

LETTER

Species packing in eco-evolutionary models of seasonally fluctuating environments

Colin T. Kremer^{1,2,3*} and
Christopher A. Klausmeier^{1,2}

Abstract

As ecology and evolution become ever more entwined, many areas of ecological theory are being re-examined. Eco-evolutionary analyses of classic coexistence mechanisms are yielding new insights into the structure and stability of communities. We examine fluctuation-dependent coexistence models, identifying communities that are both ecologically and evolutionarily stable. Members of these communities possess distinct environmental preferences, revealing widespread patterns of limiting similarity. This regularity leads to consistent changes in the structure of communities across fluctuation regimes. However, at high amplitudes, subtle differences in the form of fluctuations dramatically affect the collapse of communities. We also show that identical fluctuations can support multiple evolutionarily stable communities – a novel example of alternative stable states within eco-evolutionary systems. Consequently, the configuration of communities will depend on historical contingencies, including details of the adaptive process. Integrating evolution into the study of coexistence offers new insights, while enriching our understanding of ecology.

Keywords

Adaptive dynamics, coexistence, ESS, evolutionary ecology, limiting similarity, temporal variation.

Ecology Letters (2017) **20**: 1158–1168

INTRODUCTION

As part of the expanding synthesis of ecology and evolution (Fussmann *et al.* 2007), theoreticians and empiricists are revisiting established ecological theory to determine which classic ecological principles must be revised in light of evolution and which remain unchanged. Focusing on coexistence theory and the maintenance of diversity – two topics at the heart of community ecology – several themes are emerging. First, evolution ultimately explains the origin of species. While this may occur through neutral processes and in allopatry, sympatric speciation driven by ecology is also possible (Rundle & Nosil 2005; Schluter 2009). Consistent with these studies, eco-evolutionary theory has revealed that ecological interactions can generate disruptive selection. This sets the stage for the phenotypic divergence of competitors and perhaps ecological speciation within a community via evolutionary branching (Geritz *et al.* 1998, 2004; Abrams 2001; McGill & Brown 2007). Other studies examine the conditions under which coexistence mechanisms can evolve (Snyder & Adler 2011; Abrams *et al.* 2012; Kremer & Klausmeier 2013; Miller & Klausmeier 2017).

Second, evolution can affect the ability of extant species to coexist. Evolution can enhance species coexistence when species adjust their traits in response to their competitors, prey, predators, and environment (e.g., Lankau 2011; Barabás & D'Andrea 2016). Similarly, evolution can allow initially poorly adapted, invading species to remain within a community (Faillace & Morin 2016), or prevent the loss of species

after environmental perturbations through evolutionary rescue (Osmond & de Mazancourt 2013). In contrast, evolution can undermine species persistence (Ferrière & Legendre 2012) and coexistence (Shoresh *et al.* 2008; Abrams *et al.* 2012) when it drives convergence in species' phenotypes, reducing functional diversity within communities, eliminating species' niche differences and resulting in 'emergent neutrality' (Hubbell 2006). Subsequently, neutral species may drift to extinction (Lankau 2011), reducing species diversity. The relative abundance of neutral species affects how long they co-occur; consequently, when evolution drives rapid trait convergence it may appear to temporarily enhance coexistence. Decreased functional diversity due to evolutionary convergence occurs widely in eco-evolutionary models (e.g., Thomas *et al.* 2012; Klauschies *et al.* 2016; Scranton & Vasseur 2016), including those with temporal and spatial variation (Norberg *et al.* 2012; Kremer & Klausmeier 2013).

Are there general principles that can reconcile these competing roles of evolution as a process that both facilitates and inhibits coexistence? Fundamental ideas from ecological theory, including the competitive exclusion principle (Gause 1934) and limiting similarity (Hutchinson 1959; MacArthur & Levins 1967; Abrams 1983), may offer a way forward. Ecological theory predicts that the number of species that can coexist in any situation is less than or equal to the number of limiting, or regulating, factors present (Levin 1970; Tilman 1982; Chase & Leibold 2003). In addition, for coexistence to be robust, there are limits to the similarity of species' sensitivity

¹Kellogg Biological Station, Michigan State University, 3700 E Gull Lake Dr., Hickory Corners, MI 49060, USA

²Department of Plant Biology and Program in Ecology, Evolutionary Biology and Behavior, Michigan State University, East Lansing, MI, USA

³Department of Ecology & Evolutionary Biology, Yale University, PO Box 208106, New Haven, CT 06520, USA

*Correspondence: E-mail: kremerco@msu.edu

to or impact on these regulating factors (Meszéna *et al.* 2006; Barabás *et al.* 2012). Even when there are an effectively infinite number of distinct resources (Abrams 1988), theory typically predicts a limit to similarity.

To determine the extent to which these concepts are relevant within an eco-evolutionary context, we conduct a detailed eco-evolutionary analysis of a classic coexistence mechanism based on temporal niche partitioning in a fluctuating environment. Suggested by Hutchinson as a potential resolution to his ‘Paradox of the Plankton’, this mechanism has a long history (Hutchinson 1961; Cushing 1980; Chesson & Warner 1981; Abrams 1984; Chesson 1994, 2000; Li & Chesson 2016; Miller & Klausmeier 2017). We construct a simple model where species’ ability to grow depends on how closely their phenotype matches an environment that fluctuates deterministically over time. Coexistence here depends on a temporal storage effect: species exhibit unique responses to their environment, and experience buffered population growth and covariance between the environment and competition (Chesson 1994). Our model is inspired by research into the ecology of ectothermic species exposed to temperature fluctuations – a system of significant interest (empirically, Descamps-Julien & Gonzalez 2005; Jiang & Morin 2007; Thomas *et al.* 2012; theoretically, Thomas *et al.* 2012; Scranton & Vasseur 2016; Amarasekare & Johnson 2017). We identify communities that are both ecologically and evolutionarily stable (uninvasible), and examine how the structure of such communities depends on the environmental forcing regime (fluctuation type and amplitude). Our results demonstrate that ecological principles such as limiting similarity provide significant insights into the assembly and evolution of communities in temporally varying environments. However, this system also exhibits novel behaviours not revealed without considering evolution. We conclude that eco-evolutionary models and analyses enrich, rather than invalidate, the insights emerging from decades of ecological theory.

THE MODEL

Ecological model

We investigated competition among species for a shared resource in a fluctuating environment using a simple model:

$$\frac{1}{n_i} \frac{dn_i}{dt} = \mu_i(t, z_i) \cdot R(t) - m \stackrel{\text{def}}{=} g_i \quad (1)$$

where g_i is the per capita growth rate of species i , also referred to as its *instantaneous fitness*. For reference, all model variables (and parameter values) are listed and defined in Table S1. In brief, changes in species i ’s abundance, n_i , depend on the amount of resource available, R , a constant mortality term, m , and its growth rate, μ_i . This rate is determined by the difference between the current environmental state, $T(t)$, and the environment state the species prefers (set by trait z_i , which we define as the species’ *optimum environment*). Specifically, we use a Gaussian tolerance function: $\mu_i(t, z_i) = \mu_{\max} \cdot \exp[-(T(t) - z_i)^2/\sigma^2]$, where σ^2 controls niche width. We impose environmental fluctuations by making $T(t)$ a periodic function of time, and focus on triangle and

sine waves specifically (See Appendix S1 in Supporting Information). Finally, resource availability within this closed system is $R(t) = R_{\text{tot}} - \sum_{i=1}^k n_i$, the difference between the total resource supply, R_{tot} , and the amount of resource accumulated in biomass. This simple relationship approximates chemostat dynamics when there is rapid recycling of nutrients following mortality. In our analyses, to ensure that $R(t) > 0$, we avoid selecting biomasses as initial conditions whose total would exceed R_{tot} . Each species has an R^* , the resource level below which its population declines (in this model, $R_i^*(t) = m/\mu_i(t, z_i)$). Miller & Klausmeier (2017) studied a similar model in an environment with two discrete seasons.

While the nonlinear, non-autonomous model defined by eqn 1 is not amenable to analytical solution, numerical methods can provide solutions for various periodic environmental functions, $T(t)$, and a range of interacting species. We also apply the successional state dynamics (SSD) approach in our analyses (Klausmeier 2010; Klausmeier & Litchman 2012; Kremer & Klausmeier 2013). This approach reduces the complexity of periodic systems, making it easier to obtain stable numerical solutions (Appendix S2).

Eco-evolutionary analyses

Typical ecological analyses focus on identifying the attractors of species’ population dynamics (as described by eqn 1). In a periodically forced environment, these attractors will consist of limit cycles (chaotic attractors are also theoretically possible, but we did not detect any in our model). At an attractor, the growth rate of a persisting species averaged over one period, \bar{g}_i , must equal zero:

$$\bar{g}_i = \frac{1}{\tau} \int_0^\tau g_i dt = 0 \quad (2)$$

where τ is the period. We can identify the attractors of a community of k competing species with fixed traits $\vec{z} = \{z_1, z_2, \dots, z_k\}$ by numerically solving for the set of abundances $\vec{n} = \{n_1, n_2, \dots, n_k\}$ at the beginning of a period ($t = 0$) such that eqn 2 is satisfied for each species. The corresponding community consists of species whose populations rise and fall within a period, but form cycles that are consistent across periods. Figure 1 provides examples of ecological attractors for communities consisting of two and six species.

However, ecologically stable communities are by no means guaranteed to be evolutionarily stable: species often experience directional or disruptive selection (Kingsolver *et al.* 2001; Kingsolver & Pfennig 2007). Allowing trait change within ecological models (whether driven by evolution or invasion and community assembly) alters their behaviour in significant ways (e.g., Egas *et al.* 2004; Shores *et al.* 2008; Lankau 2011; Kremer & Klausmeier 2013), such as reducing the diversity of otherwise stable communities (see Fig. S1). Given sufficient time and accessible trait variation, a community of species that is uninvasible (Fig. 2) – if one exists – represents the end result of evolution (or invasion and assembly). This evolutionarily stable community (hereafter, ESC) consists of a set of species whose population and trait dynamics are at attractors and that is globally uninvasible. We next describe

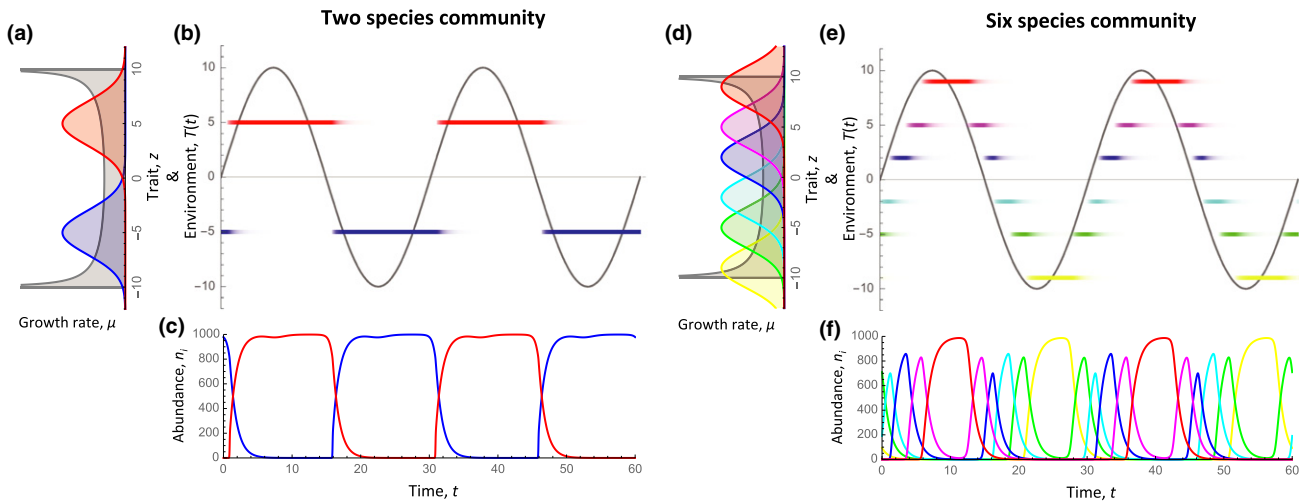


Figure 1 Examples of ecologically stable two- and six-species communities, supported by a sine wave environment. (a and d) highlight how the growth rate of each species changes with the environment (colored Gaussian curves), relative to the distribution of environmental states implied by the sine wave (gray curve). (b and e) illustrate the temporal dynamics of the environment (gray). (c and f) show species abundance patterns over time, which also appear in b&e, as bars shaded by abundance and positioned at each species' optimum environment. While the coexistence of all six species is ecologically stable, it is not evolutionarily stable. Evolution causes convergence in the traits of the species with the two lowest and two highest optimum environmental traits, z (see Fig. S1).

how to find evolutionary equilibria, determine their stability, and consequently identify ESCs.

We begin by considering the *invasion profile* created by a community of resident species. This shows graphically how the average fitness (or \bar{g}_{inv} , see eqn 2) of a rare, invading species changes across a range of possible invader traits, z_{inv} . The shape of this function around the trait values of resident species ($z_{inv} \approx z_i \in \bar{z}$) reveals whether residents experience directional, disruptive, or stabilising selection (Fig. 2). At an instant in time, the directional selection experienced by a resident species is characterised by its *instantaneous fitness gradient*

$$\left. \frac{\partial g_{inv}}{\partial z_{inv}} \right|_{z_{inv}=z_i} = \frac{2R}{\sigma^2} \cdot \mu_i \cdot (T - z_i) \quad (3)$$

This equation describes how small trait changes affect a species' instantaneous fitness. In a periodically forced environment, however, the more relevant quantity is the gradient of the time-averaged fitness \bar{g}_{inv} , which equals the time-averaged selection experienced by a resident species in eqn 3:

$$\left. \frac{\partial \bar{g}_{inv}}{\partial z_{inv}} \right|_{z_{inv}=z_i} = \left. \frac{\partial \bar{g}_{inv}}{\partial z_{inv}} \right|_{z_{inv}=z_i} = \frac{1}{\tau} \int_0^\tau \left. \frac{\partial g_{inv}}{\partial z_{inv}} \right|_{z_{inv}=z_i} dt \quad (4)$$

which provides the slope of the invasion profile in the neighbourhood of a resident species. When eqn 4 equals zero for all of the resident species i , no species experiences directional selection, representing an evolutionary equilibrium.

An evolutionary equilibrium may be evolutionarily stable or unstable depending on whether it is invulnerable or not. The quantity

$$\left. \frac{\partial^2 \bar{g}_{inv}}{\partial z_{inv}^2} \right|_{z_{inv}=z_i} \quad (5)$$

determines the shape of the fitness landscape near resident species i . If eqn 5 is less than zero, then z_i is a local maximum

of the fitness landscape indicating stabilising selection, and termed an evolutionarily stable strategy (or ESS). If eqn 5 is greater than zero, then z_i is a local minimum indicating disruptive selection (Geritz *et al.* 1998). Equation 5 is a local criterion, evaluated in the neighbourhood of resident species. However, it is possible that a species with a trait value distinct from any resident will have positive invasion fitness and be able to establish, increasing the community's diversity. Consequently, we distinguish between communities comprised of species that are only locally stable (ESSs, satisfying eqns 4 and 5), and evolutionarily stable communities (ESCs), which are globally stable, with $\bar{g}_{inv} \leq 0$ for all values of z_{inv} (Fig. 2; McGill & Brown 2007; Kremer & Klausmeier 2013). As the invasion of local communities by extant species from a regional species pool is common, we focus our analyses on identifying ESCs.

Starting with a single species, it is possible to assemble an ESC. First, we adjust the trait value of the resident species until it experiences no directional selection. If the resulting community is invulnerable, we then add another species and repeat until an ESC is achieved (Fig. 2). Finally, it is also important to consider whether an ESC is convergence stable. This occurs if selection causes small perturbations to the traits of species in the ESC to diminish (Geritz *et al.* 1998). The species comprising a convergence stable ESC represent an endpoint of evolution, diversification, and assembly in a given environment: a community that is both ecologically and evolutionarily stable.

Bifurcation analysis of ESS communities

We are interested in studying how ESC structure changes as a function of environmental variation, including different fluctuation amplitudes. We could proceed by independently assembling ESCs for each focal environment, following the

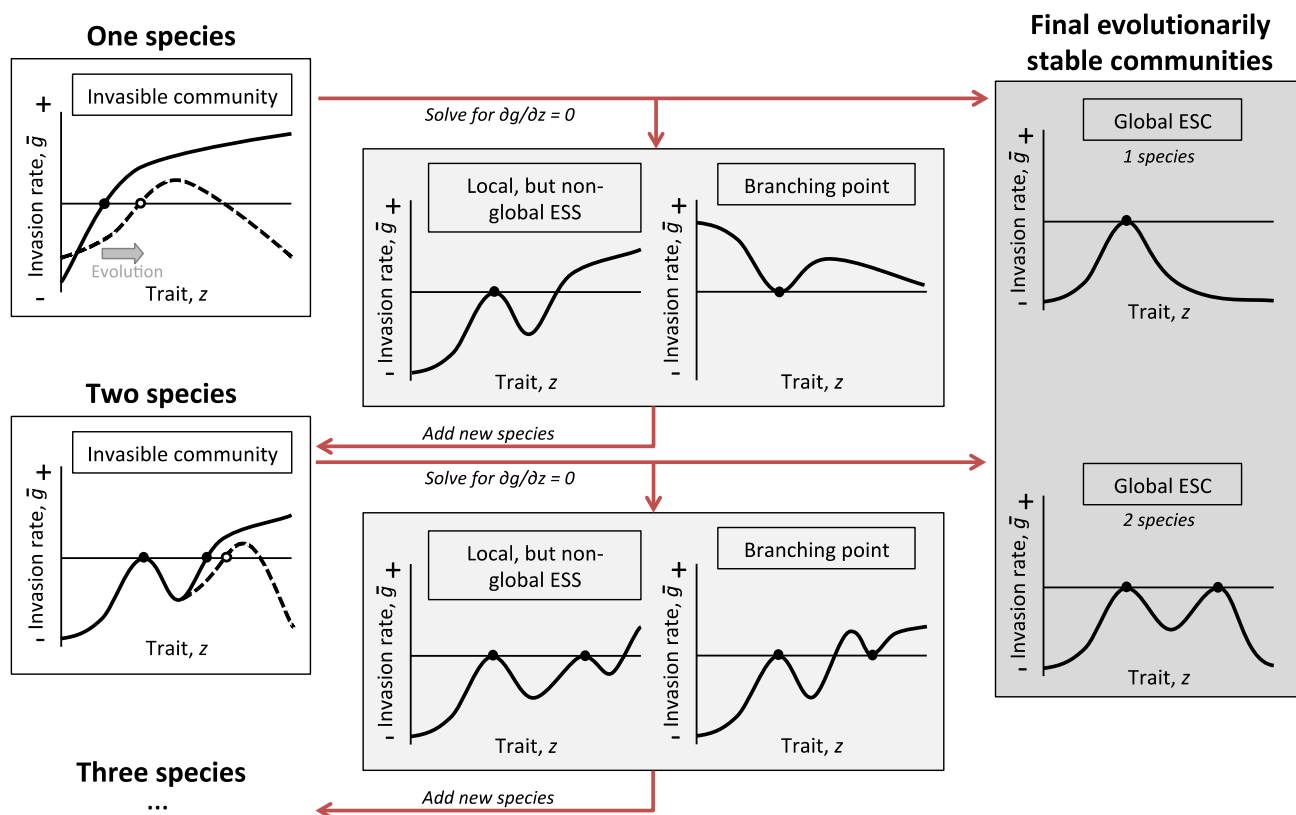


Figure 2 Evolutionarily stable communities (ESCs) can be assembled in an iterative process: (i) Start in the top left with a single, resident species whose invasion profile indicates that it experiences directional selection. (ii) Identify a new value of the resident's trait such that $\partial g/\partial z = 0$ (i.e., it is an evolutionarily stable state or ESS). If this corresponds to a global maximum of the invasion profile, a one-species ESC has been identified. Otherwise, the resident is either experiencing disruptive selection (corresponding to a branching point), or stabilising selection (corresponding to an ESS that is not globally stable, as $\bar{g}_{inv} > 0$ for some z_{inv}). In either case, the system can support additional species. (iii) Add a second resident species and solve for the pair of resident traits such that $\partial g/\partial z = 0$ for each species. (iv) Repeat this process until an n -species ESC is identified, such that $\partial g/\partial z = 0$ for all residents and $\bar{g}_{inv} > 0$ for all invader traits z_{inv} .

diversification of each community through repeated branching or non-local invasion (e.g., Fig. 2). However, this is computationally inefficient. Instead, we take advantage of the fact that small changes in environmental parameters generally lead to gradual changes in the trait values of species in an ESC (c.f. Geritz *et al.* 1999). Once we identify an ESC in one environment, we can use bifurcation continuation techniques to track changes in the composition and diversity of convergence-stable ESCs across a range of other environments (Appendix S3). Similar approaches have been used to study changes in evolutionary cases across parameter space (usually for 2–3 species: Meszéná *et al.* 1997; Geritz *et al.* 1998; Kisdi & Geritz 1999; Litchman *et al.* 2009; Kremer & Klausmeier 2013; Miller & Klausmeier 2017; but Geritz *et al.* 1999 and Jansen & Mulder 1999 reach six to eight species). We use this approach to trace out the structure of ESCs (of up to eight species).

RESULTS

In the following sections we explore how the diversity and trait distributions of ESCs change under different kinds of periodic forcing (sine vs. triangle waves), over a range of fluctuation amplitudes (T_{amp}), and under both benign (high

resource supply, R_{tot}) and harsh conditions (low R_{tot}). Just as the fundamental niche of a species consists of the range of environments where it can exist in the absence of competition, we define the *fundamental community* for a given fluctuation regime as the set of species (defined by their traits) that can survive in the absence of competitors. In a purely competitive system such as ours, the ESC will be drawn from this fundamental community. In a constant environment ($T_{amp} = 0$), classic theory tells us that no two species competing for a shared resource can coexist (Tilman 1982). However, a range of species will be able to persist individually, as long as their trait values are sufficiently similar to T_{mean} . From this fundamental community, only one species corresponds to the ESC in a constant environment: the species whose optimum environment, z , matches T_{mean} , giving it the highest possible growth rate (and, consequently, the lowest R^*). As T_{amp} increases, fluctuations will support a wider fundamental community, and multi-species ESCs arise.

Triangle wave forcing (high R_{tot})

First, we explore the structure of ESCs in fluctuating environments driven by a triangle wave. As the amplitude of environmental variation (T_{amp}) increases, we expect opportunities for

ecological coexistence to expand, and the diversity of ESCs to increase as well. This is indeed what we observe (Fig. 3). Initially, for $T_{\text{amp}} < 3.5$, there is only a single species present in the ESC; sensibly, this species has an environmental preference, z , that matches the mean of the fluctuation (i.e., $z = T_{\text{mean}} = 0$, Fig. 3a). Inspecting the invasion profile of this species at $T_{\text{amp}} = 2$, we see that it is indeed an ESC, as no other species with a different z can invade the system. Increases in T_{amp} eventually lead to a bifurcation (driven by evolutionary branching) before $T_{\text{amp}} = 4$. Within this new regime, a wide enough range of environments occurs within a period to support a two-species ESC, consisting of species with z values that are arranged symmetrically above and below the mean environmental state. Again, we can see these communities are ESCs (Fig. 3b). As we continue to increase T_{amp} , these species' traits shift further and further away from T_{mean} , until eventually a third and fourth species joins the ESC (Fig. 3c and d); these and all subsequent bifurcations that add species are driven by a loss in the global stability of ESCs and non-local invasion.

We also discovered that a given fluctuation regime does not always support a unique ESC. Instead, several convergence stable ESCs with alternative compositions can exist. For example, there are three different ESCs at $T_{\text{amp}} \approx 9.5$ (Fig. 3e). One of these is a continuation of the three species community that

exists for lower T_{amp} . However, an alternate pair of ESCs also occurs (Fig. 3e, top two panels). The trait distributions of each member of this pair are asymmetric about T_{mean} and mirror images of each other. Increasing T_{amp} drives these trait distributions towards symmetry, until the matched pair of asymmetric ESCs merge into a symmetric four-species ESC (Fig. 3d). Alternative ESCs will have different domains of attraction. As such, details of the diversification or community assembly process will determine which of the possible community structures arises in a realised community.

Figure 4a extends the bifurcation diagram of Fig. 3 to larger amplitudes of environmental forcing (T_{amp}). The width of the fundamental community steadily increases as does species diversity. The basic pattern of diversification repeats: an N -species ESC is briefly joined by a symmetric pair of asymmetric ($N + 1$)-species ESCs, which quickly merge into a single ($N + 1$)-species ESC. This persists for a range of T_{amp} , then gives way to a symmetric pair of asymmetric ($N + 2$)-species ESCs, and so on.

Sine wave forcing (high R_{tot})

The sine wave environment produces results that are similar to the triangle wave. Increasing T_{amp} expands the width of the fundamental community and a regular bifurcation pattern arises in

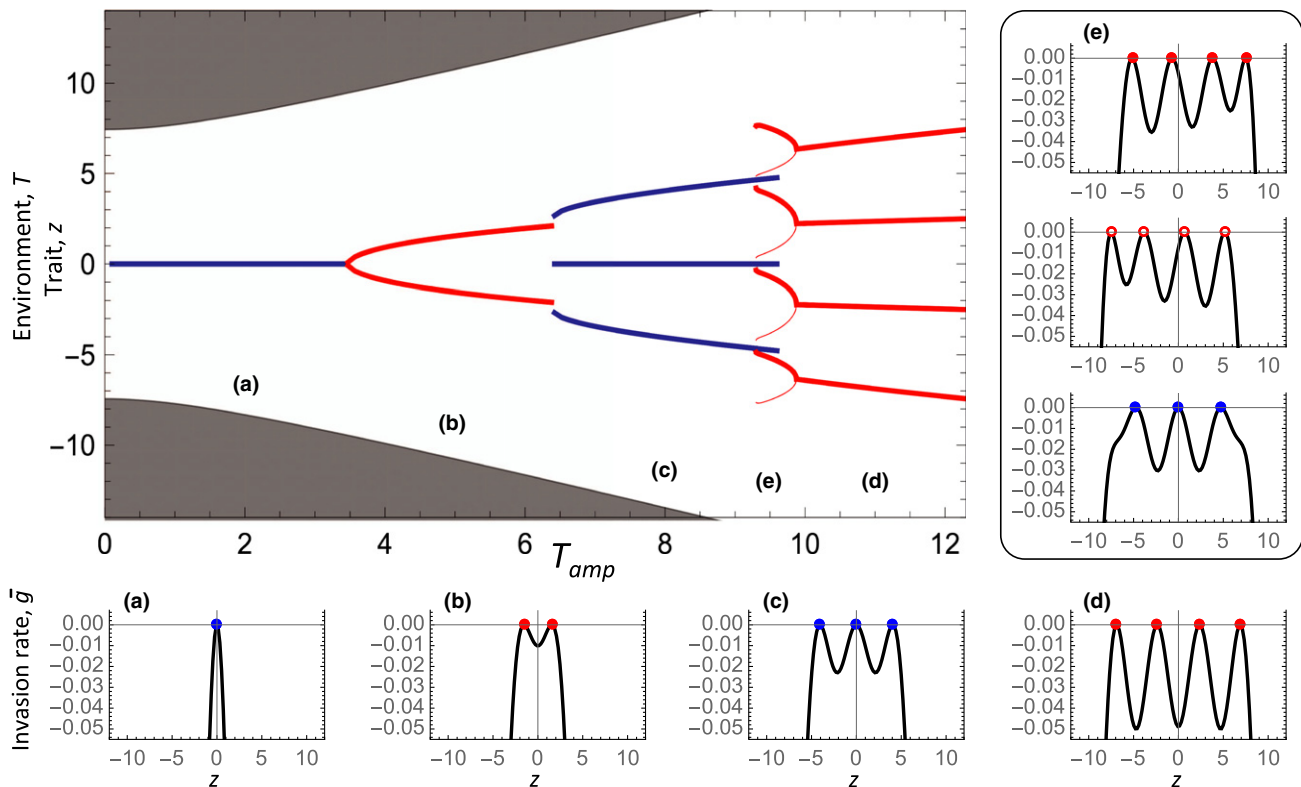


Figure 3 The number of species in evolutionarily stable communities (ESCs) increases with T_{amp} (top panel). This bifurcation diagram shows the trait values, T_{opt} , of species in these ESCs (solid lines; red and blue correspond to even and odd numbers of species, respectively). The set of trait values (z 's) that enable individual species to persist in monoculture given a particular fluctuation define the *fundamental community* at each T_{amp} . Values outside of this region are shaded in gray. Sub-panels (a–e) provide examples of the invasion profiles of increasingly diverse ESCs along the bifurcation diagram (top panel). Panels (a–d) correspond to diversity levels of 1–4 species, respectively. In each case, species' z values are arranged symmetrically around the average environmental state ($T = 0$). Asymmetric ESCs also exist; these always occur in pairs, with sets of species that are reflected around $T = 0$ (panel e). The bifurcation diagram illustrates these alternate asymmetric ESCs using heavy and thin lines (top panel; T_{amp} between $c. 9.2$ and $c. 9.8$).

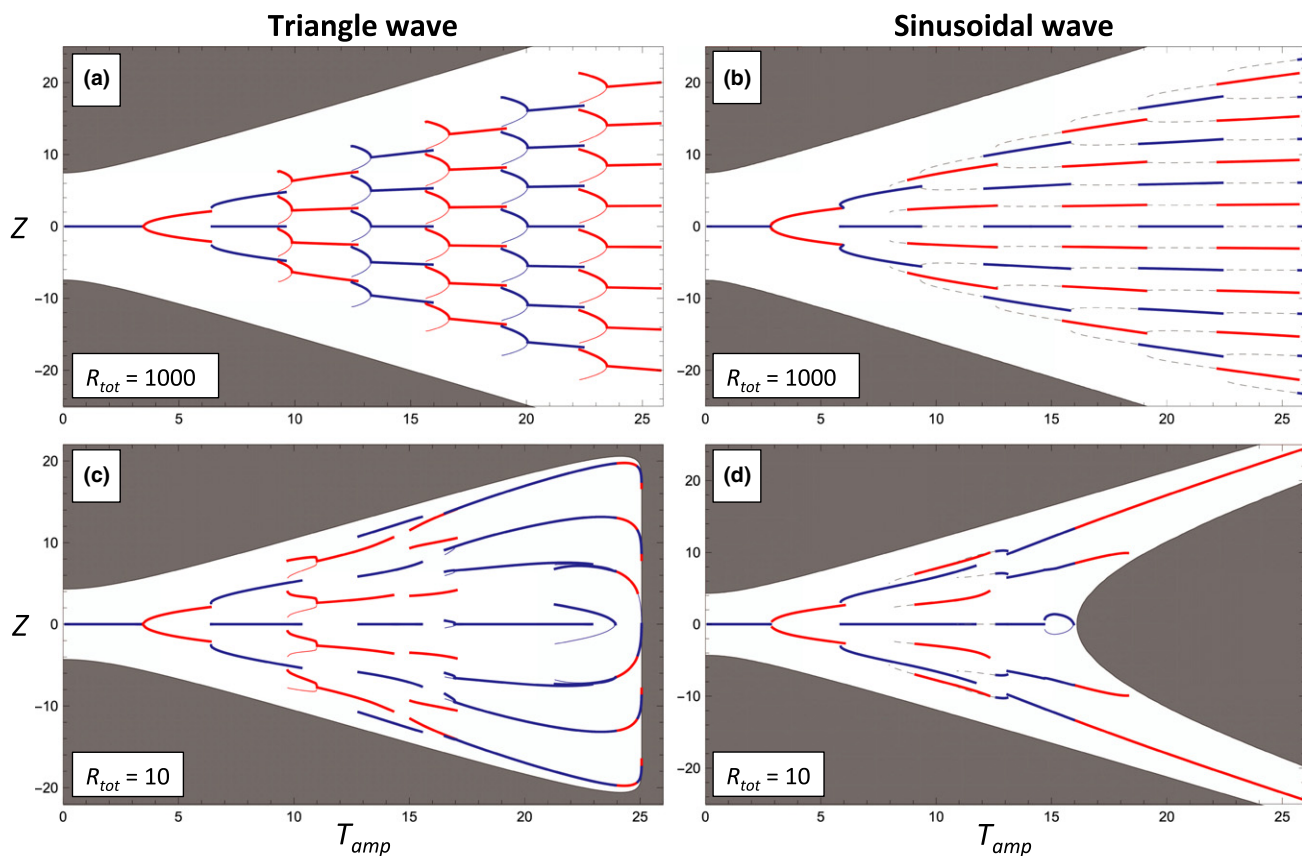


Figure 4 The structure of evolutionarily stable communities (ESCs) varies between fluctuation type (triangle vs. sine waves) and over a range of fluctuation amplitudes (T_{amp}). When resources are in plentiful supply, increasing T_{amp} widens the environmental niche, creating opportunities for species to coexist and increasing the diversity of ESCs (a and b). ESCs alternate between even (red) and odd (blue) numbers of species. Alternate, asymmetric ESCs occur during transitions between these states in the triangle wave case (a; pairs of thin and thick lines). In contrast, non-convergence stable communities connect ESCs in the sinusoidal case (b; dashed lines). Under low resource supply ($R_{tot} = 10$) it is harder for species to tolerate large fluctuations. At high T_{amp} , this results in declines in the width of the fundamental community, as well as ESC diversity (c and d). The collapse of ESC diversity occurs abruptly given triangle waves (c; around $T_{amp} = 25$). In contrast, it is much more gradual under sine waves (d). Species specialising on intermediate environments are lost first, while those specialising on extreme conditions persist even at high values of T_{amp} .

the ESCs (Fig. 4b). Diversity increases with repeated alternations between even and odd numbers of species. Alternate ESCs also occur (e.g. at $T_{amp} = 9$, both three- and four-species ESCs exist). Several subtle differences occur between the triangle and sine wave fluctuations, however (Fig. 4a and b). For example, with the triangle wave, pairs of asymmetric ESCs are implicated in transitions between even and odd communities. In contrast, with the sine wave, even and odd communities are connected by non-convergence stable ESCs (Fig. 4b).

Low resource supply (low R_{tot})

More stark differences between the triangle and sine waves are revealed at lower levels of resource supply. Suboptimal environmental conditions lower a species' growth rate, increasing its R^* . When resources are plentiful (high R_{tot}), these increases in R^* have minor consequences (because $R^* \ll R_{tot}$). However, when R_{tot} is lower species are more sensitive to environmental fluctuations: even small decreases in μ can increase R^* above R_{tot} , causing the instantaneous per capita growth rate of the population to become negative, and population size to decline. We explored how low resource supply

changes ESC structure across a range of T_{amp} for both triangle and sine waves (Fig. 4c and d). While fluctuations remain small ($T_{amp} < 8$), bifurcation patterns in ESCs are similar to the high R_{tot} case (Fig. 4a and b). However, at higher T_{amp} , fundamental community widths and ESC diversity begin to peak and decline. Interactions between resource supply and fluctuation amplitude drive these declines. Lowering R_{tot} reduces the range of conditions a species can tolerate. Additionally, the duration of suitable conditions declines as fluctuation amplitude increases (given a fixed period). Species are left with narrower temporal niches, yet must survive longer periods of mortality. This shrinks the size of the fundamental community, and restricts the potential members of ESCs.

The patterning of these declines differs dramatically between fluctuation types. ESC diversity collapses abruptly near $T_{amp} = 25$ under triangle wave forcing. However, declines are more gradual given sine waves, because low-diversity ESCs (dominated by species specialising on extreme environments) persist across higher values of T_{amp} . These distinct patterns are due to the environmental distributions each forcing function imposes. With a triangle wave, the rate of environmental change has a constant magnitude ($|dT/dt| = C$). With a sine

wave, however, the environment changes most rapidly at T_{mean} and slowly at the extremes. Consequently, triangle waves produce uniform distributions of environmental states, while sine waves create bimodal distributions (e.g., Fig. A1 in Appendix S1). This allows species with extreme trait values to remain viable in an environment with high-amplitude, sinusoidal variation. It also explains why increasing T_{amp} affects intermediate species first (e.g., above $T_{\text{amp}} \approx 16$ intermediate conditions occur so briefly that species with $z = 0$ no longer persist, even without competitors).

As the triangle wave lacks these temporal refuges, all species lose their viability nearly simultaneously, causing an abrupt collapse of the fundamental and evolutionarily stable communities. Generally, we expect that raising the maximum growth rate, lowering the mortality rate, or widening species' environmental tolerance would delay the onset of these collapses in diversity. We expect that diversity also collapses under high resource supply, but only at a much higher T_{amp} and after accumulating many more species.

Emergent patterns of limiting similarity

A wealth of research focuses on limiting similarity, the idea that there are constraints to how similar two species can be and still coexist. Because evolutionarily stable communities must also be ecologically stable (i.e., resident species must coexist), we expected to observe limiting similarity within ESCs. Our results support this idea: the trait values of species in ESCs are quite uniformly spaced along the trait axis over a wide range of T_{amp} and levels of diversity (Fig. 5). At the same time, the diversity of ESCs steadily increases with T_{amp} . New species are generally added to the community at predictable distances from current residents, but only after the

environmental niche has grown wide enough to support them. These patterns are similar in both sine and triangle waves, deviating only when diversity collapses under low nutrient supply.

Finally, the diversity level of ESCs appears to be roughly proportional to the width of the fundamental community (Fig. 5, top row), although the constant of proportionality varies slightly. This suggests that we may be able to use the width of the fundamental community (which depends on the niche requirements of an individual species, and is easy to calculate) to infer properties of even highly diverse ESCs (which are difficult to identify). This approach also captures the qualitative shape of the collapse in diversity under low R_{tot} , including the marked differences between sine and triangle waves (Fig. 6b and c). We hypothesise that these general relationships will hold for a wide range of fluctuation types (Fig. 6a). At low resource supply and high T_{amp} , environments will be unoccupied, independent of fluctuation type. At high resource supply, moving from constant to variable environments by increasing T_{amp} will produce steady increases in the diversity of ESCs. Between these extremes of resource supply, diversity will first increase, then collapse with rising T_{amp} ; the properties of this collapse will depend on details of the environmental forcing regime.

DISCUSSION

We explored evolution's effects on communities of species that coexist in fluctuating environments due to temporal storage effects (Fig. 1). Across a wide range of fluctuations, evolutionarily stable communities (ESCs) exhibit properties broadly consistent with ecological theory. This is partly unsurprising: as a special subset of possible ecologically stable communities,

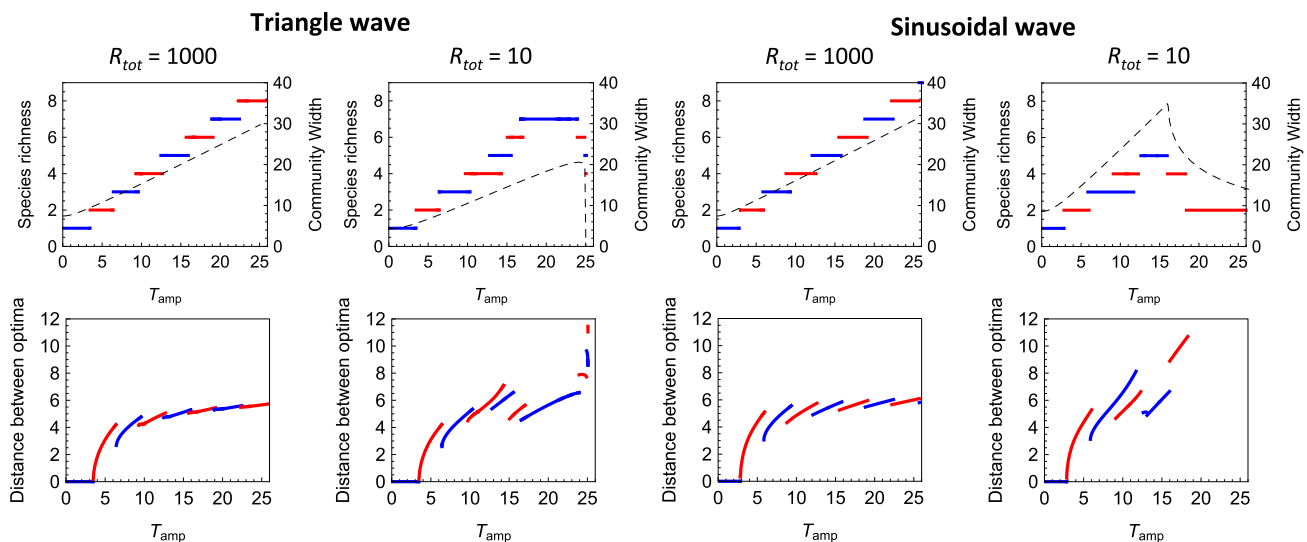


Figure 5 As revealed in the bifurcation diagrams, changes in the richness of evolutionarily stable communities (ESCs) with T_{amp} are roughly proportional to changes in the width of the fundamental community (top row, dashed lines). At the same time, the spacing between the T_{opt} values of adjacent species is highly consistent (bottom row), especially given high resource supply ($R_{\text{tot}} = 1000$) and T_{amp} . At lower values of R_{tot} , we do observe larger spacing between species, driven in the sinusoidal case by the loss of species specialising on intermediate environmental states. Overall, these patterns suggest that the diversity of ecologically and evolutionarily stable communities supported by environmental fluctuations can largely be understood by assessing the size of the environmental niche and the limiting similarity of species.

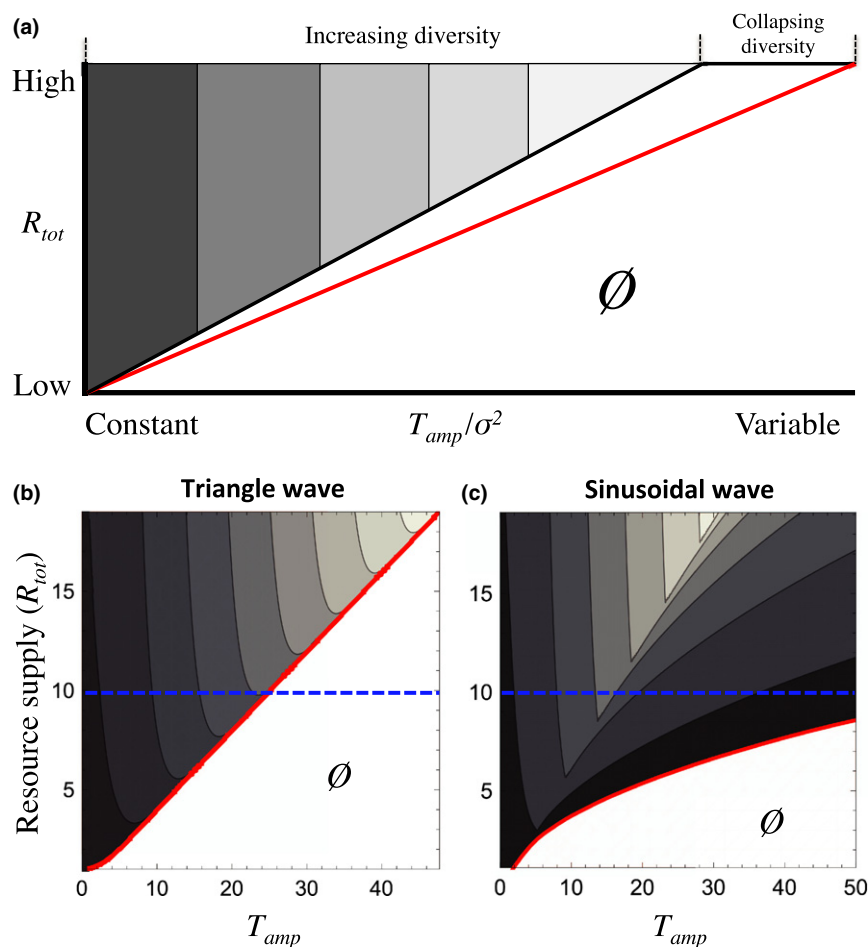


Figure 6 The amplitude of fluctuations (relative to species' niche widths) and the magnitude of resource supply together define the dimensions of the community niche, constraining diversity levels of communities (shown conceptually in (a); above the region where no species can grow, labelled ϕ , lighter colors indicate increasing diversity). These relationships can be examined for specific fluctuations, including triangle (b) and sinusoidal (c) waves. These both show similar patterns of increases in community niche width at high R_{tot} , but differences emerge in the regions where diversity begins to collapse at high T_{amp} . Note that slices across this diagram (blue dashed lines) correspond to the $R_{tot} = 10$ cases highlighted in Fig. 4 (c and d) and Fig. 5 (2nd and 4th column).

ESCs should share many of their properties. This includes pervasive evidence of limiting similarity in the trait structure of ESCs (Figs 4 and 5). Models like ours, combining a single resource and external periodic forcing, are effectively equivalent to models of competition for a continuous, one-dimensional spectrum of resources (Barabás *et al.* 2012). In this sense, they are conceptually similar to early investigations of limiting similarity in one-dimensional Lotka-Volterra models based on resource spectra (MacArthur & Levins 1967; May & MacArthur 1972; Roughgarden 1974). Although explicitly connecting these paradigms remains challenging, new approaches clarify how limiting similarity emerges within both kinds of models (Meszena *et al.* 2006; Barabás *et al.* 2012). In brief, robust coexistence depends not on how resource use affects competition (MacArthur & Levins 1967; Roughgarden 1974), but on the combination of species' sensitivity to and impact on shared resources. Calculating these terms for a model similar to ours, Barabás *et al.* (2012) illustrate that coexistence depends on the temporal storage effect, and requires that species have divergent patterns of resource sensitivity and impact over each fluctuation.

Limiting similarity enables us to propose a rule-of-thumb for predicting ESC diversity: it will be proportional to the width of the fundamental community divided by the characteristic spacing between species (Figs 5 and 6). Exact proportionalities will vary, but should be tied to the niche width of species (σ^2), which governs feasible similarity between species in ESCs. This approach works across diverse fluctuations and resource levels, and suggests that community diversity can be estimated without the challenges of identifying ESCs. Additionally, community structure may be more predictable in light of evolution than ecological theory suggests. While identical environments may support many different ecologically stable communities, as selection pushes them towards an ESC their trait distributions generally converge (e.g., Fig. S1; however see below). This also occurs in Lotka-Volterra models (Barabás & D'Andrea 2016), although evolution in multiple dimensions and among generalists/specialists may affect the regularity of trait distributions.

Our eco-evolutionary analyses also revealed properties that are not obvious from strictly ecological analyses. For example, we discovered examples of alternative ESCs, implying

that identical environments can support communities with different trait distributions (Fig. 4). These competing ESCs are analogous to the alternative stable states widely explored in ecology (Beisner *et al.* 2003). Although alternative ESCs have been found before (e.g., Kisdi & Geritz 1999), their existence is not widely appreciated. The alternate ESCs we detected are locally convergence stable, but we currently lack estimates of sizes of their basins of attraction. Ultimately, the existence of alternate ESCs implies that historical contingencies due to chance events during adaptation, diversification, and assembly will significantly affect the composition of communities. This may hamper efforts to deterministically predict community trait distributions in nature, where multiple community configurations are possible.

We have also shown that subtle properties of periodic fluctuations can have important consequences: triangle and sine waves with identical means and amplitudes can support very different communities (e.g., Fig. 4c and d). This occurs because each environmental function imposes a particular distribution of environmental states on a model. Sine waves are often employed because of their mathematical convenience and reasonable description of variation in factors like temperature and solar radiation. The fact that they also imply a bimodal environmental distribution is underappreciated. Appreciating the consequences of such distributions is critical to accurately assembling and interpreting periodic models. For example, climate change ecology (which is only beginning to disentangle the effects of altered means and amplitudes of variation, Thompson *et al.* 2013) may still not capture all of the important dimensions of environmental change.

There are several limitations to our theoretical work, which we group loosely into environmental, physiological, and evolutionary categories. Regarding the environment, we could calculate exact invasion rates despite temporal variation by focusing on deterministic, periodic fluctuations. However, stochastic environmental variation requires taking averages over long time intervals, creating computational challenges. Stochastic variation is common, can support coexistence (Scranton & Vasseur 2016), and can enhance extinction risks in auto-correlated environments. Another consideration is our use of the SSD approximation, which assumes that environmental change is slow relative to growth, death, and competitive exclusion rates (Klausmeier 2010; Klausmeier & Litchman 2012; Kremer & Klausmeier 2013; Miller & Klausmeier 2017). This is a reasonable assertion for many systems (especially microbes and insects), although not universally true. Our SSD-based results are qualitatively similar to ESC bifurcations arising from a similar model with large, but finite period (not shown). Based on related studies, high frequency, rapid fluctuations should diminish the scope for coexistence (Kremer & Klausmeier 2013; Miller & Klausmeier 2017). In contrast, high amplitude and/or low frequency fluctuations, would drive species to become rare under bad conditions, risking stochastic extinction (Miller & Klausmeier 2017).

Environmental conditions can affect many aspects of species' physiology in complex ways; however, our model employed a simplistic Gaussian relationship between the environment and maximum growth rates. Using symmetric environmental tolerance and fluctuation functions led us to expect

(and observe) ESCs that are symmetric around the mean environmental state (T_{mean}). An unusual exception did arise: symmetry breaking led to the creation of pairs of ESCs that, individually, were asymmetric around T_{mean} . However, members of these pairs were reflections around T_{mean} of each other, maintaining symmetry at a higher level (as with pitchfork bifurcations, Strogatz 2000; Kisdi & Geritz 1999 found a similar pattern). In reality, many tolerance functions are asymmetric (such as the temperature-dependence of ectotherm growth), which has important ecological consequences in variable environments (e.g., nonlinear averaging, Vasseur *et al.* 2014). Expansions of our work could explore the implications of asymmetric tolerance functions, or how the evolution of alternative strategies like dormancy affect our results.

Models of evolution also require simplifying assumptions. For example, we only considered evolution of species' environmental optimum (z). However, adaptation often affects multiple traits, including the range of conditions a species tolerates (e.g., σ^2). Phytoplankton, for example, display significant variation in their optimum temperatures and niche widths across environments (Thomas *et al.* 2016). Trade-offs between specialists and generalists are known to affect coexistence patterns in variable environments (Abrams 2006). Evolution broadened the niches of species competing for a continuous range of resources, when the cost of being a generalist was low (Ackermann & Doebeli 2004). Allowing multiple traits to evolve would affect the structure and regularity of ESCs in our model, but several patterns should remain: (1) the diversity of ESCs will remain less than or equal to predictions of ecological coexistence (c.f., Egas *et al.* 2004), and (2) species that are too similar will not coexist or appear in ESCs. While extra trait dimensions allow species to differ in more ways, sufficient similarity in even a single dimension can reduce the robustness and stability of coexistence (Meszena *et al.* 2006). Finally, regarding the mechanics of adaptation, our analyses assume that rates of evolution are slow relative to rates of environmental change. However, when evolution is sufficiently rapid, it can hamper or prevent coexistence in variable environments (Kremer & Klausmeier 2013).

This study contributes to the ongoing eco-evolutionary synthesis by re-evaluating ecological theory in light of trait evolution. For the mechanism we studied (coexistence via a temporal storage effect), adopting an eco-evolutionary perspective enriched our fundamental understanding of ecological theory, rather than contradicting it, while offering several new insights. These include demonstrating that: (1) evolution does not preclude coexistence dependent on temporal variation, (2) evolutionarily stable communities (ESCs) reveal widespread patterns of limiting similarity, and (3) alternative ESCs exist, complicating the interpretation of community trait distributions. Much work remains, however, if we are to establish general conclusions about when and how evolution affects long-standing ecological principles. This includes studying other ecological models and their assumptions, using multiple evolutionary approaches. This search for generality is critical, as we are ever more aware that evolution acts on ecologically relevant timescales. A rigorous, eco-evolutionary theoretical framework is invaluable for understanding how communities, structured by historical patterns of

variation, will react to widespread anthropogenic changes to the environment.

ACKNOWLEDGEMENTS

This is W.K. Kellogg Biological Station contribution #2000. CTK was supported by an NSF GRFP and NSF PRFB Fellowship 1402074; CAK acknowledges support from the DARPA BRICS program, the Simons Foundation (grant #343149), and NSF grants DEB-0845825 and OCE-1638958.

AUTHORSHIP

CTK & CAK conceived of, developed and analysed the models, CTK drafted the manuscript, and both authors contributed substantially to revisions.

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Editor, James Grover

Manuscript received 19 April 2017

First decision made 30 May 2017

Manuscript accepted 19 June 2017