et al.*, 2008, for a metapopulation model). Such aspects have already been included in small community-evolution models (e.g., Doebeli & Dieckmann, 1999, 2003; Johansson & Ripa, 2006; Nilsson & Ripa, 2010), indicating that the corresponding extensions to LCEMs are feasible.

Evolutionary dynamics

There is a striking diversity among LCEMs with respect to how evolutionary change is modeled, with a corresponding diversity of assumptions underlying the different approaches. In the LCEMs we have reviewed, evolution has been modeled as a diffusion process in trait space (Ito & Ikegami, 2006), as point mutations in binary strings

(Drossel *et al.*, 2001; Christensen *et al.*, 2002), as changes in the contributions of allelic effects in strings (Yoshida, 2003), as small-to-large mutational steps in continuous trait values (e.g., Loeuille & Loreau, 2005), or as gradual mutational steps in continuous trait values (e.g., Ripa *et al.*, 2009; Brännström *et al.*, 2011c).

In general, evolution can be modeled using either small or large mutational steps, and can be described as either as a deterministic or a stochastic process. When trait combinations are described as a binary string (e.g., Calderelli, 1998), evolution is necessarily modeled using large mutational steps, whereas models with continuous traits can assume mutational steps of variable size, or consider gradual evolutionary change only, such as in models that employ the canonical equation of adaptive dynamics (e.g., Ripa *et al.*, 2009). In the models that we have reviewed, those that assume large mutational steps also consider stochastic trait evolution. Conversely, models that assume small mutational steps typically consider deterministic trait evolution, with the model by Brännstrom *et al.* (2011), which assumes small mutational steps and considers stochastic trait evolution, illustrating a third combination.

Some models assume that the trait distribution of a species contains only one or a few trait combinations at any given time, resulting in communities known as oligomorphic (Ito & Dieckmann, 2007). Such oligomorphic trait distributions underlie adaptive dynamics theory and are therefore often assumed in models employing this framework (Ripa *et al.*, 2009; Ito *et al.*, 2009). In contrast, a fully continuous distribution of trait combinations within a population is assumed in only one of the models we have reviewed (Ito & Ikegami 2006), although this is a common assumption in the quantitative genetics theory of gradual evolution (Lande, 1982). In two other models (Yoshida, 2003; Loeuille & Loreau, 2005), frequent and large mutational steps, in conjunction with stochastic trait dynamics, give rise to polymorphic distributions of traits.

All LCEMs require the formation and coexistence of new species, but only the tangled nature model (Christensen *et al.*, 2002) incorporates sexual reproduction. While this common simplification is understandable in light of the additional computational complexity sexual reproduction adds to community models, future research needs to address this indisputable extra factor structuring most natural communities.

LESSONS LEARNED AND CHALLENGES AHEAD

Mechanisms promoting the evolution of community diversity

A clear advantage of LCEMs over community-assembly models is that they do not need to make *a priori* assumptions about the invading species used to build up ecological diversity. While some debate exists about advisable relative investments into ecological detail and genetic detail in models of evolutionary ecology (e.g. Waxman & Gavrilets, 2005, including responses), all community-evolution models agree on including diversification processes and their ecological determinants are key ingredients. Therefore, they provide unique opportunities for studying conditions under which diversification occurs, and conversely, help to understand constraints on the emergence and maintenance of diversity in ecological communities (Brännström *et al.*, 2011c). Such constraints emerge from the ecological and evolutionary ingredients considered in an LCEM.

One example of how diversity depends on ecological and evolutionary forces is the effect of competition. While competition has traditionally often been conceived as limiting the number of sympatrically coexisting species (Gause, 1932; Tilman, 1982), more recent research has highlighted how competition actually appears necessary to obtain diversity in community-evolution models, because it promotes speciation (Loeuille & Loreau, 2005; Ito & Ikegami, 2006; Yoder & Nuismer, 2010; Brännström *et al.*, 2011c). The crucial role of competition for the emergence of biodiversity is supported by experimental studies (Rainey & Travisano, 1998), as well as by empirical data suggesting niche displacement/limiting similarity (Abrams, 1983). A second example is provided by increased availability of energy, a purely ecological factor that has been shown to promote vertical diversity (measured by the number of trophic levels), both in community models without evolution (Oksanen *et al.*, 1981; Oksanen & Oksanen, 2000) and in community-evolution models (Drossel *et al.*, 2001; Loeuille & Loreau, 2005; Brännström *et al.*, 2011c).

With regard to evolutionary components, it is important to note that the dimensionality of a community's trait space does not directly affect the emergence of diversity. High diversity can be obtained in models utilizing only a one-dimensional trait space (Troost *et al.*, 2005; Loeuille & Loreau, 2005), a two-dimensional trait space (Ito & Ikegami, 2006; Ingram *et al.*, 2009), or many trait dimensions (Caldarelli *et al.*, 1998; Drossel *et al.*, 2001; Christensen *et al.*, 2002; Rossberg *et al.*, 2006). It has, however, been shown that the shape of trade-off functions is critical for evolutionary branching (de Mazancourt & Dieckmann, 2004), and thus for the adaptive diversification of communities, indicating that certain kinds of trade-offs may be important for the evolutionary build-up of complex communities.

Relating traits with interactions and defining trade-offs

Models based on one or two concretely identified traits (such as body size) assume that these traits play a dominant role in determining ecological interactions. The advantages of such an approach are twofold. First, because the traits are concretely identified, it is easier to derive the corresponding trade-offs from empirically supported ecological or physiological assumptions. Second, because such concretely identified traits can be measured empirically, the models can be falsified in terms of their assumptions or their predictions. For example, two assumptions of the Loeuille & Loreau (2005) model can be empirically justified: the assumption that predators will preferably feed on a restricted range of prey body sizes that are smaller than themselves (Cohen *et al.*, 2003; Emmerson & Raffaelli, 2004; Berlow *et al.*, 2004), and the assumption that body size also effects basic reproduction rates and mortality rates (Peters, 1983; Brown, 2004). Similarly, when the considered trait refers to the degree of specialization or vulnerability, trade-off functions may be based on optimal-foraging arguments (Ito & Ikegami, 2006; Kondoh, 2003).

One criticism of models based on one or two trait dimensions is that their match with reality could be limited, as interspecific interactions in nature are bound to be affected by many traits. However, static community models without evolution that use a one-dimensional niche hierarchy have been relatively successful at reproducing empirically observed food-web structures (Williams & Martinez, 2000). Real food webs are close to being interval (e.g. Stouffer *et al.*, 2006), which could be indicative of a low-dimensional trophic niche space, a high-dimensional trophic niche space, or frequent speciation events (Rossberg *et al.*, 2010; Brännström *et al.*, 2011a). It is also conceivable that the effective dimension of trophic niche space is low even if many traits determine trophic interactions (Rossberg *et al.*, 2010).

An alternative approach within the LCEM framework, close in spirit to what is done in statistical physics, is to consider a large number of traits and to obtain the evolutionary dynamics as emerging from variations of this large set (e.g. Drossel *et al.*, 2001). In such models, trade-off functions are not directly defined; instead, it is usually assumed that activation of one trait implies inhibition of another trait.

Understanding invasions and adaptations as drivers of community formation

Both community-assembly models (e.g. Post & Pimm, 1983) and LCEMs assume that the modeled communities are exposed to a series of invasions by new morphs not currently present in the community. While invaders in community-assembly models are uncorrelated with the resident community, invaders in LCEMs are often mutants that differ only slightly from their resident ancestors. Figure 2 illustrates how these two alternative approaches lead to different community structures. In Fig. 2a, the community has been assembled through invasions from an external species pool. The resultant community is wide open to further invasions. After more species have attempted to invade, the ranges of trait combinations that can successfully invade have shrunk (Fig, 2b), but the community still remains susceptible to invasions. If the community instead undergoes gradual adaptive evolution starting with a random collection of species, the picture is very different: after a while, evolution comes to a halt, with all resident species situated on invasion-fitness peaks at zero height (Fig. 2c). There are, however, still trait combinations with which invading species could successfully enter the resultant community. Combining the two processes of invasion and adaptation finally leads to a community that is completely closed, in the sense that it cannot be invaded by any additional species (Fig. 2d).

As illustrated by the figure, invasions are not fine-tuned, and thus cannot place species exactly on any fitness peaks that happen to exist. Gradual adaptive evolution, in turn, cannot cross valleys in the fitness landscape. The combination of both processes, therefore, more easily leads to communities that are completely closed to invasion, i.e., to a globally evolutionarily stable coalition. Note that the distinct fitness peaks, or niches, that are visible in Figs 2c-d, are not prescribed model ingredients, but are an emergent property of the eco-evolutionary process.

While only those community-assembly models that are trait-based can readily be extended to include evolutionary processes, all LCEMs can be extended to include invasion processes. Thus, LECMs have the potential to serve as a framework for the conceptual unification of community-assembly models and community-evolution models. This integrative approach can potentially shed new light on several research questions, such as the extent to which speciation is driven by species diversity (e.g. Emerson & Kolm, 2005) and the relationship between the rate of species invasions and local extinctions (e.g. Sax *et al.*, 2002). With more phylogenetic data becoming available (e.g. Wiens, 2004; Urban & Skelly 2006), future applications of LCEMs may help with interpreting phylogenetic patterns in communities that have emerged as the result of adaptive radiations involving both invasions and adaptations. They can also be used to investigate trait distributions in ecological communities and to study selection pressures on invasive species after their introduction into novel habitats (Phillips *et al.* 2006).

Comparing community-evolution models with empirical datasets

Indicators of ecological community structure based on binary interactions are being widely considered, both in empirical and in theoretical studies. Such indicators are often taken from graph theory (Jordano *et al*., 2003; Krause *et al*., 2003; Thébault & Fontaine, 2010; Fontaine *et al*., 2011). We know, for instance, that empirical trophic webs often tend to be compartmentalized, while empirical mutualistic webs tend to be nested (Post & Pimm, 1983; Drake, 1990; Morton & Law, 1997). Recovering these and other commonly found statistical features of natural community structures by devising suitable models has been a major goal of ecological research, a challenge in which static community models without evolution seem to succeed quite well (Williams & Martinez, 2000; Cattin *et al*., 2004). Some LCEMs succeed in this challenge too (Loeuille & Loreau, 2005; Rossberg *et al*., 2005), which raises the question of how to assess the various modeling approaches in light of the empirical data.

Recently, McGill (2010) claimed that testing biogeographical models using species-abundance distributions was of limited relevance, because too many different models, using very different ingredients, were able to reproduce key features of the observed distributions: hence, additional tests are necessary to tease apart the different models. We expect a similar difficulty to arise when comparing the community structures predicted by static community models and LCEMs: since many static community models (Williams & Martinez, 2000; Cattin *et al*., 2004) and LCEMs (Loeuille & Loreau, 2005; Rossberg *et al*., 2006) are able to reproduce empirical web structures adequately, additional tests have to be devised and undertaken to assess the relative merit of those community models, and thereby, of the theories and assumptions on which they are built.

LCEMs have a verifiability advantage over static community models, in that the latter are limited to producing binary structure (interactions between species are either absent or present), whereas community-evolution models that include population dynamics yield quantitative predictions of interaction strengths and of the relative densities or biomasses of species. Most LCEMs can, for example, reproduce skewed distributions of interaction strengths, a pattern known to be present in many food-web datasets (e.g. Paine 1992, Goldwasser & Roughgarden 1993). Predictions of the dynamics of densities or biomasses through time may also be used for empirical tests. Further, when these models are based on concretely identified traits, model-predicted trait distributions can be directly compared with their empirical counterparts (Loeuille & Loreau, 2006; Rossberg *et al*., 2008, Troost *et al*., 2008).

Finally, we note that most static community models use community-scale parameters (such as diversity and connectance, most commonly) as input to obtain other quantitative indicators of community structure as output, leaving unexplained the former's origin. In contrast, LCEMs may help understand the origin of diversity and connectance as emergent properties of the considered eco-evolutionary process (Loeuille & Loreau, 2005; Beckerman *et al*., 2006; Petchey *et al*., 2008).

Community-evolution models and the stability of ecological communities

Recent ecological threats such as global warming and a rapidly growing human population mean that now, more than ever, it is important to understand the conditions under which ecosystems may persist and remain stable. There are experimental, empirical, and theoretical reasons to think that evolution may affect the stability or the dynamics of populations constituting ecological communities. In an experiment, Takehito Yoshida and collaborators showed that evolution strongly influences population cycles (Yoshida *et al*., 2003). Empirical data on lemming cycles suggest that adaptations to food quality may have been an important cause of such periodic fluctuations (Seldal, 1994). The question of the influence of evolution on stability has been extensively studied in small community-evolution models (van Baalen & Sabelis, 1993; Ferrière & Gatto, 1993; Doebeli & Koella 1995; Abrams & Matsuda, 1997; Fussmann *et al*., 2007). While a general message is difficult to discern, it has been suggested that evolution of prey vulnerability/defense is more likely to destabilize population dynamics, while evolution of predator consumption is more likely to stabilize it (Abrams, 2000). LCEMs offer an open opportunity to study these and related questions in a realistic context of fully fledged ecological communities.

While small community-evolution models allow us to discover key ingredients that change the effects of evolution on stability, such as spatial heterogeneity, nonlinear functional responses, or trophic position, it is important to study the same questions in more complex settings. One reason is that the number of feedback loops is limited when considering just two species, while many indirect effects constraining stability occur in larger communities. Another reason is May's (1973) demonstration that diversity is an important component of the stability of communities, with larger communities tending to be less stable.

Already, LCEMs seem to be producing different results compared with small community-evolution models regarding the effects of evolution on stability: in general, the effects of evolution on stability are very diverse and are currently far from being obvious, leaving open such important questions as whether coevolution stabilizes population dynamics (Saloniemi, 1993; van Baalen & Sabelis, 1993; Hochberg & Holt, 1995; Schreiber & Vejdani 2006) or destabilizes population dynamics (Abrams & Matsuda, 1997). In contrast, LCEMs including the WebWorld model (Quince *et al*., 2005), Loeuille & Loreau's model (Loeuille & Loreau, 2005; Brännström *et al*., 2011c) and Kondoh's model (Kondoh, 2003) all produce complex and fairly stable assemblages. One plausible reason for this is that evolution in these models produces skewed interaction-strength distributions (Loeuille, 2010a), which is known to be stabilizing in real food webs (McCann *et al*., 1998). However, satisfaction with LCEMs for providing a simple answer to this tricky question must be qualified by recognizing that natural communities contain many kinds of interactions beyond the trophic interactions typically emphasized in these models. It has been suggested that in such multi-interaction communities, evolution may be stabilizing when diversity is low, but destabilizing at higher levels of diversity (Loeuille 2010b).

What lies ahead: conservation and management

Interactions between organisms are not only shaping ecological coexistence and the structure of communities, but may themselves change in response to the selective pressures they impose. The conservation and management of populations can benefit from these insights. In particular, a good understanding of the demography and evolution of large communities may allow predicting what effects alien species or environmental changes will have on the dynamics and composition of ecological communities. Such an understanding may be imperative in times when species displacement is being considered a possible means of mitigating the detrimental impacts of climate change (Willis *et al*., 2009; Thomas, 2011).

There are many instances in which the translocation of a species has led to large-scale modifications of ecological communities because of interactions between community and evolutionary dynamics. One of the more well-known examples is the introduction of the cane toad (*Bufo marinus*) in Australia. In 1935, some 3000 specimens were released in northern Queensland in an attempt to manage the native cane beetle (*Dermolepida albohirtum*), a pest of sugar cane (Lever, 2001). Not only did the toads fail to control the pest they were supposed to prey upon, but they rapidly invaded western Australia and became a pest themselves (Lampo & De Leo, 1998). Evolution matters to understand the different steps of such invasive dynamics. First, the plasticity in the toad's behavior played a critical role in their propagation. Second, the invasive speed of the cane toads has increased over the years through adaptive changes in leg length (Phillips *et al*., 2006). The cane toad is not the only example of an invasive species for which adaption has played a major role; similar conclusions have been reached for other invasive organisms (Blossey & Notzold, 1995; Colautti *et al*., 2004; Joshi *et al*., 2005; Liu & Stiling, 2006). Evolutionary responses may also bring invasions to a halt. For instance, the evolution of soapberry bugs seems to increase the resistance of recipient communities to invasion by exotic vine species in Australia (Carroll *et al*., 2005). Although evolutionary effects are notoriously difficult to disentangle from other adaptive processes or species-replacement dynamics, many results now suggest they may play a critical role in understanding issues related to invasion and conservation (Stockwell *et al*., 2003; Müller-Schärer *et al*., 2004).

For exploited populations, a body of published work is elucidating the evolutionary effects of selective harvesting (Koskinen *et al*., 2002; Coltman *et al*., 2003; Barot *et al*., 2004; Olsen *et al*., 2004, Poos *et al*., 2010). In many cases, models have shown that exploitation imposes a selective pressure on the targeted species to mature earlier and at a smaller size, and this expectation has to some extent been confirmed by the analyses of corresponding trends in empirical data (Barot *et al*., 2004; Olsen *et al*., 2004). As LCEMs suggest that body size can play an important role in determining ecological interactions and the resultant structure of food webs (Loeuille & Loreau, 2005; Rossberg *et al*., 2008; Brännström *et al*., 2011c), evolution of body size due to selection pressures exerted by human exploitation may cascade through communities with largely unknown consequences for the maintenance of diversity and the functioning of natural ecosystems (Laugen *et al*., 2012).

Dunne *et al*. (2002) show that a sequential removal of species may entail the rapid collapse of a whole food web, in particular if the removed species are very connected. However, this intuitively plausible expectation may not apply if species can adapt and reorganize their food web's feeding interactions in such a way as to prevent the secondary extinctions. Such a reorganization of interactions may result from behavioral changes, phenotypic plasticity, or adaptive evolution. It is feasible to model these processes using evolutionary food-web models (e.g., Kondoh, 2003). Alternatively, there may be scenarios in which species evolution hinders, rather than promotes, the persistence of species. Evolutionary suicide (Parvinen, 2005) and evolutionary murder (e.g. Dercole *et al*. 2006, Ferrière *et al*., 2007) are two known ways through which species evolution leads to extinctions. In the context of a large community, these mechanisms may still operate, and if they do, they will increase the vulnerability of such a community to secondary extinctions. Future developments of evolutionary models of ecological communities in general, and of LCEMs in particular, have the potential and capacity to address such conservation and management issues, while models that do not take into accounts traits and their evolution will remain fundamentally limited in these regards.

ACKNOWLEDGMENTS

We thank and acknowledge Thilo Gross, Hiroshi C. Ito, and Axel G. Rossberg for valuable contributions to an early version of this manuscript. Å. B. and U. D. gratefully acknowledge support from the European Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks), funded through the European Community's Sixth Framework Programme (Contract MRTN-CT-2004-005578). U. D. gratefully acknowledges additional support by the European Commission, the European Science Foundation, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund. N. L. acknowledges support by Université Pierre et Marie Curie and by the CNRS.

REFERENCES

Abrams, P.A. 1983. The theory of limiting similarity. *Annu. Rev. Ecol. Syst.*, **14**: 359-376.

Abrams, P.A. 2000. The evolution of prey-predator interactions: theory and evidence. *Annu. Rev. Ecol. Syst.*, **31**: 79-105.

Abrams, P.A. 2003. Effects of altered resource consumption rates by one consumer species on a competitor. *Ecol. Lett.*, **6**: 550-555.

Abrams, P.A. and Matsuda, H. 1997. Prey adaptation as a cause of predator-prey cycles. *Evolution*, **51**: 1742-1750.

Abrams, P.A., Matsuda, H. and Harada, Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.*, **7**: 465-487.

Armstrong, R.A. and McGehee, R. 1980. Competitive exclusion. *Am. Nat.*, **115**: 151-170.

van Baalen, M. and Sabelis, M.W. 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *Am. Nat.*, **142**: 646-670.

Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. 2004. Long-term trend in the maturation reaction norm of two cod stocks. *Ecol. Appl.*, **14**: 1257-1271.

Bastolla, U., Lässig, M., Manrubia, S.C. and Valleriani, A. 2005. Biodiversity in model ecosystems, I: coexistence conditions for competing species. *J. Theor. Biol.*, **235**: 521-30.

Beckerman, A.P., Petchey, O.L. and Warren, P.H. 2006. Foraging biology predicts food web complexity. *P. Natl. Acad. Sci. USA*, **103**: 13745-13749.

Bell, G., and Gonzalez A. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science*, **332**: 1327-1330.

Berlow, E.L., Neutel, A.M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. and Petchey, O. 2004. Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, **73**: 585-598.

Blossey, B. and Notzold, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *J. Ecol.*, **83**: 887-889.

Borrvall, C., Ebenmann, B. and Jonsson, T. 2000. Biodiversity lessens the risk of cascading extinctions in model food webs. *Ecol. Lett.*, **3**: 131-136.

Brännström Å. and Dieckmann U. 2005. Evolutionary dynamics of altruism and cheating in social amoebas. *Proc. R. Soc. Lond. B*, **272**: 1609-1616.

Brännström Å., Carlsson L., and Rossberg A.G. 2011a. Rigorous conditions for food-web intervality in high-dimensional trophic niche spaces. *J. Math. Biol.* **63**: 575-592.

Brännström Å., Gross T., Blasius B. and Dieckmann U. 2011b. Consequences of fluctuating group size for the evolution of cooperation. *J. Math. Biol.* **63**: 263-281.

Brännström, Å., Loeuille, N., Loreau, M. and Dieckmann, U. 2011c. Emergence and maintenance of biodiversity in an evolutionary food web model. *Theor. Ecol.*, **4**: 467-478.

Bronstein, J.L., Dieckmann, U. and Ferrière, R. 2004. Coevolutionary dynamics and the conservation of mutualisms. In *Evolutionary Conservation Biology* (R. Ferrière, U. Dieckmann and D. Couvet, eds.), pp. 305-326. Cambridge: Cambridge University Press.

Brown, J.H., 2004. Toward a metabolic theory of ecology. *Ecology*, **85**: 1771-1789.

Brown, J.S. and Vincent, T.L. 1992. Organization of predator-prey communities as an evolutionary game. *Evolution*, **46**: 1269-1283.

Caldarelli, G., Higgs, P.G. and McKane, A.J. 1998. Modelling coevolution in multispecies communities. *J. Theor. Biol.*, **193**: 345-358.

Carroll, S.P., Loye ,J.E., Dingle, H., Mathieson, M., Famula, T.R. and Zalucki M.P. 2005. And the beak shall inherit – evolution in response to invasion. *Ecol. Lett.* **8**: 944-951.

Koskinen, M.T., Haugen, T.O. and Primmer, C.R. 2002. Contemporary fisherian life-history evolution in small salmonid populations. *Nature*, **419**: 826-830.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. and Gabriel, J.P. 2004. Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**: 835-839.

Christensen, K., Di Collobiano, S.A., Hall, M. and Jensen, H.J. 2002. Tangled nature: a model of evolutionary ecology. *J. Theor. Biol.*, **216**: 73-84.

Cohen, J.E., Briand, F. and Newman, C.M. 1990a. *Community Food Webs: Data and Theory*, Berlin: Springer.

Cohen, J.E., Jonsson, T. and Carpenter, S.R. 2003. Ecological community description using the food web, species abundance and body size. *P. Natl. Acad. Sci. USA*, **100**: 1781-1786.

Cohen, J.E., Luczak, T., Neman, C.M. and Zhou, Z.M. 1990b. Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka-Volterra cascade model. *Proc. R. Soc. Lond. B*, **240**: 607-627.

Cohen, J.E., and Newman, C.M. 1985. A stochastic theory of community food webs: I. models and aggregated data. *Proc. R. Soc. Lond. B,* **224**: 421-448.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. and MacIsaac, H.J. 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.*, **7**: 721-733.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. and Festa-Bianchet, M. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**: 655-658.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.*, **8**: 1175–1182. de Mazancourt, C. and Dieckmann, U., 2004. Trade-off geometries and frequency-dependent selection. *Am. Nat.*, **164**: 765-778.

de Mazancourt, C., Loreau, M. and Dieckmann, U. 2001. Can the evolution of plant defense lead to plant-herbivore mutualism? *Am. Nat.* **159**: 109-123.

Dercole, F. 2003. Remarks on branching-extinction evolutionary cycles. *J. Math. Biol*., **47**: 569-580.

Dercole, F., Ferrière, R., Gragnani, A. and Rinaldi, S. 2006. Coevolution of slow-fast populations: evolutionary sliding, evolutionary pseudo-equilibria and complex Red Queen dynamics. *Proc. R. Soc. Lond. B* **273**: 983-990.

Dickie, I.A., Fukami, T., Wilkie, J.P., Allen, R.B. and Buchanan, P.K. 2011. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecol. Lett*., **15**: 133-141.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354-357.

Dieckmann, U., Heino, M. and Parvinen, K. 2006. The adaptive dynamics of function-valued traits. *J. Theor. Biol*., **241**: 370-389.

Dieckmann, U., Marrow, P. and Law, R. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the Red Queen. *J. Theor. Biol*., **176**: 91-102.

Doebeli, M. and Dieckmann, U. 2003. Speciation along environmental gradients. *Nature*, **421**: 259-264.

Doebeli, M., Hauert, C. and Killingback, T. 2004. The evolutionary origin of cooperators and defectors. *Science,* **306**: 859-862.

Doebeli, M. and Koella, J.C. 1995. Evolution of simple population dynamics. *Proc. R. Soc. Lond. B*, **260**: 119-125.

Drake, J.A. 1990a. Communities as assembled structures: do rules govern pattern? *Trends Ecol. Evol.*, **5**: 159-164.

Drake, J.A. 1990b. The mechanics of community assembly and succession. *J. Theor. Biol*., **147**: 213-233.

Drossel, B., Higgs, P.G. and McKane, A.J. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. *J. Theor. Biol.*, **208**: 91-107.

Drossel, B. and McKane, A.J. 1999. Ecological character displacement in quantitative genetic models. *J. Theor. Biol.*, **196**: 363-376.

Drossel, B., McKane, A.J. and Quince, C. 2004. The impact of nonlinear functional response on the long-term evolution of food web structure, *J. Theor. Biol.*, **229**: 539-548.

Dunne, J.A. 2006. The network structure of food webs. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs,* (M. Pascual and J.A. Dunne, eds), pp. 27-86, Oxford: Oxford University Press.

Dunne, J.A., Williams, R.J. and Martinez, N.D. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, **5**: 558-567.

Egas, M., Dieckmann, U. and Sabelis, M.W. 2004. Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. *Am. Nat*., **163**: 518-531.

Elton, C.S. 1958. *Ecology of Invasions by Animals and Plants,* London: Chapman and Hall.

Emerson, B.C. and Kolm, N. 2005. Species diversity can drive speciation. *Nature,* **434**: 1015-1017.

Emmerson, M. and Raffaelli, D. 2004. Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.*, **73**: 399-409.

Ferrière, R., Bronstein, J.L., Rinaldi, S., Law, R. and Gauduchon, M. 2002. Cheating and the evolutionary stability of mutualisms. *Proc. R. Soc. Lond. B*, **269**: 773-780.

Ferrière, R. and Gatto, M. 1993. Chaotic population dynamics can result from natural selection. *Proc. R. Soc. Lond. B*, **251**: 33-38.

Ferrière, R., Gauduchon, M. and Bronstein, J.L. 2007. Evolution and persistence of obligate mutualists and exploiters: competition for partners and evolutionary immunization. *Ecol. Lett.*, **10**: 115-126.

Fontaine, C., Guimaraes Jr, P.R., Kefi, S., Loeuille, N., Memmott, J., van der Putten, W.H., van Veen, F.J.F. and Thebault, E. 2011. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.*, **14**: 1170-1181.

Fussmann, G.F., Loreau, M. and Abrams, P.A. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.*, **21**: 465-477.

Gaba, S. and Ebert, D. 2009. Time-shift experiments as a tool to study antagonistic coevolution, *Trends Ecol. Evol.*, **4**: 226-232

Gause, G.F. 1932. Experimental studies on the struggle for existence. *J. Exp. Biol.*, **9**: 389-402.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35-57.

Goldwasser, L, and Roughgarden J. 1993. Construction and analysis of a large Carribbean food web. *Ecology* **74**: 1216-1233.

Gomulkiewicz, R., and Holt R.D. When does evolution by natural selection prevent extinction? *Evolution* **49**: 201-207.

Gyllenberg, M., Parvinen, K. and Dieckmann, U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.*, **45**: 79-105.

Hairston, N.G.J., Ellner, S.P., Geber, M.A., Yoshida, T. and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, **8**: 1114-1127.

Hall, S.J. and Raffaelli, D. 1993. Food webs: theory and reality. *Adv. Ecol. Res.*, **24**: 187-239.

Hartvig, M., Andersen, K.H. and Beyer, J.E. 2011. Food web framework for size-structured populations. *J. Theor. Biol.*, **272**: 113-122.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. and Lawton, J.H. 1999. Plant diversity and productivity experiments in European grasslands. *Science*, **286**: 1123-1127.

Hochberg, M.E. and Holt, R.D. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. *Evol. Ecol.*, **6**: 633-661.

Ingram, T., Harmon, L.J. and Shurin, J.B. 2009. Niche evolution, trophic structure, and species turnover in model food webs. *Am. Nat.*, **174**: 56-67.

Ito, H.C. & Dieckmann, U. 2007. A new mechanism for recurrent adaptive radiations. *Am. Nat.* **170**: E96-E111.

Ito, H.C. and Ikegami, T. 2006. Food web formation with recursive evolutionary branching. *J. Theor. Biol.*, **238**: 1-10.

Ito, H.C., Shimada, M. and Ikegami, T. 2009. Coevolutionary dynamics of adaptive radiation for food-web development. *Pop. Ecol.*, **51**: 65-81.

Iwasa, Y., Cohen, D. and Leon J.A. 1985. Tree height and crown shape, as results of competitive games. *J. Theor. Biol.*, **112**: 279-298.

Johansson, J. and Ripa, J. 2006. Will sympatric speciation fail due to stochastic competitive exclusion? *Am. Nat.*, **168**: 572-578.

Jordano, P., Bascompte, J. and Olesen, J.M. 2003. Invariant properties in coevolutionary of plant-animal interactions. *Ecol. Lett.*, **6**: 69-81.

Joshi, J. and Vrieling, K. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecol. Lett.*, **8**: 704-714.

Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science*, **299**: 1388-1391.

Krause, A.E., Frank, K.A., Mason, D.M., Ulanowicz, R.E., Taylor, W.W. 2003. Compartments revealed in food-web structure. *Nature*, **426**: 282-285.

Krivan, V. and Diehl, S. 2005. Adaptive omnivory and species coexistence in tri-trophic food webs. *Theor. Pop. Biol.*, **67**: 85-99.

Lampo, M. and De Leo, G.A. 1998. The invasion ecology of the toad *Bufo marinus*: from South America to Australia, *Ecol. App.*, **8**: 388-396.

Laugen, A.T., Engelhard, G.H., Whitlock, R., Arlinghaus, R., Dankel, D.J., Dunlop, E.S., Eikeset, A.M., Enberg, K., Jørgensen, C., Matsumura, S., Nusslé, S., Urbach, D., Baulier, L., Boukal, D.S., Ernande, B., Johnston, F.D., Mollet, F., Pardoe, H., Therkildsen, N.O., Uusi-Heikkilä, S., Vainikka, A., Heino, M., Rijnsdorp, A.D. and Dieckmann, U. 2012. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish Fish.*, in press.

Law, R. 1979. Optimal life histories under age-specific predation. *Am. Nat.,* **114**: 399-417.

Law, R. and Blackford, J.C. 1992. Self-assembling food webs: A global viewpoint of coexistence of species in Lotka-Volterra communities. *Ecology,* **73**: 567-578.

Law, R. and Morton, R.D. 1996. Permanence and the assembly of ecological communities. *Ecology,* **77**: 762-775.

Lever, C. 2001. *The Cane Toad: The History and Ecology of A Successful Colonist.* Yorkshire: Westbury Publishing.

Liu, H. and Stiling, P. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Inv.,* **8**: 1535-1545.

Loeuille, N. 2010a. Consequences of adaptive foraging in diverse communities. *Funct. Ecol.*, **24**: 18-27.

Loeuille, N. 2010b. Influence of evolution on the stability of ecological communities. *Ecol. Lett.*, **13**: 1536-1545.

Loeuille, N. and Loreau, M. 2005. Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci. USA,* **102**: 5761-5766.

Loeuille, N. and Loreau, M. 2006. Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecol. Lett.*, **9**: 171-178.

Loeuille, N. and Loreau, M. 2009. Emergence of complex food web structure in community evolution models. In *Community Ecology,* (Verhoef, H.A. & Morin, P.J., eds). pp. 163-178. Oxford: Oxford University Press.

Loeuille, N., Loreau, M. and Ferrière, R. 2002. Consequences of plant-herbivore coevolution on the dynamics and functioning of ecosystems. *J. Theor. Biol.*, **217**: 369-381.

Lundberg, P., Ranta, E. and Kaitala, V. 2000. Species loss leads to community closure. *Ecol. Lett.*, **3**: 465-468.

MacArthur, R.H. 1955. Fluctuation of animal populations and a measure of community stability. *Ecology,* **36**: 533-536.

Martinez, N.D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.,* **61**: 367-392.

May, R.M. 1973. *Stability and Complexity in Model Ecosystems*, Princeton, N.J.: Princeton University Press.

McCann, K. 2000. The diversity-stability debate. *Nature,* **405**: 228-233.

McCann, K. and Hastings, A. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B,* **264**: 1249-1254.

McCann, K., Hastings, A. and Huxel, G.R. 1998. Weak trophic interactions and the balance of nature. *Nature,* **395**: 794-798.

McGill, B.J. 2010. Towards a unification of unified theories of biodiversity. *Ecol. Lett.*, **13**: 627-642.

McGill, B.J. and Brown, J.S. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Annu. Rev. Ecol. Evol. Syst.,* **38**: 403-435.

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define "fitness" for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198-202.

Montoya, J.M., Pimm, S.L. and Solé, R.V. 2006. Ecological networks and their fragility. *Nature,* **442**: 259-264

Morris, R.J., Lewis, O.T. and Godfray, H.C.J. 2004. Experimental evidence for apparent competition in a tropical forest food web. *Nature,* **428**: 310-313.

Morton, R.D. and Law, R. 1997. Regional species pool and the assembly of local ecological communities. *J. Theor. Biol.*, **187**: 321-331.

Müller-Schärer, H., Schaffner, U. and Steinger T. 2004. Evolution in invasive plants: implications for biological control. *Trends Ecol. Evol.*, **19**: 417-422.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature,* **368**: 734-737.

Nilsson, J. and Ripa, J. 2010. The origin of polymorphic crypsis in a heterogeneous environment. *Evolution,* **64**: 1386-1394.

O'Brien, E.E. and Brown, J.S. 2008. Games roots play: effects of soil volume and nutrients. *J. Ecol.*, **96**: 438-446.

Odum, E. 1953. *Fundamentals of Ecology,* Philadelphia, PA: Saunders.

Oksanen, L., Fretwell, S.D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, **118**: 240-261.

Oksanen, L. and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.*, **155**: 703-723.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, **428**: 932-935.

Paine, R.T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology,* **69**: 1648-1654.

Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature,* **355**: 73-75.

Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheor*., **53**: 241-264.

Parvinen, K., Dieckmann, U. and Heino, M. 2006. Function-valued adaptive dynamics and the calculus of variations. *J. Math. Biol*. **52**: 1-26.

Petchey, O.L., Beckerman, A.P., Riede, J.O. and Warren, P.H. 2008. Size, foraging and food web structure. *Proc. Natl. Acad. Sci. USA,* **105**: 4191-4196.

Peters, R.H. 1983. *The Ecological Implications of Body Size*, Cambridge, U.K.: Cambridge University Press.

Peterson, A.T, Ortega-Huerta, M.A, Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier R.H., and Stockwell D.R.B. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature,* **416**: 626-629.

Phillips, B.L., Brown, G.P., Webb, J.K. and Shine, R. 2006. Invasion and the evolution of speed in toads. *Nature,* **439**: 803-803.

Pimentel, D. 1961. Animal population regulation by the genetic feed-back mechanism. *Am. Nat.,* **95**: 65-79.

Pimm, S.L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities,* Chicago, IL: University of Chicago Press.

Pimm, S.L. and Lawton, J.H. 1977. Number of trophic levels in ecological communities. *Nature*, **268**: 329-330.

Pimm, S.L. and Lawton, J.H. 1978. On feeding on more than one trophic level. *Nature*, **275**: 542-544.

Polis, G.A. 1991. Complex desert food webs: an empirical critique of food web theory. *Am. Nat.*, **138**: 123-155.

Poos, J.J., Brännström, Å. and Dieckmann, U. 2011. Harvest-induced maturation evolution under different life-history trade-offs and harvesting regimes. *J. Theor. Biol.* **279**: 102-112.

Post, W.M. and Pimm, S.L. 1983. Community assembly and food web stability. *Math. Biosci*., **64**: 169-192.

Proulx, S.R., Promislow, D.E.L. and Phillips, P.C. 2005. Network thinking in ecology and evolution. *Trends Ecol. Evol.*, **20**: 345-353.

Quince, C., Higgs, P.G. and McKane, A.J. 2005. Topological structures and interaction strength in model food webs. *Ecol. Model.,* **187**: 389-412.

Rainey, P.B. and Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. *Nature*, **394**:69-73.

Reznick, D., Nunney, L. and Tessier, A. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol*., **15**: 421-425.

Ripa, J., Storlind, L., Lundberg, P. and Brown. J.S. 2009. Niche coevolution in consumer-resource communities. *Evol. Ecol. Res.,* **11**: 305-323.

Rosenzweig, M.L. 1978. Competitive speciation. *Biol. J. Linn. Soc*., **10**: 275-289.

Rosenzweig, M.L. 1971. The paradox of enrichment. *Science,* **171**: 385-387.

Rossberg, A.G., Brännström, Å. and Dieckmann, U. 2010. Food-web structure in low-and high-dimensional trophic niche spaces, *J. R. Soc. Interface,* **7**: 1735-1743.

Rossberg, A.G., Ishii, R., Amemiya, T. and Itoh, K. 2008. The top-down mechanism for body-mass-abundance scaling. *Ecology,* **89**: 567-580.

Rossberg, A.G., Matsuda, H., Amemiya, T. and Itoh, K. 2006. Food webs: experts consuming families of experts. *J. Theor. Biol.,* **241**: 552-563.

Roughgarden, J. 1972. Evolution of niche width. *Am. Nat.,* **106**: 683-718.

Rummel, J.D. and Roughgarden, J. 1983. Some differences between invasion-structured and coevolution-structured competitive communities: a preliminary theoretical analysis. *Oikos*, **41**: 477-486.

Sax, D.F., Gaines, S.D. and Brown, J.H. 2002. Species invasions exceed extinctions on island worldwide: a comparative study of plants and birds. *Am. Nat.* **160**: 766-783.

Saloniemi, I. 1993. A coevolutionary predator-prey model with quantitative characters. *Am. Nat*., **141**: 880-896.

Schreiber, S.J. and Vejdani, M. 2006. Handling time promotes the coevolution of aggregation in predator-prey systems. *Proc. R. Soc. Lond. B,* **273**: 185-191.

Seldal, T., 1994. Grazing-induced proteinase-inhibitors – a possible cause for lemming population-cycles. *Oikos,* **70**: 3-11.

Slatkin, M. 1980. Ecological character displacement. *Ecology*, **61**: 163-177.

Stegen, J.C., Enquist, B.J. and Ferrière, R. 2009. Advancing the metabolic theory of biodiversity. *Ecol. Lett.,* **12**: 1001-1015

Steiner, C.F., Stockwell, R.D., Kalaimani, V. and Aqel, Z. 2011. Dispersal promotes compensatory dynamics and stability in forced metacommunities. *Am. Nat.*, **178**: 159-170.

Stockwell, C.A., Hendry, A.P., and Kinnison, M.T. 2003. Contemporary evolution meets conservation biology.

Trends Ecol. Evol., **18**: 94-101.

Stouffer, D.B., Camacho, J., Guimera, R., Ng, C.A. and Nunes Amaral, L.A. 2005. Quantitative patterns in the structure of model and empirical food webs. *Ecology*, **86**: 1301-1311.

Stouffer, D.B., Camacho, J. and Nunes Amaral, L.A. 2006. A robust measure of food web intervality. *Proc. Natl. Acad. Sci. USA*, **103**: 19015-19020.

Sugihara, G., Bersier, L.F. and Schoenly, K. 1997. Effects of taxonomic and trophic aggregation on food web properties. *Oecologia*, **112**: 272-284.

Taper, M.L. and Case, T.J. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology*, **66**: 355-371.

Taylor, P.J. 1988. The construction of turnover of complex community models having generalised Lotka-Volterra dynamics. *J. Theor. Biol.*, **135**: 569-588.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, **329**: 853-856.

Thomas, C.D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol. Evol.*, **26**: 216-221.

Tilman, D., 1982. *Resource Competition and Community Structure*, Princeton, NJ: Princeton University Press.

Troost, T.A., Kooi, B.W. and Dieckmann, U. 2008. Joint evolution of predator body size and prey-size preference. *Evol. Ecol.*, **22**: 771-799.

Troost, T.A., Kooi, B.W. and Kooijman, S.A.L.M. 2005. Ecological specialization of mixotrophic plankton in a mixed water column. *Am. Nat.*, **166**: E45-E61.

Urban, M.C. and Skelly D.K. 2006. Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology*, **87**: 1616-1626.

Van Valen, L. 1973. A new evolutionary law. *Evol. Theory*, **1**: 1-30.

Warren, P.H. and Lawton, J.H. 1987. Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, **74**: 231-235.

Waxman, D. and Gavrilets, S. 2005. 20 questions on adaptive dynamics. *J. Evol. Biol.*, **18**: 1139-1154.

Wiens, J.J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, **58**: 193-197.

Williams, R.J. and Martinez, N.D. 2000. Simple rules yield complex food webs. *Nature*, **404**: 180-183.

Williams, R.J. and Martinez, N.D. 2006. Diversity, complexity, and persistence in large model ecosystems. In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, (M. Pascual and J.A. Dunne, eds), pp. 163-185. Oxford: Oxford University Press.

Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S. and Huntley, B. 2009. Assisted colonization in a changing climate: a test-study using two UK butterflies. *Conserv. Lett.*, **2**: 46-52.

Winemiller, K.O. and Polis, G.A. 1996. Food webs: what can they tell us about the world? In *Food Webs: Integration of Patterns and Dynamics*, (G.A. Polis and K.O. Winemiller, eds), pp. 1-22. New York: Chapman and Hall.

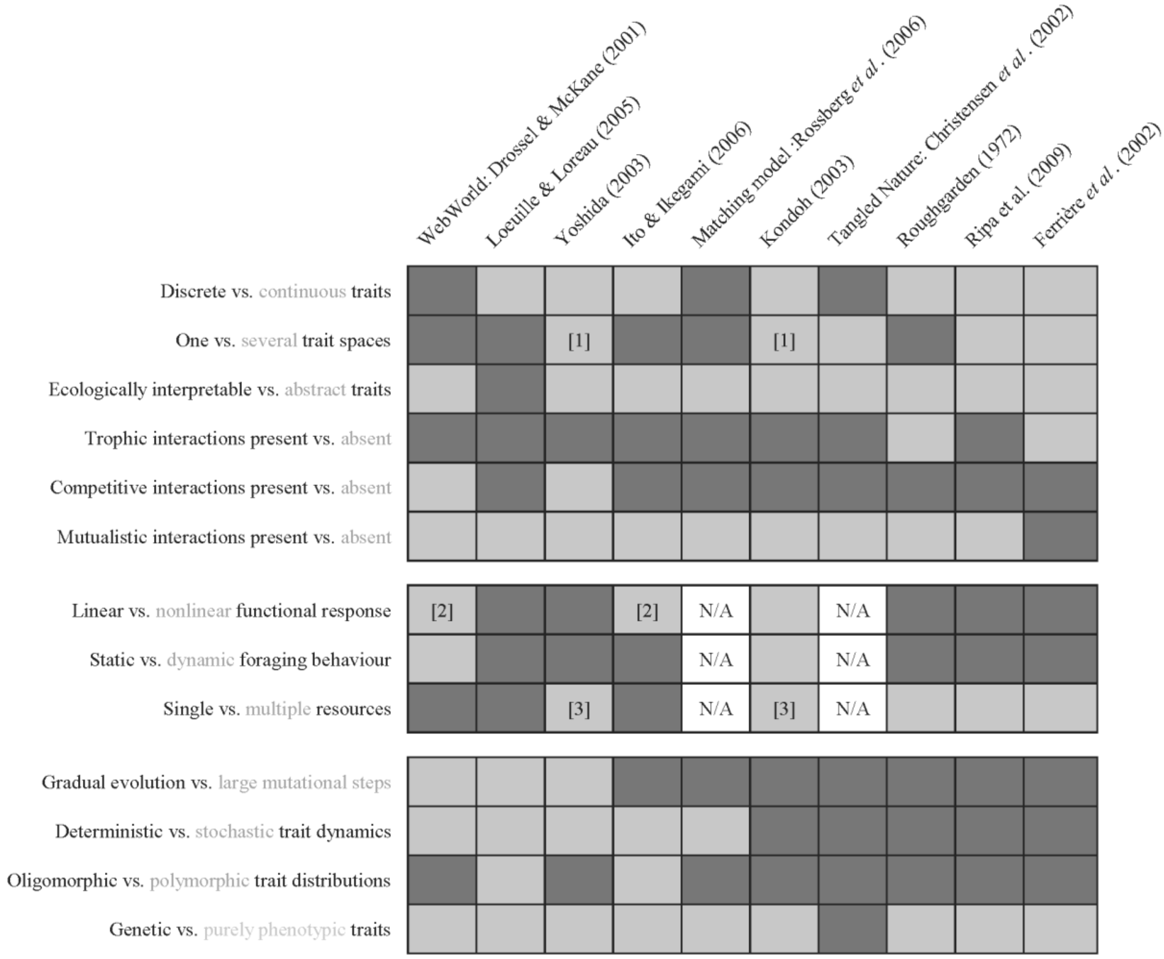
Yoder, J.B. and Nuismer, S.L. 2010. When does coevolution promote diversification? *Am. Nat.*, **176**: 802-817.

Yodzis, P. 2000. Diffuse effects in food webs. *Ecology*, **81**: 261-266.

Yoshida, K. 2006. Ecosystem models on the evolutionary time scale: a review and perspective. *Paleontol. Res.* **10**: 375-385.

Yoshida, K. 2003. Evolutionary dynamics of species diversity in an interaction web system. *Ecol. Modell.* **163**: 131-143

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. and Hairston, N.G. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, **424**: 303-306.



	WebWorld: Drossel & McKane (2001)	Loeuille & Loreau (2005)	Yoshida (2003)	Ito & Ikegami (2006)	Matching model :Rossberg *et al* . (2006)	Kondoh (2003)	Tangled Nature: Christensen *et al* . (2002)	Roughgarden (1972)	Ripa et al. (2009)	Ferrière *et al* . (2002)
Discrete vs. continuous traits	■	□	□	□	■	□	■	□	□	□
One vs. several trait spaces	■	■	□ [1]	■	■	□ [1]	□	■	□	□
Ecologically interpretable vs. abstract traits	□	■	□	□	□	□	□	□	□	□
Trophic interactions present vs. absent	■	■	■	■	■	■	■	□	■	□
Competitive interactions present vs. absent	□	■	□	■	■	■	■	■	■	■
Mutualistic interactions present vs. absent	□	□	□	□	□	□	□	□	□	■
Linear vs. nonlinear functional response	□ [2]	■	■	□ [2]	N/A	□	N/A	■	■	■
Static vs. dynamic foraging behaviour	□	■	■	■	N/A	□	N/A	■	■	■
Single vs. multiple resources	■	■	□ [3]	■	N/A	□ [3]	N/A	□	□	□
Gradual evolution vs. large mutational steps	□	□	□	■	■	■	■	■	■	■
Deterministic vs. stochastic trait dynamics	□	□	□	□	□	■	■	■	■	■
Oligomorphic vs. polymorphic trait distributions	■	□	■	□	■	■	■	■	■	■
Genetic vs. purely phenotypic traits	□	□	□	□	□	□	■	□	□	□

[1] Each species has a unique associated trait
[2] Linear functional responses are studied for comparison
[3] Resource species undergo evolution

Table 1: Overview of characteristic features of selected large community-evolution models. Features are presented in three groups, encompassing traits and interactions (top), demographic dynamics (middle), and evolutionary dynamics (bottom).

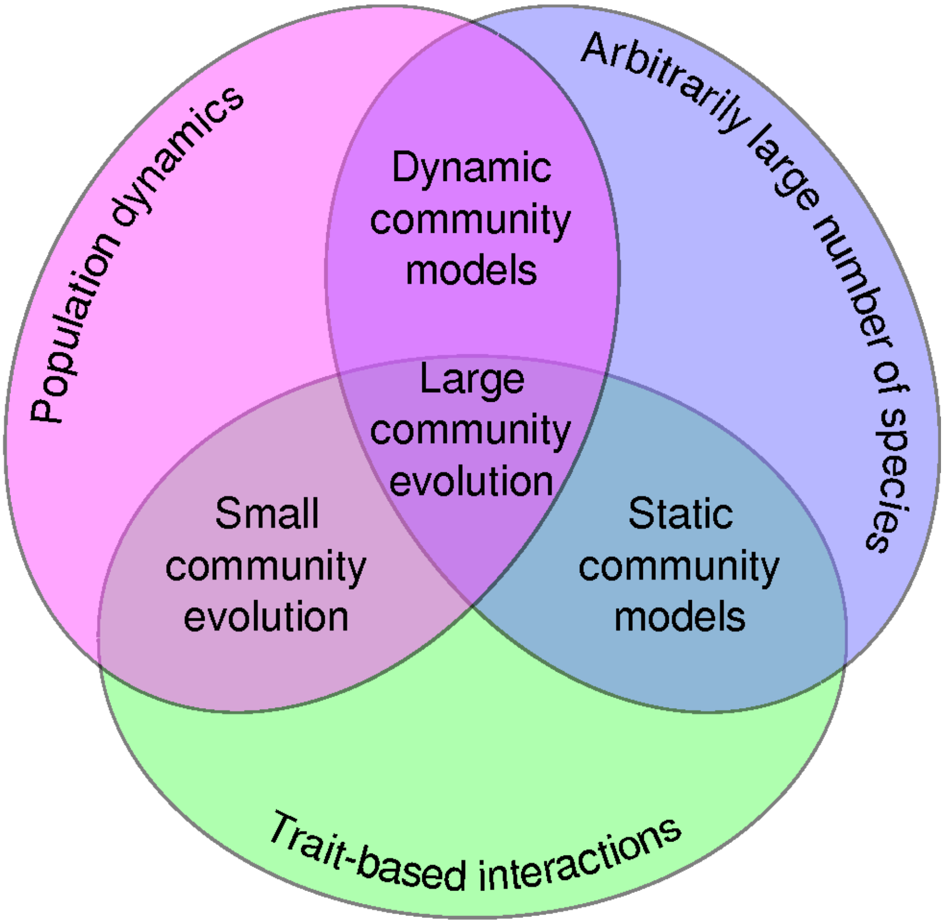


Figure 1: Schematic illustrations of the community models considered in this review. We start out by surveying static and dynamic ecological models, which do not possess an evolutionary component. After this, we move on to evolution in small community models. Finally, we review large community-evolution models (LCEMs), which synthesize elements of all aforementioned model types.

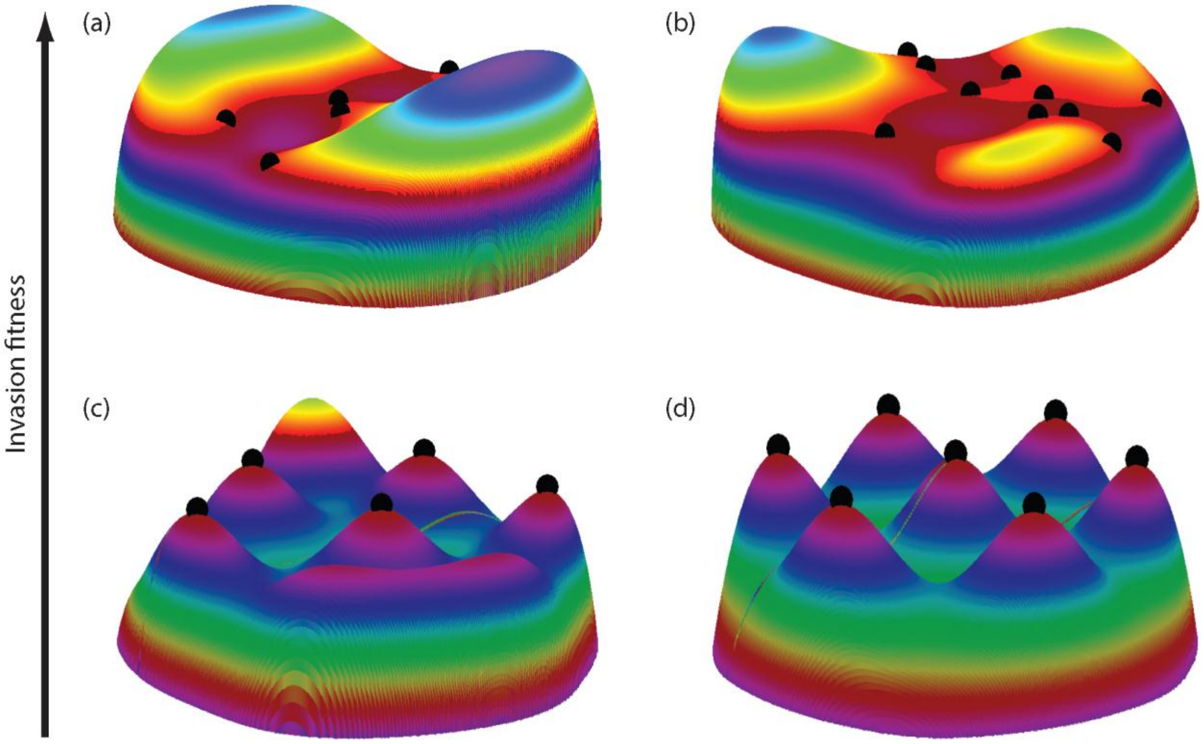


Figure 2: Invasion-fitness landscapes of assembled and evolved communities. The filled circles indicate the trait combinations of resident species in four ecological communities (a-d) in a two-dimensional shared trait space spanning the horizontal plane. The height of the colored surface at any given point in the trait space thus corresponds to the initial growth rate that a rare species with those trait values would have on average, were it to invade the system. Areas with positive invasion fitness (bright colors) are open to invasions, whereas areas with negative invasion fitness (dimmed colors) are closed to invasions. Populations of the resident species are assumed to be at ecological equilibrium, and accordingly have an invasion fitness of zero. The community in (a) is the result of just a few invasions from an external species pool. The community's state after a larger number of invasion attempts is illustrated in (b). In both (a) and (b), large parts of the trait space can still be invaded. The community in (c) shows the result of gradual evolution, e.g., from the original five species in (a). Through gradual evolution, species climb the fitness landscape, with this uphill movement coming to a halt when each species becomes situated on a local peak of the fitness landscape. As shown in (c), the resulting landscape may still contain unoccupied peaks. A species from an external species pool providing suitable trait combinations may invade the vicinity of such unoccupied peaks, through subsequent gradual evolution reach the peak, and thereby reduce the peak's fitness to zero. Such an outcome is illustrated in (d), which shows a community that is the result of repeated invasions and gradual evolution, and which in this manner has become closed not only to further invasions, but also to further adaptive evolution. The model underlying all four panels is a simple Lotka-Volterra competition model with trait-dependent carrying capacity and competition kernel: the former is given by the positive part of an upside-down bivariate unit paraboloid, $k(x,y) = \max(0,1-(x^2+y^2))$, and the latter by a bivariate cubic exponential function, $a(dx,dy) = \exp(-\mathrm{sqrt}(dx^2+dy^2)/c)^3)$, where c is chosen so that the standard deviation of a is 0.3. The invasion fitness at the trait combination (x,y) is then given by $f(x,y) = 1-n_{\mathrm{eff}}(x,y)/k(x,y)$, where $n_{\mathrm{eff}}(x,y)$ is the sum of $a(x'-x,y'-y)n_{\mathrm{eq}}(x',y')$ over all resident species (x',y') with equilibrium densities $n_{\mathrm{eq}}(x',y')$, where the latter are set so that $f(x',y') = 0$ for all resident species.