

REVIEW AND
SYNTHESIS

Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity

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Abstract

Biological diversity depends on the interplay between evolutionary diversification and ecological mechanisms allowing species to coexist. Current research increasingly integrates ecology and evolution over a range of timescales, but our common conceptual framework for understanding species coexistence requires better incorporation of evolutionary processes. Here, we focus on the idea of *evolutionarily stable communities* (ESCs), which are theoretical endpoints of evolution in a community context. We use ESCs as a unifying framework to highlight some important but under-appreciated theoretical results, and we review empirical research relevant to these theoretical predictions. We explain how, in addition to generating diversity, evolution can also limit diversity by reducing the effectiveness of coexistence mechanisms. The coevolving traits of competing species may either diverge or converge, depending on whether the number of species in the community is low (undersaturated) or high (oversaturated) relative to the ESC. Competition in oversaturated communities can lead to extinction or neutrally coexisting, ecologically equivalent species. It is critical to consider trait evolution when investigating fundamental ecological questions like the strength of different coexistence mechanisms, the feasibility of ecologically equivalent species, and the interpretation of different patterns of trait dispersion.

Keywords

Adaptive dynamics, adaptive landscape, character displacement, coexistence, eco-evolutionary dynamics, ecological equivalence, ESS.

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INTRODUCTION

To understand the origin and maintenance of biological diversity, it is necessary to dissect the integrated effects of evolutionary and ecological processes. Genetic diversity is ultimately generated by mutation, and the fate of new mutations is determined by a combination of drift and selection. Selection takes many forms and is often driven by ecological interactions such as competition, predation and mutualism. These interactions therefore influence how species evolve and can thereby enhance or diminish the diversity (species richness) of communities. Meanwhile, ecological interactions themselves are affected by the (co-)evolutionary change of species. Although these general principles have been long understood (Darwin 1859; Brown & Wilson 1956; Hutchinson 1965), disentangling the interplay of ecological and

evolutionary processes in natural communities remains a difficult challenge.

A greater appreciation of the possibility of rapid evolution (Reznick *et al.* 1990; Hairston *et al.* 1999; Grant & Grant 2002) has invigorated the study of eco-evolutionary dynamics, or the interplay of ecological and evolutionary processes on similar timescales (Fussmann *et al.* 2007; Lankau 2011; Schoener 2011). The reciprocal effects of environmental conditions on trait evolution, and of trait change on environmental conditions, can lead to eco-evolutionary feedbacks that are essential for understanding the outcome of species interactions (Yoshida *et al.* 2003; Bull *et al.* 2006; Post & Palkovacs 2009, Hanski 2011). Ecological theory has increasingly included evolutionary processes by assuming that the parameters representing species' traits are not constant over time, but rather evolve in response to selection caused by abiotic and biotic

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conditions (Abrams 1986; Brown & Vincent 1992; Geritz *et al.* 1998). Such analyses may assume that evolution is either slow relative to ecological dynamics, or contemporaneous with ecological dynamics (Abrams 2001). Importantly, these analyses often find that incorporating evolutionary change can result in different outcomes from those expected under ecological models with fixed traits (Abrams 1990; Fox & Vas-seur 2008; terHorst *et al.* 2010; Schreiber *et al.* 2011; Kremer & Klausmeier 2013; Barabás & D'Andrea 2016). Similarly, evolutionary theory has begun to incorporate ecology by relaxing the assumption of fixed population size (Bell 2013). Evolution then depends on absolute rather than relative fitness and can impact population dynamics. This perspective has led to new insights concerning the evolution of the fundamental niche (e.g. Holt & Gaines 1992; Bell 2017).

In this article, we aim to synthesise developments in eco-evolutionary theory, focusing on a set of related insights that illuminate key questions in community ecology and evolutionary biology. Specifically, we explore the idea of an *evolutionarily stable community* (ESC), which represents the theoretical endpoint of evolution in a community context. Analysing ESCs helps us understand evolutionary dynamics even if real communities may rarely reach this endpoint, just as analysing ecological equilibria helps us understand population dynamics even though real populations may not be at equilibrium. We show that the ESC framework deepens our understanding of mechanisms of coexistence, saturation of community diversity, and coevolution of competitors' traits. After defining the ESC concept, we show how it can be used, revealing that evolution may reduce the potential of coexistence mechanisms to promote species diversity. We then synthesise a variety of prior work to ask whether commonly studied coexistence mechanisms remain robust under trait evolution. Next, we focus on the eco-evolutionary dynamics leading to ESCs and show that competitors can either diverge or converge in their traits, depending on whether communities are undersaturated or oversaturated, respectively, relative to the ESC. Finally, to better connect these insights to natural systems, we review relevant empirical work from a number of fields and suggest research avenues related to species introductions, secondary contact, and adaptive radiation.

Our review complements and updates several prior reviews on the topic of competitive coexistence and evolution. Abrams (1990) critiqued the idea that competition should cause resource utilisation traits to be evenly spaced or overdispersed and noted that evolution of coexisting competitors may lead to trait convergence. Similarly, Mayfield & Levine (2010) argued that competition may cause coexisting competitors to have traits (and phylogenetic relatedness) more similar than expected based on the regional species pool, if those traits determine overall competitive ability in a particular environment. Lankau (2011) reviewed different mechanisms by which rapid evolution can prevent competitive exclusion. Our review builds on previous work by connecting short-term eco-evolutionary dynamics to the long-term stability of coexistence, by reviewing and contrasting the ecological and evolutionary stability of different kinds of coexistence mechanisms, by emphasising conditions under which evolution can diminish

diversity, and by suggesting ways to test theoretical predictions.

WHAT ARE EVOLUTIONARILY STABLE COMMUNITIES (ESCS)?

To understand the effects of evolution on community structure, it is useful to start by considering the potential endpoint of evolution (Maynard Smith & Price 1973; Vincent & Brown 1988), before looking at the dynamics that may lead to this point. This is analogous to typical analyses of ecological models, where the long-term pattern of population abundance(s) is characterised (stable equilibrium, limit cycles, alternate stable states, etc.). In most eco-evolutionary models, if mutation and speciation or immigration produce sufficient trait variation and species richness, a community will eventually reach a final state such that new populations (with unique traits) cannot invade. This is the 'end' result of eco-evolutionary dynamics in a community context, and we refer to it as an *evolutionarily stable community* (ESC). In theoretical terms, an ESC is a set of species whose population and trait dynamics are at an attractor that is globally uninvadable (Kremer & Klausmeier 2017). Often, evolution reaches an 'endpoint' in an ESC only because fundamental tradeoffs or constraints affect the traits that determine fitness, which prevents directional trait change from proceeding indefinitely. In addition, models typically assume that environmental conditions have a stationary distribution, that is, there is no long-term directional change in environmental properties (environmental change is discussed in section Other features of ESCs). Finally, we assume that ESCs are convergence stable (Geritz *et al.* 1998), which means the community is stable to small perturbations of species' trait values (evolutionary dynamics leading to ESCs are discussed in section Undersaturated communities experience diversification/invasion until the ESC is reached).

A common and instructive approach for analysing ESCs is to assume that evolution is slow relative to ecological dynamics (Geritz *et al.* 1998). Assuming asexuality, ESCs can then be identified by considering whether new phenotypes can invade an existing set, and solving for the set of phenotypes that is uninvadable. An example invasion analysis is presented in Fig. 1, and the theory of invasion analysis is discussed further in Box 1. Allowing sexual reproduction and/or intraspecific trait variation (quantitative genetics) can, in some cases, alter the diversity and structure of an ESC, which we discuss in section Intraspecific trait variation can undermine species coexistence.

Evolution on 'rapid' ecological timescales can also be considered when analysing ESCs, for example, by modelling trait dynamics of each population with a quantitative genetic approximation (Abrams 2001). Under these conditions the eco-evolutionary attractor may include species whose trait values fluctuate in perpetuity, due to environmental fluctuations (Kremer & Klausmeier 2013) or endogenous population cycles (Dieckmann *et al.* 1995). The concept of an uninvadable ESC is still useful under rapid evolution, because with sufficient time and speciation/immigration the community will often converge on an uninvadable set of populations

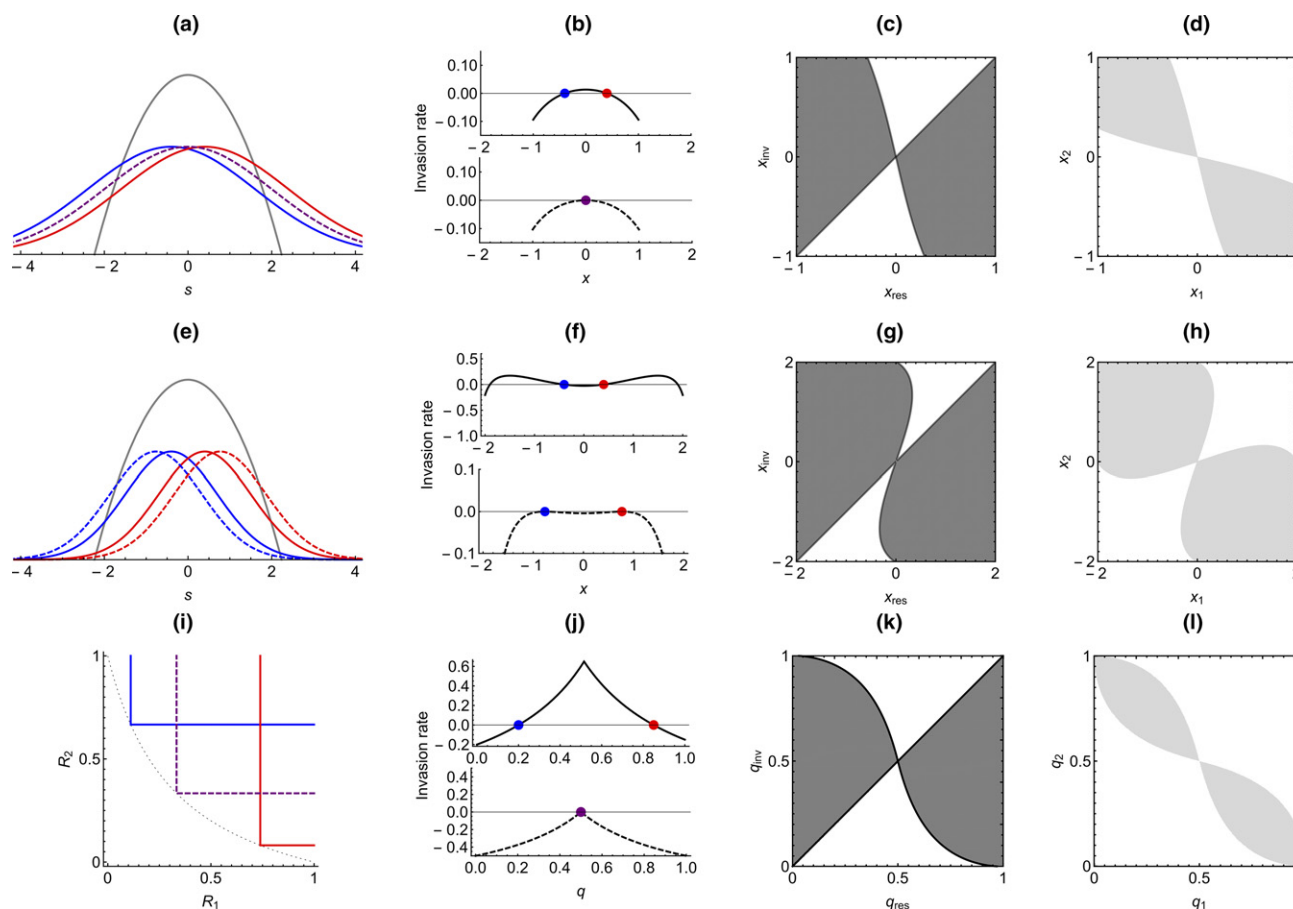


Figure 1 Evolutionary stability of coexistence. (a) Competition kernels for three species (blue, red, purple) and carrying capacity curve (black) as a function of resource axis s . The solid curves (blue and red) represent example species that coexist ecologically, while the dashed curve (purple) is the ESC. (b) Invasion rate as a function of trait x when the blue and red species are resident (top panel) or when the purple species is resident (bottom). (c) Pairwise invasibility plot for invader trait x_{inv} vs. resident trait x_{res} (positive invasion rates in grey). (d) Mutual invasibility plot for two species with traits x_1 and x_2 (mutual invasibility in grey). (e–h) are analogous to (a–d), but with narrower competition kernels that lead to a two-species ESC. (i–l) are analogous to (a–d), but illustrate a model where species compete for two essential resources R_1 and R_2 . Relative competitive ability for R_1 is determined by trait q , which sets uptake and demand for each resource (Appendix S1). The colored lines in (l) show the zero-net-growth isoclines for species constrained to the dotted black tradeoff curve. Further explanation of the plot is given in Boxes 2 and 3, and the equations in Appendix S1.

whose abundances and traits are at dynamic attractors (such as periodic limit cycles). However, the diversity and structure of the ESC may depend on the rate of evolution, which we discuss in section Intraspecific trait variation can undermine species coexistence. By incorporating dynamic eco-evolutionary attractors, ‘Red Queen’ evolutionary dynamics can be considered in an ESC framework, for situations where Red Queen dynamics are defined as endless evolution within populations driven by biotic interactions (Stenseth & Smith 1984; Dieckmann *et al.* 1995). It is also possible for evolutionary cycles to arise in which selection drives diversification, and then drives one competitor extinct, followed by diversification, and so on (Kisdi *et al.* 2002). Endless cycles of diversification and extinction are outside of what we define as ESCs.

In what follows we begin by considering the ESC that is predicted to emerge under particular ecological conditions, while remaining agnostic about the processes leading to the ESC. This leads to our first key observation: (1)

Evolutionarily stable diversity is often lower than the maximum ecologically stable diversity. We then consider how ESCs can be assembled, and note that: (2) Undersaturated communities (with fewer species than their ESC) experience diversification or invasion until the ESC is reached; and (3) Oversaturated communities (with more species than their ESC) experience extinctions and/or convergence towards neutrality of some species. Finally, we review some important properties of ESCs: (4) ESCs share features of standard ecological equilibria, including bifurcations and alternative stable states, but these aspects are little studied; and (5) Intraspecific trait variation can undermine species coexistence, particularly in variable environments. In each case, we summarise current theoretical results, describe corresponding empirical examples (where they exist) and outline outstanding theoretical and empirical questions. Finally, we consider the implications of ESCs for studying trait dispersion patterns and offer concluding thoughts on future directions.

Box 1 Invasion analysis and evolutionarily stable communities.

When considering coexistence, an important question is whether species can coexist in a way that is both ecologically stable and stable with respect to selection on the traits that determine competition. Ecologically stable coexistence is often defined by mutual invasibility (Armstrong & McGehee 1980). Invasibility is tested by imagining that one species is present in the system (the resident) at equilibrium, and evaluating whether another species (the invader) can increase from very low density under these conditions. If each species can invade when rare, then neither species will be able to drive the other extinct, and they will stably coexist.

Mutual invasibility depends on species' parameter values, which are determined by those species' traits (phenotypes). Ecological models typically assume that all individuals of a population have the same phenotype. One way to consider the outcome of trait evolution is to consider a continuum of trait values that could arise through mutation/immigration. In this context, phenotypes can be considered strategies in an evolutionary game (Maynard Smith & Price 1973; Vincent & Brown 1988). The outcome of trait evolution can be explored by evaluating invasibility across the set of trait values. For every possible resident phenotype, one can quantify the invasibility of every invader phenotype. One can then ask if there is a resident phenotype that cannot be invaded by any other phenotype. If this is the case, then a species with this trait value represents a (globally) evolutionarily stable strategy (ESS), and the evolutionarily stable coexistence of multiple populations with different trait values is impossible. If there is no single-species ESS, one can then ask whether there is a pair of strategies that can mutually invade each other, yet resist invasion by any third strategy. If so, then the coexistence of this pair of phenotypes is evolutionarily stable, and we refer to them as an evolutionarily stable community (ESC; for consistency we will also refer to single uninhabitable phenotypes as ESCs). This process of testing invasibility can be iterated until an ESC is found (cf. Fig. 2 in Kremer & Klausmeier 2017). In some cases no ESC exists, resulting in evolutionary cycles (e.g. Kisdi *et al.* 2002), or more than one ESC exists, leading to alternative stable states (e.g. Kremer & Klausmeier 2017).

Although invasion analysis using populations defined by a single trait value is a tractable and informative approach, ESCs can also be analysed using approaches that incorporate more realistic complexity, such as trait evolution on ecological time-scales or intraspecific trait variation. Sometimes these approaches make different predictions about ESCs, which we discuss in sections Undersaturated communities experience diversification/invasion until the ESC is reached, Other features of ESCs, and Intraspecific trait variation can undermine species coexistence. For example, 'rapid' evolution can be modelled using a quantitative genetic approximation in which the mean trait of a population is modeled explicitly and evolves in the direction that increases individual fitness, at a rate equal to the fitness gradient multiplied by the additive genetic variance (Abrams 2001). This kind of model can yield fluctuating abundance and trait dynamics, for example, due to seasonal forcing or predator-prey cycles. To analyse ESCs, invasion analysis can be performed by calculating the fitness of a range of possible invading populations, appropriately averaged over a single cycle (Kremer & Klausmeier 2013). This kind of model can also be used to simulate transient eco-evolutionary dynamics, as we do in Figs. 2, 3, and 5.

EVOLUTIONARILY STABLE DIVERSITY IS OFTEN LOWER THAN ECOLOGICALLY STABLE DIVERSITY

A common and important result of eco-evolutionary modelling is that the number of phenotypically distinct species that coexist at the projected evolutionary endpoint (ESC) is fewer than the number of species that could coexist, in principle, in the absence of evolution (Slatkin 1980; Taper & Chase 1985; Mougi & Nishimura 2006; Shores *et al.* 2008; van den Berg & van den Bosch 2009; Ravigné *et al.* 2009). This is not a statement about the trajectory evolution will take, but rather about how many species can stably coexist in a particular ecological context. For example, under the conditions shown in Fig. 1a the red and blue species show stable ecological coexistence (see Box 2 for detailed explanation of this model). However, this two-species community can be invaded by an intermediate phenotype that, once established, would not be invasible by a population with any other phenotype (dotted purple curve in Fig. 1a). Furthermore, gradual evolution driven by selection will lead a population towards this phenotype (Box 2). In total, the scenario shown in Fig. 1a–d illustrates that while many different species pairs may be able to coexist ecologically, evolution favours their replacement by a single

species with an uninhabitable phenotype. Therefore, if sufficient genetic variation exists for a species to evolve the uninhabitable phenotype, then it is reasonable to argue that ultimately it will evolve and displace any other species in the community (assuming a stationary environment). The difference between ecologically stable communities and ESCs is important for natural communities, because observed diversity may be transient if a community has not yet reached an ESC, a possibility we discuss further below. Likewise, a coexistence mechanism that may explain diversity based on a purely ecological model may not be evolutionarily stable.

The diversity of ESCs will depend on environmental conditions and the tradeoff(s) underlying coexistence (de Mazancourt & Dieckmann 2004). For example, simply reducing the niches of species in the previous example (making competition kernels narrower) enables a pair of species to form an ESC (Fig. 1e–h). In Fig. 1e the solid blue and red lines represent two species that can coexist, but are invasible by other phenotypes. The dotted blue and red lines show the two species belonging to the ESC under these new conditions. Further narrowing of the competition curves allows an even greater number of species to coexist at the ESC (e.g. as found in Taper & Chase 1985).

Box 2 Example invasion analysis: competition for a spectrum of resources

Figure 1 a–h reanalyses a common heuristic model of competition, coexistence, and trait evolution. The model assumes that species compete for a spectrum of resources that vary along a single dimension. For example, the resource spectrum could be thought of as seeds of different sizes, which are fed upon by birds with beaks of different sizes (Fig. 1a, Appendix S1). Models of this type have been thoroughly analysed to understand the conditions allowing competitors to coexist (e.g. MacArthur & Levins 1967; Chesson 1990; Abrams & Rueffler 2009), and a review of these results is beyond the scope of this article (see Barabás *et al.* 2012; Leimar *et al.* 2013). We focus instead on how trait evolution affects emergent community structure in this scenario. Figure 1a shows the carrying capacity curve that defines the environmental context and the competition kernels of three example species. We assume that the trait x that varies across species is the position of the peak of the competition kernel, and that the width, height, and shape of this curve are constant. We assume that all individuals of a species can be characterised by the same trait x . Under certain conditions, this Lotka–Volterra model approximates an explicit consumer–resource model, where the strength of interspecific competition is quantified as the overlap between species in their consumption curves (Appendix S1, MacArthur & Levins 1967; but see Ackermann & Doebeli 2004 and Abrams & Rueffler 2009). Figure 1b shows an invasion profile, which plots invasion rate as a function of a species' trait value given a community of resident species. This profile is an adaptive landscape across the range of possible phenotypes (Arnold *et al.* 2001), with the fitness of a phenotype defined as the invasion rate of a population with that phenotype (Metz *et al.* 1992). The top panel shows the invasion profile when the red and blue species are already present in the community (i.e. they are the 'resident' community), and the bottom panel shows the invasion profile when the purple species is the resident. The red and blue pair can be invaded by any species with an intermediate trait value (yielding positive invasion rates), while the purple species is uninvadable. Fig. 1c shows a pairwise invasibility plot (PIP; Geritz *et al.* 1998) for the model, which summarises invasibility for all potential pairs of invader/resident trait values. In contrast to Fig. 1b, the PIP exclusively considers a single resident species at a time. A PIP is a useful illustration of potential evolutionary dynamics, because it shows whether a phenotype can be invaded (in which case it is not an evolutionary endpoint), and also whether a phenotype can be attained through gradual evolution (if a series of invasions by small mutations will move a population towards the phenotype). The trait value of the purple species ($x = 0$) is an evolutionarily stable strategy (Maynard Smith & Price 1973) because a resident with this trait value cannot be invaded by a population with any other trait value. This strategy is also convergence stable (Geritz *et al.* 1998), because small evolutionary steps driven by selection will always lead to this trait value (residents with $x \neq 0$ can always be invaded by nearby populations with a trait closer to 0). Finally, this phenotype could also be reached through larger evolutionary steps, because this strategy can invade all other strategies. Figure 1d shows a mutual invasibility plot for the model, where all trait pairs that can coexist ecologically are shaded in grey. Figure 1e–h are analogous to Fig. 1a–d, but with narrower competition kernels that change the evolutionary attractor, allowing the evolutionarily stable coexistence of two species. In contrast to a–d, in E–H the trait value $x = 0$ is a branching point rather than an ESS, and is still convergence stable (Geritz *et al.* 1998). This means that if a single species were initially present, selection would drive it up the adaptive landscape towards $x = 0$, but once it reaches this point the fitness peak becomes a fitness valley, which is noticeable in Fig. 1f as a slight depression between the red and blue points. The evolutionary dynamics that can lead from a branching point to an ESC are discussed in section Undersaturated communities experience diversification/invasion until the ESC is reached.

Recent studies have explored the evolutionary stability of a variety of well-known coexistence mechanisms. In Table 1 we compile a non-exhaustive list of the coexistence mechanisms thought to be important in many natural communities and how they are affected by trait evolution. We contrast the maximum possible diversity set by the competitive exclusion principle (Hardin 1960; Levin 1970; Armstrong & McGehee 1980) with the evolutionarily stable diversity. Some competition models can in principle allow an unlimited number of species to coexist because there is continuum of resources or limiting factors (Armstrong & McGehee 1980; Abrams 1988, Barabás *et al.* 2012). For example, there may be a continuum of resource types (as in Fig. 1A–H), or a single resource used by species whose relative fitness varies continuously over space or time due to abiotic factors. For the type of model in Fig. 1a–h, where there is a continuous spectrum of resources, there are certain parameter values under which a continuum of species or phenotypes can coexist. However, these solutions are structurally unstable, meaning that small changes to

parameter values (e.g. species traits) causes the continuum of coexisting species to collapse (Barabás *et al.* 2012). Even under more realistic conditions, such as those depicted in Fig. 1a–h, the number of species that can coexist ecologically is often roughly double the evolutionarily stable diversity (each species in the ESC can often be replaced by a pair of flanking species).

In general, Table 1 highlights an often overlooked fact: evolution generates diversity, but also restricts its magnitude. In the presence of trait evolution, some mechanisms can only maintain diversity if there is a strong enough underlying tradeoff. For example, the classic keystone predation mechanism only maintains diversity if the tradeoff between competitive ability and predator resistance is strong enough (Abrams and Chen 2002). This implies that better understanding and quantifying tradeoff strength and shape will be essential for understanding coexistence. Although the diversity maintained by a mechanism can depend on how competition, tradeoffs, and environmental heterogeneity are modelled, it seems likely

Table 1 Summary of maximum ecological diversity vs. evolutionarily stable diversity for various coexistence mechanisms. ‘CEP Diversity’ is the maximum number of coexisting species set by the competitive exclusion principle. ‘ESC Diversity’ is the diversity of an evolutionarily stable community for the same model.

Coexistence Mechanism	CEP diversity	ESC diversity	References
Multiple resources			
Two essential resources	2 sp	1 sp	Abrams (1987), Schreiber & Tobiason (2003)
N essential resources	N sp	1 sp	Conjecture; Shores <i>et al.</i> (2008)
Two substitutable resources	2 sp	1 sp if weak tradeoff, 2 sp if strong tradeoff	Abrams (1987), Schreiber & Tobiason (2003)
One-dimensional continuum of substitutable resources	Unlimited	Typically $\approx L/(2\sigma)$ where L = total niche space, 2σ = niche width	MacArthur & Levins (1967), Barabás & Mészéna (2009)
Shared predators			
Keystone predation	2 sp	1 sp if weak tradeoff, 2 sp if strong tradeoff	Abrams and Chen (2002), Ehrlich <i>et al.</i> (2017)
One-dimensional continuum of specialist predators	Unlimited	$\approx L/(2\sigma)$ where L = total niche space, 2σ = predator feeding kernel width	Conjecture
Temporal variability			
Growth rate vs. competitive ability trade-off in periodic environment	Unlimited	1–2 sp with reasonable tradeoff (> 2 with extreme tradeoffs)	Armstrong & McGehee (1980), Chesson (1994, Kremer & Klausmeier (2013)
Temporally varying environmental factor (discrete environmental states)	Number of environmental states	\leq Number of environmental states	Miller & Klausmeier (2017)
Temporally varying environmental factor (continuous environment)	Unlimited	$\approx L/(2\sigma)$	Kremer & Klausmeier (2017)
Spatial variability			
Spatially varying environmental factor	Unlimited	Unlimited as dispersal $\rightarrow 0$	Abrams 1988; Mouquet & Loreau 2003; Norberg <i>et al.</i> 2012;
Spatiotemporal variability			
Competition-colonisation trade-off	Unlimited	Unlimited if strict competitive hierarchy, fewer if weaker trade-off	Kinzig <i>et al.</i> 1999; Adler & Mosquera 2000

that broad categories of mechanisms differ in the level of diversity they can explain in the presence of trait evolution. Notably, competition for essential resources does not maintain any diversity when there are two resources, and likely does not allow for coexistence with any number of resources, as species converge on a single best competitor phenotype. This has important implications for primary producers, which often compete for essential resources such as nutrients (Tilman 1980). Mechanisms that can potentially maintain very high diversity are specialist natural enemies and spatial variation in competitive superiority, as long as dispersal is not too high (Table 1). These observations suggest that, empirically, the development of communities will depend not only on whether their constituent species can coexist stably, but whether they are more or less diverse than the ESC, and the pace of immigration and adaptation.

Although evolutionarily stable diversity is often less than the maximum possible diversity, there are cases where trait evolution can lead to emergent eco-evolutionary dynamics that increase diversity (Abrams 2006; Klauschies *et al.* 2016). For example, a generalist predator may be more likely to coexist with multiple specialists under rapid evolution of its feeding preference (Abrams 2006). In addition, rapid evolution can prevent a competitor from going extinct by allowing

character displacement instead of competitive exclusion (Lankau 2011). This process is important but distinct from the comparisons in Table 1, where we consider the maximum diversity across all possible combinations of competitors’ traits, as opposed to transient dynamics of particular species.

UNDERSATURATED COMMUNITIES EXPERIENCE DIVERSIFICATION/INVASION UNTIL THE ESC IS REACHED

Theory

In any given environment, communities that contain fewer species or phenotypes than their ESC are *undersaturated*. Trait evolution within populations combined with speciation and/or immigration will tend to move undersaturated communities towards an ESC. We intentionally defined ESCs independently from the mechanisms by which they arise, as a variety of ecological and evolutionary processes could all lead to the same ESC. Here, however, we outline these processes while considering whether ESCs are likely to occur in nature.

In models with a multispecies ESC, if only a single species is initially present, it will often evolve until it reaches a branching point at which it experiences disruptive selection

(Geritz *et al.* 1998). In other words, as it climbs a peak on the adaptive landscape, the landscape shifts and the peak becomes a valley. Among asexual species, speciation follows easily through evolutionary branching (Geritz *et al.* 1998; Waxman & Gavrilovs 2005). However, the conditions for sympatric speciation are more complex in sexual species, where recombination continually produces less fit intermediate phenotypes. The production of less fit offspring may, however, select for assortative mating. Under some conditions (e.g. strong disruptive selection, tight linkage between mate choice and genes under disruptive selection) assortative mating is able to evolve, allowing speciation (reviewed in Coyne & Orr 2004; Chapter 4; Kopp *et al.* 2018).

Alternatively, a species could remain at a branching point indefinitely, until allopatric/peripatric speciation facilitates reproductive isolation (e.g. by the accumulation of genetic incompatibilities). If secondary contact eventually occurs then selection will reduce competition among these similar species by causing character displacement (Brown & Wilson 1956; Case & Taper 2000). For example, simulation of the trajectory of trait evolution for the model in Fig. 1e shows trait divergence until the species reach the two uninvasible phenotypes (results not shown). If the ESC for this community contained more than two phenotypes, then iteration of this process of allopatric speciation, secondary contact, and character displacement would result in adaptive radiation and the 'filling' of niche space (Schluter 2000; Rundell & Price 2009). Allopatric speciation could also occur before an ancestor species reaches a branching point; secondary contact would still allow for the sister species to diverge towards the ESC phenotypes or subsequent branching points. Finally, competitors in a community are often distantly related, and the ESC concept is not restricted to single diversifying clades. Therefore, analogous processes of invasion and character divergence producing an ESC can occur if the invaders arise due to immigration rather than speciation. This could occur, for example, due to the breakdown of a geographic barrier or the chance arrival of colonists to an island.

In the light of the processes just described we can consider the conditions that will tend to facilitate or inhibit the development of undersaturated communities into ESCs, and consequently determine whether ESCs are likely to occur in nature. The rate at which populations reach their ESC phenotypes (whether directly or via branching) will be affected by the strength of selection and the amount of heritable trait variation that is maintained and/or produced through mutation (Abrams 2001). In addition to the rate of trait change within populations, the generation of reproductively isolated populations could be a key rate-limiting process, and therefore any factor affecting speciation rates could affect ESC assembly. This may include geological processes that fragment populations as well as biological factors that determine the ease with which reproductive isolation emerges (Coyne & Orr 2004). The amount of trait evolution and diversification that must occur before an undersaturated community reaches its ESC will depend on the diversity of the ESC, and consequently the sources of environmental heterogeneity and the tradeoffs underlying coexistence (Table 1). Finally, some ESCs may not be reachable through gradual evolution and branching (e.g.

Geritz *et al.* 2007), and the community may converge on a locally stable but globally invisable configuration, a phenomenon which is analogous to being stuck on a local optimum of a fitness landscape (Wright 1932). In these cases ESC assembly will require immigrants from other regions or processes that allow the crossing of fitness valleys such as drift or environmental fluctuation (Wright 1932; Whitlock 1997).

It may be useful to think of ESCs as theoretical entities that are most relevant to an intermediate evolutionary timescale, towards which communities evolve under particular genetic constraints. On longer timescales, contingency may prevail over determinism (Losos 2017), for example if rare sequences of epistatic mutations act as 'key innovations' (Wheat *et al.* 2007; Blount *et al.* 2008; Turner *et al.* 2015), changing the evolutionary game enough that the ESC changes fundamentally, and processes of selection and extinction/diversification temporarily accelerate. Likewise, significant environmental change may alter an ESC enough to drive many species extinct and 'reset' the assembly process. In macroevolutionary terms, ESCs are similar to the outcome of diversification within adaptive zones (Simpson 1953), but with the distinction that ESCs focus on co-occurring competitors, and multiple clades may contribute to community assembly.

Empirical evidence: Do real communities reach evolutionarily stable diversity?

Do real communities actually diversify to evolutionarily stable endpoints, or are ESCs merely a theoretically useful fiction? A closely related question is whether communities are saturated with species, or whether rates of production of genetic variance, speciation, and immigration are low enough (or extinction high enough) to limit communities from reaching evolutionarily stable diversity.

Microbial microcosms may hold the most potential for strong tests of ESCs. Microbial evolution experiments, for example, with *Pseudomonas fluorescens* and *Escherichia coli*, have found repeatable adaptive radiations of a single ancestor into a similar set of specialised descendants (ecomorphs) (MacLean 2005; Herron & Doebeli 2013; Kassen 2014). Repeated adaptive radiations are consistent with diversification to an underlying ESC. In cases of repeated radiations, an evolved community could be tested for invasibility by generating a range of phenotypes and seeing whether they can increase from low abundance in the resident community. Although it is impossible to generate the full range of potential invaders, in part due to the large number of dimensions of phenotypic variation, nonetheless, an uninvasible community in such an experiment would be valuable evidence for an ESC. In contrast, long-term experiments with *E. coli* find that the fitness of populations increases continuously though at a decelerating rate, over 60 000 generations, which is evidence against reaching an ESC (Good *et al.* 2017). A continuous increase in fitness does not necessarily mean that an ESC does not exist, but it does suggest that reaching an evolutionary optimum may take a very long time, delayed by mutations that open up new evolutionary paths (Meyer *et al.* 2012), diminishing-returns epistasis (Kryazhimskiy *et al.* 2014), or clonal interference slowing evolutionary trajectories (Good *et al.* 2017).

Performing long-term evolutionary experiments in natural communities is much more difficult, but indirect evidence testing for ESCs could be gained by studying the history of trait evolution in a group of interacting species. There are several examples of repeated adaptive radiations that occurred when a lineage colonised multiple islands or lakes, for example, in Caribbean anoles (Mahler *et al.* 2013), holarctic sticklebacks (Schluter 2000), and Hawaiian spiders (Gillespie 2004). Repeated diversification to a set of phenotypes is certainly consistent with predictions from eco-evolutionary theory (e.g. Doebeli 2011), although it is hard to assess whether the diversified biota is uninviable. Although they are tantalising examples, repeated adaptive radiations are rare, and rarely occur on different continents (Losos 2010). In diverse biotas (such as those on continents or in the ocean) it is likely that multiple clades radiate simultaneously while competing for the same resources, such that trait evolution within a single clade will yield an incomplete picture of community coevolution. In this case, to understand the trajectory of trait coevolution it will be necessary to measure the traits that determine competitive outcomes when organisms from multiple clades compete, and to study the joint evolution of these traits.

If ESCs are prevalent in nature then diversity at regional scales should exhibit equilibrium dynamics, in the absence of drastic environmental change or evolution of key innovations. Rabosky & Hurlbert (2015) argued that this is the case, and that richness is governed by ecological limits, but Harmon & Harrison (2015) presented multiple lines of evidence that diversity at local and regional scales is in fact unsaturated. Patterns of trait evolution within single species should also reflect whether communities tend to reach ESCs, because individual species in an ESC should experience stabilising selection over the long term, although short-term dynamics may be directional due to environmental fluctuation (i.e. the ESC may be a periodic or stochastic attractor). For example, it has been found that short-term trait change within species can be large, but tends to occur as bounded fluctuations rather than consistent directional shifts, while large directional shifts occur in rare bursts (Kinnison & Hendry 2001; Hunt 2007; Uyeda *et al.* 2011). These patterns are consistent with species constrained by a (stochastic) trait attractor that infrequently undergoes dramatic shifts, perhaps due to environmental change or key innovations.

Because ESCs can also be approached through immigration and species sorting, studies of community assembly should be investigated for repeatable selection dynamics. For example, Fukami *et al.* (2005) found that as experimentally restored herbaceous plant communities developed over time, the functional composition of replicate communities converged, while their taxonomic compositions remained distinct, perhaps due to priority effects. This suggests that particular combinations of phenotypes are favoured by community assembly, potentially resulting in uninviable communities, and hence, ESCs. Ecological assembly processes may also combine with divergent trait evolution. In a diversity manipulation with grassland plants, species' traits diverged more in mixtures than in monocultures, consistent with ecological species sorting combining with trait evolution, which could eventually lead to a set of uninviable populations (Zupping-Dingley *et al.* 2014).

OVERSATURATED COMMUNITIES EXPERIENCE EXTINCTIONS AND/OR CONVERGENCE

Theory

We can contrast diversification in an undersaturated community with the situation where a community is *oversaturated* with species relative to the ESC. A simple illustrative scenario considers what happens in the short term when two or more species compete for essential resources, but the ESC is a single phenotype (Fig. 1i–l; detailed model description in Box 3). This kind of scenario has received some theoretical attention (Abrams 1986, 1990; terHorst *et al.* 2010; Klauschies *et al.* 2016). Contrary to the general expectation that competition drives trait divergence, in this case selection leads to trait convergence (Fig 2; MacArthur & Levins 1967). Despite competition, selection can drive convergence because fitness increases with similarity to the uninviable phenotype, even if a competing species already possesses that phenotype. The dynamics of this process are potentially complex, because multiple species are effectively evolving to occupy the same niche (terHorst *et al.* 2010).

Figure 3 shows three example trajectories for convergent evolution under the essential resources model. In case A, two

Box 3 Example invasion analysis: competition for essential resources.

Figure 1 i–l is analogous to Fig. 1a–d, but illustrates a model where species compete for two resources, R_1 and R_2 , which are essential (i.e. they are required for growth and cannot be substituted). For example, nutrients such as nitrogen and phosphorus are essential resources for the growth of autotrophs, because they cannot be substituted for one another (Tilman 1980). We reanalyse this model to show that the ESC concept applies generically to different ecological mechanisms and also to illustrate transient eco-evolutionary dynamics (Fig. 2 and 3). In Fig. 1i we assume that species trade-off in their competitive ability for R_1 and R_2 (dotted black line), and that competitive ability can be summarised by their zero-net-growth isoclines (blue, red, purple lines), which are the resource concentrations at which growth balances mortality (further details in Appendix S1). This model allows two species to coexist, if each consumes relatively more of the resource for which it has a larger requirement. How is competition for essential resources altered by trait evolution? If we assume that resource consumption follows optimal foraging rules (Tilman 1982), then an invasion analysis shows that there is a single species that is uninviable, again reducing diversity as in Fig. 1b (Fig. 1j; Abrams 1987; Vincent *et al.* 1996; Klausmeier *et al.* 2007; Shores *et al.* 2008). The phenotype of this species (purple dotted line in Fig. 1i) is intuitive, because it is balanced such that growth is co-limited by the two resources. In other words, this species is not wasting its limited resource acquisition efforts consuming a resource that is not limiting its growth. Fox & Vasseur (2008) show how different results may be obtained from this model if resource consumption rates evolve but resource requirements do not.

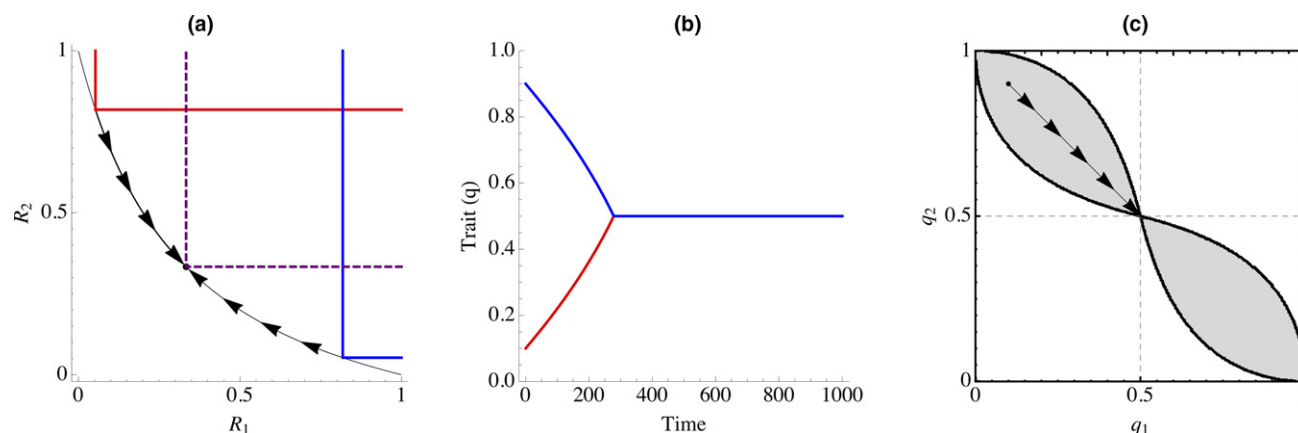


Figure 2 Eco-evolutionary dynamics leading to character convergence. (a) is drawn as in Fig. 11, with black arrows showing how the two initial species (red and blue) are selected to converge to the intermediate phenotype given by the dashed purple line. (b) Shows the dynamics of trait evolution, with eventual convergence to the same trait value ($q = 0.5$). In (c) the trajectory of trait evolution is overlaid on a mutual invasibility plot. In this case, the initial species pair (upper left dot) coexist ecologically, and evolution proceeds through the coexistence region (grey) as the two species converge to $q = 0.5$. Equations and parameter values that produce the results in this figure are given in Appendix S1.

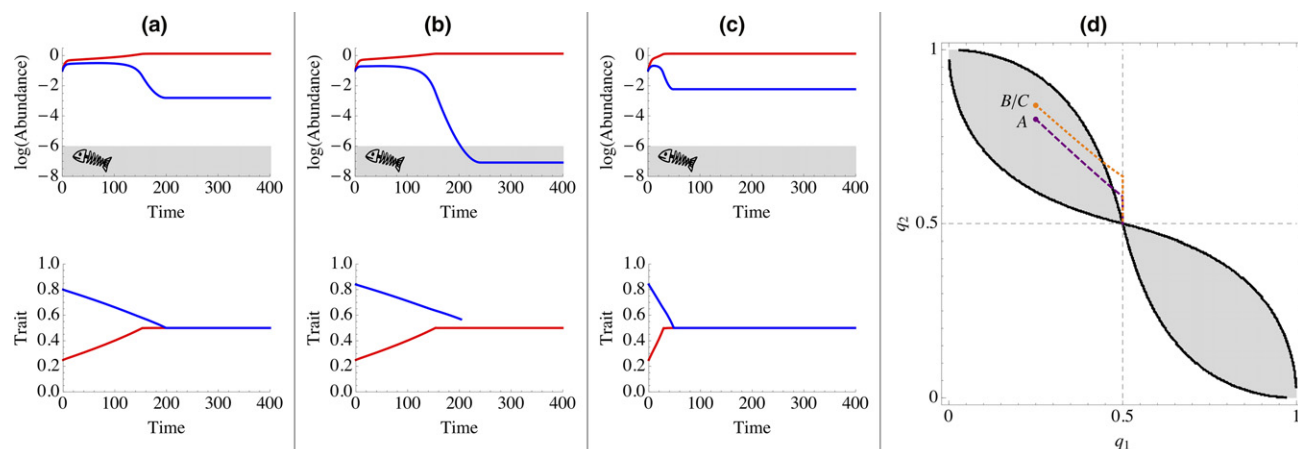


Figure 3 Character convergence and extinction or persistence under different conditions. (a–c) show how the abundances (top panels) and evolving traits (bottom panels) of two competitors (red and blue lines) vary over time, under different conditions. Relative to (a), (b) changes the initial trait value of the blue species, while (c) increases the rate of evolution relative to (b). (d) plots the trajectories of trait evolution from (a–c) on a mutual invasibility plot, with all trait trajectories ending at $q = 0.5$. As shown on panel (d), scenarios B and C yield the same coevolutionary trajectory of trait change, but the difference in the rate of evolution results in different persistence outcomes. Further discussion of the figure is in the main text; equations that produce the results in this figure are given in Appendix S1.

species initially coexist with trait values that are on opposite sides of the ESC. In other words, one is a better competitor for R_1 (e.g. nitrogen) and the other is a better competitor for R_2 (e.g. phosphorus). They are both selected to move towards the intermediate trait value at which nitrogen and phosphorus are co-limiting. As selection drives each species towards the ESC, their evolving trait values follow a trajectory that remains largely within the region of coexistence, and their abundances remain relatively even. Eventually species 1 (red) nears the trait attractor first, at which point the abundance of species 2 (blue) declines rapidly, until its trait also reaches the ESC. Once both species have reached the ESC they interact neutrally because their traits are now identical. Because our model is deterministic, a neutral interaction means that the abundance of each species remains constant over time; in reality, genetic drift and demographic stochasticity would cause the relative abundance of the two species to drift. One species,

typically the rarer one, will eventually experience stochastic extinction, although the time it takes for this to happen could be astronomically long if population sizes are large (Hubbell 2001).

Case B shows the effect of different initial trait values, where species 2 starts at an even greater distance from the attractor than species 1. In this case, species 1 reaches the ESC at the same time as in case A, but species 2 lags behind, dropping to an extremely low abundance before reaching the attractor. Presumably a species this rare would rapidly go extinct under natural conditions, with extinction risk compounded by an increase in genetic drift at small population sizes. Finally, case C shows how the initial conditions in case B, which disfavour species 2, can be ameliorated by an increase in the rate of evolution. The traits of the two species follow essentially the same trajectory as in case B, but the abundance of species 2 does not decrease nearly as much

because it converges more rapidly on the attractor occupied by species 1. This outcome is a kind of evolutionary rescue, where trait evolution can rescue a population from a declining trajectory (Gomulkiewicz & Holt 1995). Theory and empirical studies have documented conditions under which evolutionary rescue is possible, both in isolation (Gomulkiewicz & Holt 1995; Bell & Gonzalez 2009) and in the presence of competition (Osmond & de Mazancourt 2013; Van Den Elzen *et al.* 2017); trait convergence may require similar conditions.

The possibility of trait (or character) convergence has large implications for our understanding of species diversity and its relationship to functional diversity (Abrams 1990; terHorst *et al.* 2010; Klauschies *et al.* 2016). Specifically, selection for character convergence is a way to generate neutral species diversity among species that are initially ecologically different (Fig. 3, cases a and c). For this example we used a competition model that has a single optimal phenotype towards which competitors evolve. However, the same principles apply to communities with more diverse ESCs. In general, whenever the community contains more species than the number of phenotypes that make up the ESC, selection for trait convergence should occur. The number of species that actually reach the ESC phenotype(s) before going extinct will likely depend upon the rates of evolution of each species and whether some species are positioned to reach the ESC long before their competitors. Prior work has discussed special conditions under which ecological equivalence might evolve, such as selection towards a common trait value under dispersal limitation (Hubbell 2006) or the reproductive isolation of sister species that are still ecologically equivalent (Leibold & McPeck 2006). However, in an oversaturated community there should be selection for character convergence regardless of the details of the competitive mechanism and the initial similarity of the species. The same phenomenon may occur if multiple species are within the domain of attraction of a single adaptive peak, and therefore converge on the same phenotype even though a large mutational jump would allow them to access an unoccupied peak on the fitness landscape (Geritz *et al.* 1998; Leimar *et al.* 2012).

Empirical evidence: Do community oversaturation and character convergence occur in nature?

We now outline some situations in which character convergence may be likely to occur.

Secondary contact

One possibility is during secondary contact of closely related species. The process of speciation usually has an allopatric phase (Coyne & Orr 2004), and the geographic separation of populations may result in character divergence through adaptation to environmental differences across space (Schluter 2001), or perhaps by genetic drift alone (Turelli *et al.* 2001). Reproductive isolation can involve a complex mix of processes (Coyne & Orr 2004), but for our purposes we will focus on what happens when reproductively isolated species with allopatric distributions come into sympatry, perhaps due to the breakdown of a dispersal barrier or environmental change. Under these conditions the effect of competition on trait

evolution will depend on the degree of niche divergence permitted by the environment. If the ESC contains more than one species, character displacement may occur. Numerous examples of character displacement exist (Pfennig & Pfennig 2009), although definitive evidence for this process is actually limited (Stuart & Losos 2013). On the other hand, if the ESC in the sympatric range consists of a single species, then species that diverged in allopatry will be selected to converge in sympatry (Grant 1972). As discussed above, competitive exclusion may occur before species fully converge (Fig. 3). Competitive exclusion is consistent with many examples of morphologically similar species that have allopatric distributions (Rundell & Price 2009). In contrast, there is little evidence of trait convergence during secondary contact, but testing for convergence may bring important examples to light. Evidence of character convergence may be sparse because convergence may be harder to detect than divergence, for example if convergence erases trait differences that are relatively modest or not visually evident. Convergence may also be under-reported, if divergence is the expected effect of competition (Dayan & Simberloff 2005). Empirical arguments in favour of convergence should attempt to fulfil the conditions laid out for character displacement more generally (Schluter 2000; Germain *et al.* 2017). One possible example comes from voles, where morphological differences between congeners are smaller when comparing individuals from the sympatric regions of these species' ranges (Spaeth 2009). There is some evidence for convergence in signalling traits in birds (Grether *et al.* 2013), which may be due to selection on interspecific aggression in the context of resource competition, which is presumably controlled by other traits. It has also been argued that morphological and trophic convergence of sympatric cichlids is widespread in Lake Tanganyika, although it is not clear if secondary contact is a likely mechanism (Muschick *et al.* 2012). It is noteworthy that if closely related species do not diverge in allopatry, then competitive dynamics in sympatry should be neutral, which is also the ultimate outcome of trait convergence. Siepielski *et al.* (2010) found that species in the damselfly genus *Enallagma* were ecologically equivalent, while being ecologically differentiated from species in the genus *Ischnura*. They suggested that ecological equivalence could be caused by speciation without subsequent or concurrent ecological differentiation. Their results are also consistent with speciation leading to modest ecological differences that are erased by convergence in sympatry. It may also be the case that selection for convergence of competitive traits will lead to a breakdown of reproductive isolation, because selection for reproductive isolation is often associated with ecological divergence (Funk *et al.* 2006).

Biotic interchange and species introductions

When biogeographic dispersal barriers break down, biotas that have evolved in isolation for millions of years have the potential to invade one another, a phenomenon termed biotic interchange (Vermeij 1991). Biotic interchange can lead to substantial increases in regional species diversity (Vermeij 1991; Tilman 2011), which could result in oversaturated communities. At the same time, invasion between biotas tends to be asymmetric, such that species from one biota are more

likely to expand into new territory (Vermeij 1991), although these invasions rarely result in extinction of competitors (Tilman 2011). These patterns suggest that trait convergence is an outcome worth investigating in the context of biotic interchange, but that large increases in diversity may be the result of differential saturation of the original biotas.

The introduction of non-native species presents additional opportunities to test questions such as whether communities are saturated with species (Sax & Gaines 2008) and how species evolve when placed in new environments (Strauss *et al.* 2006; Buswell *et al.* 2011). Many studies have documented trait change in introduced species (Simmons & Thomas 2004; Phillips *et al.* 2010; Buswell *et al.* 2011), as well as trait change of native species in response to introductions (Strauss *et al.* 2006; Leger 2008). However, little is known about mutual trait change or the lack thereof in native and introduced species that are known to compete. If native communities are already at an ESC, then an introduced species may be selected to converge towards a native competitor, while if native communities are undersaturated then an introduction may lead to character divergence between the introduced species and their native competitors. Testing these possibilities will require information on the traits and competitive interactions of native and introduced species, and the selection pressures or trajectories of trait change in response to these interactions. Similar considerations apply when relatively isolated environments such as islands are colonised from neighbouring areas. For example, in the *Anolis* lizard communities of the West Indies, Schoener (1969) found that individuals of each species tend to be convergently smaller on islands with a diversity of *Anolis* species, when compared to individuals of the same species on single-species islands. He postulated that this pattern may be due to convergent selection for smaller size when absolute food abundance is reduced, resulting in a scarcity of larger prey. Likewise, the foraging traits of bluegill fish converge to that of competing alewife populations, as competition selects for the ability to consume smaller zooplankton prey (Huss *et al.* 2014).

OTHER FEATURES OF ESCS

Until now, our discussion has focused primarily on scenarios where a single ESC persists over time in a particular environment. This is the simplest case; however, as with ecological models in general, more complex phenomena can arise. These are worth noting, yet remain little studied outside of the theoretical literature.

Alternative ESCs

Complex models sometimes predict the existence of multiple ESCs with different levels of diversity and/or trait composition supported by the same environment. These are analogous to the concept of alternative stable states within ecological models with multiple equilibria. A few theoretical studies show that alternative stable ESCs can arise in models of competition in seasonal environments (Kremer & Klausmeier 2017), a heterogeneous two-patch model (Kisdi & Geritz 1999), and in metapopulations where seed size and dispersal

evolve (Levin & Muller-Landau 2000). The existence of alternate ESCs suggests a number of patterns. For example, due to variable initial conditions, undersaturated communities in otherwise identical environments may follow distinct trajectories of divergence/invasion. This would imply that community trait distributions may not be uniquely predictable based on knowing the dominant environmental conditions and ecological mechanisms at play. Some evidence consistent with alternate ESCs comes from coevolutionary experiments with six species of soil bacteria, in which replicate communities diverge on evolutionary timescales into a few alternative community types (Celiker & Gore 2014). Alternative ESCs may help explain why adaptive radiation, and phenotypic evolution more generally, seems predictable in some circumstances but not others (Lässig *et al.* 2017; Losos 2017), because alternative ESCs are one way for contingency to arise in eco-evolutionary outcomes. Sufficiently large perturbations may also push a community between the basins of attraction corresponding to alternate ESCs. This could cause modest changes in species' traits, or the convergence/divergence of resident species when opposing ESCs support different levels of diversity.

Environmental change

The structure of an ESC depends on environmental conditions (Fig. 1; van den Bosch *et al.* 2010), and so environmental change can lead to a shift in the composition of an ESC (de Mazancourt *et al.* 2008). If environmental change causes a reduction in the diversity of an ESC (e.g. as caused by a reduction in the breadth of available seed sizes in Fig. 1) this could lead to extinction or convergent trait change if the community transiently contains more species than is evolutionarily stable. Experimental resource additions to plant communities often lead to reductions in species and functional diversity (Crawley *et al.* 2005; Suding *et al.* 2005; Isbell *et al.* 2013), but whether these responses also lead to evolutionary trait convergence is unknown. Alternatively, environmental changes that increase the diversity of an ESC would create empty niches, rendering a community invisable by immigrants with the proper traits, or causing resident species to evolve towards branching points. Testing for trait divergence or convergence due to environmental change will require measuring competitors' trait values before and after natural or experimental environmental change.

INTRASPECIFIC TRAIT VARIATION CAN UNDERMINE SPECIES COEXISTENCE

Intraspecific trait variation can be heritable or not, and maintained by mutation-selection balance or by random environmental effects on trait expression. So far we have tacitly assumed that there is enough heritable trait variation produced within species to allow them to evolve to the ESC or converge on neutrality, but not so much to directly affect coexistence. Yet recent studies have shown that intraspecific trait variation can prevent species coexistence (Hart *et al.* 2016) and make the trait divergence of competitors less likely (Sasaki & Dieckmann 2011), because intraspecific variation effectively increases the niche width of competitors.

In heterogeneous environments, heritable intraspecific trait variation can further undermine species coexistence. As seen in Table 1, temporal and spatial variation are potentially strong mechanisms of species coexistence. Figure 4 shows the effect of genetic variation on species coexistence along a linear one-dimensional spatial environmental gradient, a simplified scenario using the model of Norberg *et al.* (2012). For small genetic variance, V , nine species coexist along the gradient with no evidence of local adaptation (within species trait values do not vary along the gradient) (Fig. 4a). As genetic variance increases, local adaptation becomes increasingly evident (Fig. 4b–e) and functional species diversity declines, slowly at first (Fig. 4b and c) followed by an abrupt collapse (Fig. 4d and e). Thus trait diversity can be maintained either within species (high genetic variance and low species richness) or between species (low genetic variation and high species richness). Kremer & Klausmeier (2013) found analogous results in a model of temporal variability.

Implications of ESCs for interpreting patterns of trait dispersion

Ideally the processes that structure communities could be inferred from patterns in the co-occurrence of species and the traits they possess. It is often assumed that strong resource competition should cause the resource utilisation traits of coexisting species to be relatively overdispersed, because competition imposes a limit on the similarity of competitors that can stably coexist (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). Although limiting similarity and ‘even spacing’ of competitors is a commonly employed concept, it has been criticised on theoretical grounds, because it is easy to construct scenarios where competitors are actually more likely to coexist if they are similar (Abrams 1990; Mayfield & Levine 2010). Recent theory has also argued that coexistence may be ‘lumpy’, in the sense that there are groups of species whose members are very similar, while the groups themselves are overdispersed in trait space (Scheffer & van Nes 2006; Barabás *et al.* 2013; Klauschies *et al.* 2016; Scranton & Vas-seur 2016).

The ESC framework and the points we have discussed above help us reconcile these different perspectives by considering trait distributions in the context of evolutionary stability. It is certainly the case that competition may select for the convergence or divergence of competitors’ traits (Figs 1–3), which means that overdispersed trait distributions are not a satisfactory test for the presence of competition. As we have discussed in depth, convergence is expected when communities are oversaturated relative to the ESC. It is also worth noting that convergence may be a common outcome when competitors are evolving along multiple trait axes that involve multiple mechanisms of coexistence (D’Andrea & Ostling 2016). For example, in Fig. 5 competitors evolve along both a resource use axis (as in Fig. 1a–h) and a second axis representing resistance to specialist enemies such as pathogens or specialised herbivores (Kursar *et al.* 2009). Along the resource axis, species converge on three well-spaced phenotypes, with groups of 4–5 species each possessing the same resource trait. However, rather than representing sets of neutrally stable species, species with the same resource trait coexist due to divergence along the second trait axis.

Although overdispersed trait distributions are not the only outcome of competition, nonetheless there are reasons to expect that multi-species ESCs will feature regular patterns in trait space. Adding heritable intraspecific variation to a competition model tends to reduce the number of species that can coexist, but species that do coexist are more regularly distributed in trait space compared to randomly assembled non-evolving communities (Barabás & D’Andrea 2016). Likewise, the final community in Fig. 5 exhibits more regularity than the initial community, even though the peaks along the resource axis include multiple species. A related point is that ‘lumpy’ coexistence may be evolutionarily unstable in most cases, because the lumps of similar species are clustered around a single phenotype in the ESC. For example, in Fig. 1d and l the ESC is a single phenotype, but pairs of species on opposite sides of the ESC can be arbitrarily similar and still coexist ecologically. However, as evolution proceeds these species are expected to converge on the ESC, at which point their dynamics become neutral (Fig. 2).

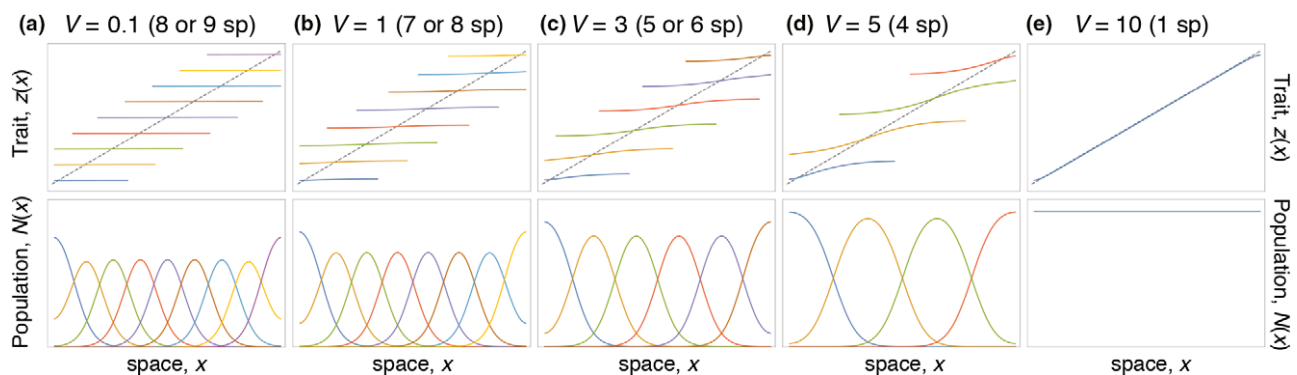


Figure 4 Outcome of coupled eco-evolutionary dynamics along a spatial environmental gradient as a function of additive genetic variance, V . The grey dashed line in the top panels represents the local trait optimum (trait value with highest fitness at that location). Lines of different colours correspond to functionally different species, whose traits and population sizes vary in space. The plotted results are the equilibrium patterns of species’ mean trait values across space (top row) and species’ abundances across space (bottom row). The columns correspond to increasing values of intraspecific trait variation (V), which is the additive genetic variance within a population at a location in space. Details of the model underlying this figure can be found in Norberg *et al.* (2012). Note that cases a–c each have alternative ESCs with one fewer species (not shown here, see Mathematica code).

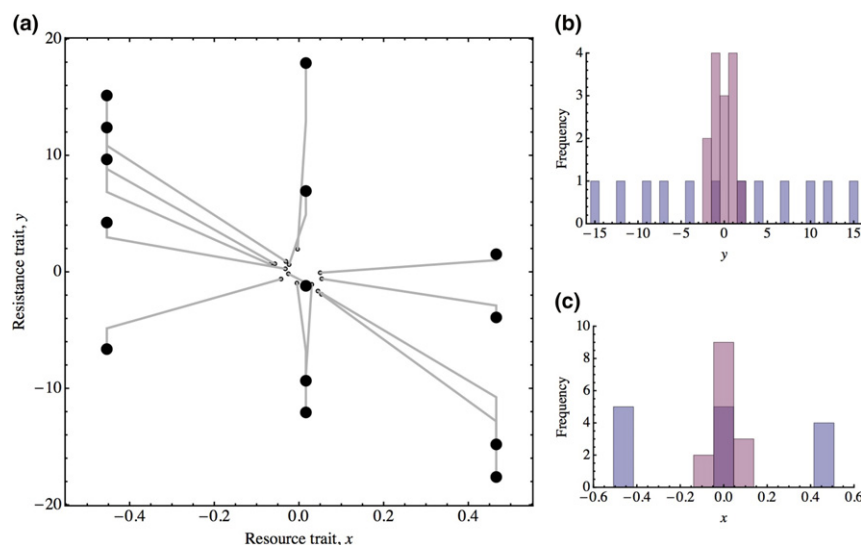


Figure 5 Divergence and convergence in multiple trait dimensions. (a) Evolution determines the trajectory 14 species follow from their randomly chosen initial trait values (small circles) to their ending points (large circles). Trait x is the resource optimum as in Fig 1a, while trait y determines resistance to specialist predators. Along the resistance trait axis all species eventually occupy distinct locations, while along the resource axis the community has diverged/converged to occupy 3 peaks in trait space. Sharp turns in the trait trajectories occur when species reach the adaptive peak for trait x before the final location for trait y . (b) Histogram showing the initial (purple) and final (blue) distribution of resistance trait y in the community. (c) Histogram showing the initial (purple) and final (blue) distribution of resource trait x in the community. Equations and parameter values that produce the results in this figure are given in Appendix S1.

These observations apply equally to communities where the ESC contains multiple phenotypes, and reiterate the general observation that evolutionarily stable diversity (of non-neutral species) is typically less than the number of species that can coexist ecologically. In sum, we argue that the study of community trait distributions is valuable, but with the recognition that mixtures of convergence and divergence may be common, and that observed patterns may be snapshots of a trajectory leading to an ESC.

Future directions

Theory has outpaced empirical work on coexistence and eco-evolutionary dynamics, and we suggest three major areas where increased empirical attention is necessary to assess theoretical predictions: testing alternative coexistence mechanisms, testing whether ESCs occur in nature, and testing for convergent evolution of competitors. It is likely that any community has multiple coexistence mechanisms that maintain diversity, but theory suggests that some mechanisms can maintain substantially more evolutionarily stable diversity than others (Table 1). A renewed focus on spatial differences in competitive ability and specialised enemies may be particularly fruitful in explaining diversity, especially for systems where resource partitioning is unlikely to be important. It is also important to develop approaches that test whether real communities reach ESCs. For laboratory microcosms, combining experimental radiations with invasibility experiments can help assess whether evolved communities are evolutionarily stable. Analogous experiments in natural systems are likely intractable, but measuring trajectories of trait evolution and selection gradients for co-occurring competitors would help test whether competitors are diverging or not, and whether competitors are

collectively experiencing long-term stabilising selection (as predicted for an ESC), or directional or disruptive selection. We would expect that communities that have been assembling and evolving for prolonged periods in a relatively constant environment would be more likely to reach an ESC, while communities that have experienced recent invasions or substantial environmental change may exhibit stable coexistence but continued evolution of community members. Finally, there are several situations in which convergent evolution of competitors may occur due to community oversaturation, and should be investigated: secondary contact of sister species, invasions or breakdowns of biogeographic barriers, and perhaps environmental change. Testing for convergent trait evolution in laboratory microcosms, for example among phytoplankton competing for essential nutrients, would also be an important proof of concept.

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AUTHOR CONTRIBUTIONS

All authors contributed to the conceptualisation and writing of the manuscript. CTK and CAK created the figures and underlying model code.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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