

An Eco-evolutionary System with Naturally Bounded Traits

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Received: date / Accepted: date

Abstract We consider eco-evolutionary processes that include natural bounds on adaptive trait distributions. We implement ecological axioms, that a population grows if it is replete with resources, and doesn't grow if it has none. These axioms produce natural bounds on the trait means that suggest that the assumption of gamma-distributed traits, where the trait variance is a function of the trait mean, is more appropriate than the usual assumption of normally distributed traits, where the trait variance is independent of the trait mean.

We use a Lotka-Volterra model to simulate two plant populations, whose trait means evolve according to an evolutionary model, to simulate populations adapting during invasions. The results of our model simulations using gamma-distributed traits suggest that adapting populations may endure bottlenecks by increasing their fitness and recovering from near extinction to stably coexist. The inclusion of eco-evolutionary processes into ecosystem models generates K^* theory which predicts the long term states of populations that make it through evolutionary bottlenecks. Otherwise, the final states of populations that do not make it through bottlenecks are predicted by the non-evolutionary R^* theory.

Keywords eco-evolutionary modelling · K^* theory · gamma-distribution · trait variance · fitness · coexistence · competition · invasion

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1 Introduction

The seminal papers by Lande [24,25] that are often cited as a basis for eco-evolutionary approaches [2,17,9] assumed that traits were normally distributed in populations, and consequently that the trait variance was independent of the trait mean. Some authors, for example [3,4,6,7,9], have considered models in which the genetic variation depends on the mean trait value, and applied arbitrary upper and lower bounds on trait distributions. Others have considered bounded tradeoffs in fluctuating environments [23], or have evolved the moments of the distributions separately [30].

A key difference of the approach used here is that an ecosystem modelling framework based on simple ecological axioms provides natural bounds on trait distributions. These natural conditions may impose lower or upper bounds, or both, depending on the population and its trophic interactions.

Our approach to modelling ecosystems is based on the simple 'ecological axiom' that the growth of each population in an ecosystem model depends on an explicitly modelled resource, so that when maximal resource is available the population increases, and when no resource is available the population reduces [10]. These requirements naturally place bounds on the values that parameters representing traits can take - in some cases the sign of a parameter is constrained, and in others it imposes relationships (inequalities or bounds) between parameter values. These provide mathematical limits to the values that parameters can take that biological, physiological and ecological processes must respect. While in our simple models these bounds are respected mathematically, in practice parameter values are likely to be constrained from approaching their bounds too closely by physiological, ecological or environmental processes.

The natural bounds on parameters inherent in this resource-limited approach suggests that the common assumption that traits are normally distributed needs to be revised. While the initial traits that represent the interaction between an invading and invaded population might be normally distributed, this framework suggests that natural selection will often operate to impose a bounded distribution on trait values. Further, Fisher's fundamental theorem of natural selection [14,19] suggests that in order to constrain natural selection the variance of a bounded trait must approach zero as the trait value approaches its bound. In this manuscript we examine eco-evolutionary processes in a simple model that represents a resident and an invading population in which the traits have natural bounds and are represented by gamma-distributions in accordance with Fisher's constraint.

The mechanisms that allow competing populations to coexist have been a central theme in ecology almost from its inception in its modern form. Gause's Principle of Competitive Exclusion [18] articulates an ecological view of coexistence of competitors that appears inconsistent with the diversity maintained in plankton [20]. Eco-evolutionary approaches have contributed some interesting modifications to traditional ecological modelling approaches in which the traits of populations are fixed [1,22,35,40].

A population that extends its range needs to adapt to its new habitat [5, 21, 34], including to populations that it may never have encountered previously. The success of an invading population may depend more heavily on its ability to respond to natural selection driven by interactions with incumbent populations than on physiological tolerance or plasticity [26]. Further, some evidence suggests that continuing adaptation in established ecosystems may be driven more by relative changes in fitness between populations rather than by variations in relative fitness driven by changes in the environment [15].

Population invasions with evolutionary change produce modifications to the genetic structure of the invading population as a consequence of a combination of evolutionary forces [34, 12]. How a population that invades an incumbent population, that it has never previously encountered, interacts with that population and *vice versa*, is a function of traits that have been developed in another environment. Trait variance is central to natural selection [19]. Invading populations that are ill-suited to competing with an incumbent population can undergo selection by eliminating the least well suited fraction. Such founder events and associated genetic bottlenecks produce adaptive evolution that can reduce genetic variation in invading populations [11]. The bottlenecks remove less fit individuals from the population. Then modification to the average traits of the population can alter the outcomes of population invasions as trait variance facilitates selection of a population that can more effectively compete in the new environment.

Here we derive a simple Lotka-Volterra model [29, 42] in a resource-limited framework with eco-evolutionary processes that operate on naturally bounded, γ -distributed traits. We use the model to investigate how populations react to invasions, where both invading and incumbent populations encounter the other population for the first time. We consider scenarios in which a population invades another population in an environment to which they are both adapted, but as these populations have never previously met, we assume that the traits that determine how the populations interact are the result of random processes. Consequently these traits start as approximately normally distributed with substantial variance, as their means are remote from the bounds. However, as eco-evolutionary processes execute, average trait values may move towards their bounds. If they do the initial normal trait distributions become constrained by the bound, and become more asymmetrically distributed as the bound is approached and the variance of the trait reduces.

A key result is that resource-limited eco-evolutionary models predict quite different longer-term outcomes (here labelled K^* theory) to non-eco-evolutionary models of invasion such as R^* theory [37–39]. Our results identify the important role of evolutionary bottlenecks that determine whether R^* or K^* theory predicts the long-term outcome of invasions, and provide hypotheses that are testable by experiment. Our post-invasion populations stably coexist and are optimally-adapted, in contrast to the oscillating solutions of Merico et al. [30], Vasseur et al. [40] and Kremer and Klausmeier [23].

1.1 Resource-limited Modelling

Here we outline the framework that imposes ecological bounds on the trait values in the model - a detailed exposition of the framework is provided in [10]. The resource-limited ecosystem modelling approach is implemented by the following process:

- We identify a limiting resource, most commonly a limiting nutrient, that we use as a common currency to measure all populations. We sum the limiting nutrient cycling in both the living populations and the non-living nutrient pool, and scale all the (living and nonliving) variables by this total;
- Each population grows (dies) according to the constraints of the other populations and the environment, represented here in its simplest form by the non-living nutrient pool, independently of how we measure the populations and the scale of the ecosystem;
- The mass of limiting nutrient is conserved as it flows through the food web; we assume that immigration equals emigration and nutrient influx equals nutrient efflux (most delineated ecosystems recycle at least 90% of their limiting nutrient [28,41]);
- The growth of every population is explicitly limited by the resources available to it - when its resources are maximal the population increases, when its resources are zero, the population decreases;
- Negative nutrient concentrations are not permitted, that is, when any living population or the nutrient in the abiotic resource pool are zero, these variables can only increase.

The first three principles ensure the set-up of model ecosystem equations that are internally consistent. The fourth provides checks to ensure that the populations have sensible properties, that they are viable but not immortal. The final principle ensures that there is no capacity for living populations to "borrow" resources from the environment, and reflects that the total amount of limiting nutrient is finite. Note that the fifth condition, that precludes negative values, does not imply that the system may take negative values and that we over-ride these, as is apparently done in some complex ecological simulation model examples. The condition in our example arises from the structure of the equations and is a property of the system.

2 A Simple Eco-evolutionary Model of Invasion

2.1 The Ecosystem Model

We consider a model of two plant populations, one of which x_1 is incumbent in an established ecosystem, which the other x_2 seeks to invade. For simplicity, we assume that both populations depend on the same resource. We measure the living populations and abiotic resource pool R in a common currency, the amount of limiting resource that they have sequestered. The

approximation that the total amount of resource cycling in the food web is fixed and finite allows us to scale the total amount of resource in the system to be one and represent each population as a fraction of the total resource. For two competing populations, this defines a simple (closed) ecospace $E = \{x_1, x_2; 0 \leq x_1, x_2, R \leq 1; x_1 + x_2 + R = 1\}$ in which all of the ecologically valid population behaviour occurs.

A simple Lotka-Volterra model in a resource-limited framework captures the interactions and dynamics of the living populations [6, 40]. The development of these models is explained in detail in [10]; we just provide an outline here sufficient to demonstrate that this ecologically-based framework produces natural bounds on trait values. The populations interact through indirect resource exploitation competition for R , and direct interference competition represented by \hat{a}_{12} and \hat{a}_{21} :

$$\begin{aligned}
 \frac{dx_1}{dt} &= x_1 f_1(x_1, x_2, R), \\
 &= x_1(r_1 R - \hat{a}_{11}x_1 - \hat{a}_{12}x_2), \\
 &= x_1(r_1[1 - x_1 - x_2] - \hat{a}_{11}x_1 - \hat{a}_{12}x_2), \\
 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2), \\
 \frac{dx_2}{dt} &= x_2 f_2(x_1, x_2, R), \\
 &= x_2(r_2 R - \hat{a}_{21}x_1 - \hat{a}_{22}x_2), \\
 &= x_2(r_2[1 - x_1 - x_2] - \hat{a}_{21}x_1 - \hat{a}_{22}x_2), \\
 &= x_2(r_2 - a_{21}x_1 - a_{22}x_2).
 \end{aligned} \tag{1}$$

We substitute the relation $R = 1 - x_1 - x_2$, implicit in the ecospace, to eliminate explicit reference to R in the equations and define new coefficients $a_{11} = r_1 + \hat{a}_{11}$, $a_{12} = r_1 + \hat{a}_{12}$, $a_{21} = r_2 + \hat{a}_{21}$, and $a_{22} = r_2 + \hat{a}_{22}$. These coefficients explicitly include the indirect competition for resources (the r_i component of the a_{ij}), both within (a_{11} and a_{22}) and between (a_{12} and a_{21}) populations, and the direct interaction competition (\hat{a}_{12} and \hat{a}_{21}) between populations. Both populations depend on R to be able to grow, and as $R = 1 - x_1 - x_2$ we note that the maximum resource for both populations $R = 1$ is available at the origin of the ecospace $\{0, 0\}$ and the minimum resource for both populations occurs on the boundary of the ecospace where $x_1 + x_2 = 1$.

We implement the fourth of our simple ecological axioms above, that if a population x_i does not have any resource available (i.e. $R = 0$) it reduces (i.e. $f_i|_{R=0} < 0$), and that when the world is full of its resource (i.e. $R = 1$) the population increases (i.e. $f_i|_{R=1} > 0$). Applying these principles to (1) and evaluating f_1 and f_2 at the respective resource extremes $R = 0$ and $R = 1$, the vertices of the triangular ecospace E bounded by $x_1 = 0$, $x_2 = 0$ and $x_1 + x_2 = 1 \Rightarrow R = 0$ provides naturally arising constraints on the values that the parameters can take:

$$0 < r_1 < a_{11}, a_{12}, \quad \text{and} \quad 0 < r_2 < a_{21}, a_{22}. \tag{2}$$

Populations that do not comply with these constraints are either immortal if $f_i|_{R_i=0} \geq 0$, or unviable if $f_i|_{R_i=1} \leq 0$. The parameters that represent the average values of the "arms-race" traits that represent how the resident and invading populations interact, a_{12} and a_{21} , are naturally bounded on the left by the minimum trait values r_1 and r_2 respectively. Recalling that these parameters may be decomposed into indirect competition components r_1 and r_2 , and direct competition components \hat{a}_{12} and \hat{a}_{21} , we see that each population is potentially able to reduce its direct competition component to zero.

2.2 Evolution of Traits with Bounded Distributions

We follow the derivation of Lande [24] (see Appendix) and consider the evolution of the average value of a heritable phenotypic character \bar{z} in response to selection. When the phenotype has a γ -distribution the average trait value is given by $\bar{z}(t) = \alpha/\beta$ where α is a shape parameter and β is a rate parameter that together determine the distribution. The general form of the γ -distribution assumes a lower bound of zero, but parameters in resource-limited models may have lower bounds other than zero (equation (2)). We derive an equation describing how the average value of a trait that is γ -distributed changes over time in the Appendix. Allowing for a non-zero lower bound z_L for \bar{z} and, assuming continuous trait variation, we get:

$$\frac{d\bar{z}}{dt} = h^2 \left(\frac{\bar{z}(t) - z_L}{\beta} \right) \frac{\partial \ln \bar{W}}{\partial \bar{z}(t)}, \quad (3)$$

where h^2 is the realised additive heritability of the character and \bar{W} is the average fitness of the population. The consequence of having a bounded trait is that the variance becomes a function of the average trait value (specifically $\sigma^2 = (\bar{z} - z_L)/\beta$) and ensures that phenotypes with bounded distributions are not able to exceed their bounds during computer simulations. Together, the heritability of the trait (h^2), the variance of the trait values $((\bar{z} - z_L)/\beta)$, and the magnitude of the sensitivity of the average population fitness to the average trait value ($\partial \ln \bar{W} / \partial \bar{z}$), determine how quickly the average trait value changes. The trait mean and variance are always positive, so the sign of the sensitivity determines whether the trait value increases or decreases.

2.3 Average Population Fitness

When considering heuristic models (in which much detail has been abstracted and subsumed into generic descriptions of processes) it is appropriate to use simple heuristic representations of average population fitness [2, 16, 8, 32]. Many of these approaches define the average population fitness to be part or all of the population growth function f_i . Simply defining the fitness function $\bar{W}_i = f_i$, as is used in [3], is not appropriate for an eco-evolutionary model as the logarithm of the population fitnesses would be undefined at the ecological coexistence

steady state (where $f_i = 0$ for all i), so here we use the exponential form [40, 31]:

$$\ln \bar{W}_i = f_i \Rightarrow \bar{W}_i = e^{f_i}. \quad (4)$$

This fitness function only has optima at the bounds of its range, so ecological and fitness equilibria cannot coincide while the trait variance is non-zero - the evolutionary component of the model will continually exert pressure to move the ecological equilibrium to a higher fitness evolutionary state as long as there remains some variance in the population.

2.4 The Resource-limited Eco-evolutionary Model

We define the eco-evolutionary model by using the fitness function (4) in equations (3) for the trait means a_{12} and a_{21} applied to the LVCN ecosystem model (1) of two interacting populations x_1 and x_2 :

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - a_{11}x_1 - a_{12}x_2), \\ \frac{dx_2}{dt} &= x_2(r_2 - a_{21}x_1 - a_{22}x_2), \\ \frac{da_{12}}{dt} &= -h_1^2 \left(\frac{a_{12} - r_1}{\beta_1} \right) x_2, \\ \frac{da_{21}}{dt} &= -h_2^2 \left(\frac{a_{21} - r_2}{\beta_2} \right) x_1. \end{aligned} \quad (5)$$

Here $(a_{12} - r_1)/\beta_1$ and $(a_{21} - r_2)/\beta_2$ are the variances of the parameter distributions, with means a_{12} and a_{21} , that describe each trait. The sensitivities of the average population fitnesses to the average population traits are simply $\partial f_1/\partial a_{12} = -x_2$ and $\partial f_2/\partial a_{21} = -x_1$. We have assumed the intra-population competition parameters do not change, although in more complicated scenarios they may be allowed to change [43].

2.5 Eco-evolutionary Coupling

Bilateral coupling lies at the heart of the eco-evolutionary approach [36]; to be a valid eco-evolutionary model the population dynamics influence the phenotype evolution and *vice versa*. The blocks of the Jacobian, or community, matrix evaluated at the eco-evolutionary equilibrium point $\{x_1^*, x_2^*, a_{12}^*, a_{21}^*\}$ reveal that this is the case for the model (5):

$$J = \begin{bmatrix} -a_{11}x_1^* & -a_{12}^*x_1^* & -x_1^*x_2^* & 0 \\ -a_{21}^*x_2^* & -a_{22}x_2^* & 0 & -x_1^*x_2^* \\ 0 & -h_1^2 \left(\frac{a_{12}^* - r_1}{\beta_1} \right) & -h_1^2 \left(\frac{1}{\beta_1} \right) x_2^* & 0 \\ -h_2^2 \left(\frac{a_{21}^* - r_2}{\beta_2} \right) & 0 & 0 & -h_2^2 \left(\frac{1}{\beta_2} \right) x_1^* \end{bmatrix}. \quad (6)$$

The terms in the upper left block of J describe how the populations influence each other, and similarly the block in the lower right of J describes how changes in the arms-race parameters affect each other. The terms in the upper right quadrant of J represent the feedback of the changes in the traits on the dynamics of the population, and the terms in the bottom left quadrant of J represent the feedback of the population dynamics on the evolution of the phenotypes. In terms of these criteria, equations (5) represent a *bona fide* eco-evolutionary system.

2.6 Predicting Post-Invasion Populations

The eco-evolutionary model (5) suggests that each population will seek to minimise the detrimental effect of the competing population on it, by reducing the interaction parameters of each population, so $a_{12} \rightarrow r_1$ and $a_{21} \rightarrow r_2$ as $t \rightarrow \infty$. This provides an insight into the post-invasion carrying capacity of the environment for the two populations. The equilibrium populations for the two coexisting populations in (1) are:

$$\left\{ x_1^* = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, x_2^* = \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}} \right\}. \quad (7)$$

Prior to the invasion x_1 exists as a stable population at its equilibrium value $r_1/a_{11} = K_1$, which we conventionally call its environmental carrying capacity prior to invasion. Similarly, we might estimate a carrying capacity for the invading population x_2 based on its equilibrium population in its natural environment with no competitors $r_2/a_{22} = K_2$. The adaptation processes that occur during the invasion have the limits $\lim_{t \rightarrow \infty} a_{12} = r_1$ and $\lim_{t \rightarrow \infty} a_{21} = r_2$. Substituting these limits into x_1^* in (7) gives the post-invasion equilibrium population x_1^{**} in terms of the pre-invasion carrying capacities (and analogously for x_2^{**}):

$$x_1^{**} = K_1 \left(\frac{1 - K_2}{1 - K_1 K_2} \right) = K_1^*, \text{ and } x_2^{**} = K_2 \left(\frac{1 - K_1}{1 - K_1 K_2} \right) = K_2^*. \quad (8)$$

Equation (8), which we call K^* theory, predicts the sizes of the coexisting populations after the completion of the eco-evolutionary processes that move the average trait values to their bounds. This provides an alternative to Tilman's R^* theory [37–39] that predicts the outcome of some competition scenarios when no trait adaptation occurs. Specifically, R^* theory predicts that x_1 would win scenario (b) and x_2 would win scenario (c) in Figure 1. Alternatively, K^* theory predicts the long-term population sizes in all scenarios where the populations survive the eco-evolutionary bottleneck (see below).

Table 1 Parameter values used for the four scenarios in Fig. 1. These values are fixed in each eco-evolutionary simulation except for a_{12} and a_{21} , where the table values are the initial values.

SCENARIO	r_1	a_{11}	a_{12}	r_2	a_{21}	a_{22}	β_1	β_2
Competitive exclusion	1	1.75	2.00	1.25	4.00	2.00	0.50	1.40
R^* theory - x_1 wins	1	1.67	2.00	1.25	3.50	3.00	0.50	1.00
R^* theory - x_2 wins	1	2.50	2.75	1.50	2.00	2.00	0.50	0.14
Coexistence - x_1 dominates	1	2.50	1.50	1.25	3.00	2.75	0.50	1.75

3 Simulations

Four scenarios that represent attempts by a population x_2 to invade an ecosystem with an incumbent population x_1 are considered. We classify these based on the predicted outcomes according to non-eco-evolutionary theory:

- (a) Competitive exclusion: either the incumbent population x_1 or the invading population x_2 could survive with the outcome being determined by the initial population sizes;
- (b) R^* theory predicting that the incumbent population x_1 will survive and the invader x_2 will fail to invade;
- (c) R^* theory predicting that the invading population x_2 will successfully establish in the ecosystem, replacing the incumbent population x_1 , which will go extinct;
- (d) Competitive coexistence predicting that x_2 will successfully invade but the incumbent population x_1 will survive and both populations will coexist.

The ecospace diagrams for the four non-eco-evolutionary invasion scenarios are shown in Fig. 1. These diagrams show the outcomes of the invasion attempts if no adaptive evolution occurs. The vector fields in Fig. 1(a and b) predict that the invader x_2 will quickly go extinct and x_1 will survive unaffected, Fig. 1(c) predicts that the x_2 population will invade and rapidly increase and drive x_1 to extinction, while Fig. 1(d) predicts that x_2 will invade, but remain at very low populations levels and coexist with an x_1 population that is barely affected by the invasion.

Heritability in the simulations is fixed at $h_1 = 0.2 = h_2$ for all simulations as is the variance parameter β_1 for the x_1 population. The variance parameter β_2 of the x_2 population is adjusted for each simulation to ensure that the variances of both populations are the same at the start of the simulation. The parameter sets used for the scenarios depicted in Fig. 1 are provided in Table 1.

The post-invasion populations that equation (8) suggests from the eco-evolutionary model are quite different to the non-adaptive predictions of Fig. 1. However, these contrasting end-point predictions do not provide a complete story - we need to integrate the system numerically and consider the detail of the transition from the short term dynamics predicted by the ecology to the long-term dynamics predicted by the eco-evolution.

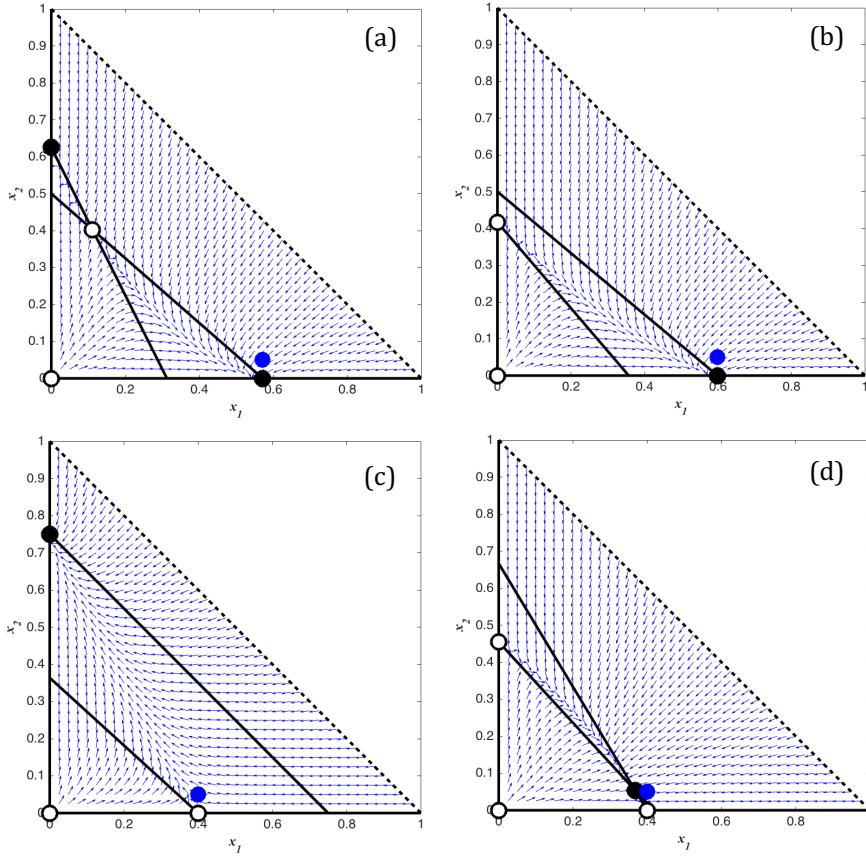


Fig. 1 Ecospace diagrams illustrating the initial conditions (blue dots) and stable invasion outcomes (black dots) under ecological theory used for the four scenarios: (a) competitive exclusion - either x_1 or x_2 could survive depending on initial conditions, but for this initial condition x_1 will survive and x_2 will fail to invade; (b) competitive exclusion - R^* theory predicts that x_1 will win and x_2 will go extinct; (c) competitive exclusion - R^* theory predicts that x_2 will win and x_1 will go extinct; (d) competitive coexistence - both populations survive but x_1 will dominate in non-adaptive scenarios. The lines are zero isoclines, the dots are stable (black) or unstable (white) equilibria or initial conditions (blue). The vector field (blue arrows) show how the system changes in time. The initial population values have x_1 set to its carrying capacity (i.e. $x_1^* = K_1 = r_1/a_{11}$) and $x_2^* = 0.05$. Technically R^* is only relevant to panels (b) and (c), but we will use the term generically to mean the outcome of non-evolutionary competition. See Table 1 for parameter values.

4 Simulation Results and Discussion

The time series results of numerical integrations of the eco-evolutionary model for the four scenarios are shown in Fig. 2. In each case adaptation allows the invading population x_2 to successfully establish itself in the ecosystem, without sending the incumbent population x_1 to extinction. This result, that eco-evolutionary processes allow coexistence of populations that would otherwise

not coexist, has been reported by Vasseur et al. [40] in a Lotka-Volterra model with normally distributed "neighbour-dependent selection", and by Kremer and Klausmeier [23] in resource-based model with bounded trade-offs between growth rates and resource utilisation in a varying environment. In this context, our result that eco-evolution facilitates coexistence supports the above work, although we note that our optimally-adapted post-invasion populations stably coexist in contrast to the oscillating solutions of Merico et al. [30], Vasseur et al. [40] and Kremer and Klausmeier [23]. This marked difference in predictions is readily testable by experiment.

A significant novel result of our simulations is that we achieve coexistence without applying arbitrary bounds on the trait adaptation, and that we obtain stable population size and traits as a result of adaptation. Importantly, both populations end up stably coexisting at post-invasion levels predicted by equation (8), which we call K^* theory. When trait adaptation is included in the models, non-evolutionary ecological theory (for example, R^* theory) may be useful to predict the short term outcome of the potential invasion, but the long term outcome is generally quite different. In the event that eco-evolutionary experiments produce stable post-invasion populations, then K^* theory is also experimentally testable.

A further novel result of our simulations is that the invading population x_2 adapts more quickly than the incumbent population x_1 in all scenarios, as it is subject to intense pressure by the much larger incumbent population. The deleterious effect of x_1 on x_2 very rapidly prunes that component of the x_2 population that has attributes that make them poor competitors with x_1 . As these individuals are deleted from the population, the mean trait value and the trait variance reduce, reducing the x_2 population but also selecting for a population that can successfully compete with x_1 .

During the period of x_2 adaptation, the x_1 population experiences weak selection pressure, as the population of x_2 is very small and has minimal effect on the trait distribution of x_1 . However, once the x_2 population has adapted and begins to grow exponentially it begins to exert selection pressure on x_1 , and its average trait value and variance reduce. This continues until the two populations reach an arms-race detente, and come to the stable coexistence state predicted by equation (8).

A key result of the simulation is revealed in Fig. 2. The population sizes at the end of the eco-evolutionary process (the right sides of the upper panel of each triptych) can lag behind the evolution of population properties that determine those states. This is counter to the common assumption that ecological time scales are much faster than evolutionary time scales. This assumption is implemented in this model, with the ecological rate coefficients for population growth (r_1 and r_2) being 10 to 100 times greater than the evolutionary coefficients that determine the rate of trait change $h^2(\bar{z}(t=0) - z_L)/\beta$ (Table 1).

The disconnect between the evolutionary state and the ecological state is due to the invasion bottleneck, during which the invading population adapts while the incumbent population does not. Once the invading population has

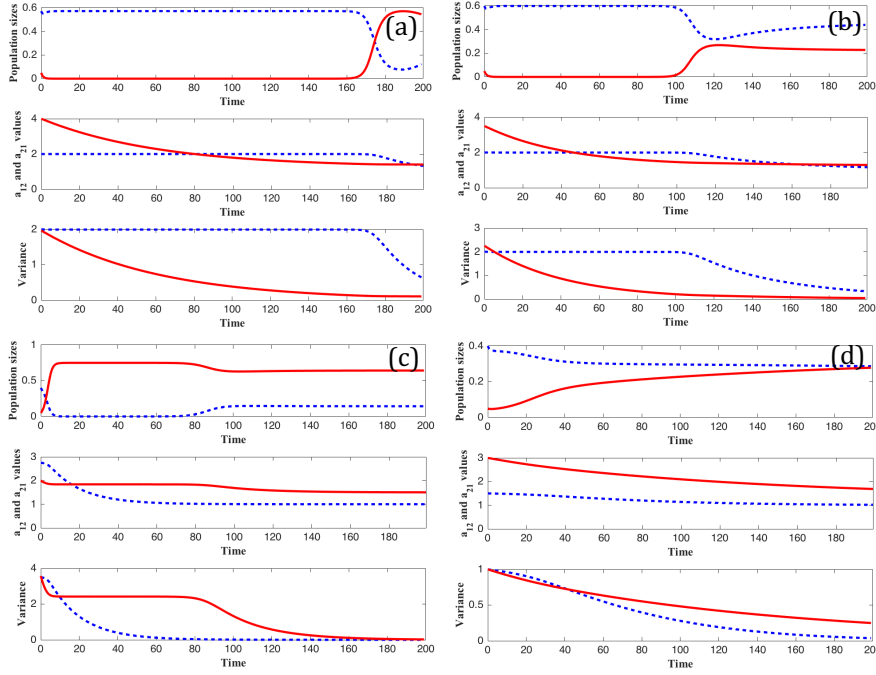


Fig. 2 Outcomes of the eco-evolutionary model for the four scenarios shown in Figure 1. The upper graph in each triptych shows the populations x_1 (dashed blue) and x_2 (solid red); the middle graph shows the trait means a_{12} (dashed blue) and a_{21} (solid red), and the bottom graph shows the trait variance of a_{12} (dashed blue) and a_{21} (solid red). Both populations survive in all cases, but this result does not take into account the probability that populations that remain very small for long periods of time may go extinct as a result of random effects. Essentially the left part of each population graph reflects the predictions of R^* theory, and the right part reflects the predictions of K^* theory.

developed a successful average trait value its population size exponentially increases, leaving the incumbent population poorly equipped to cope with the invader, and consequently then experiencing stronger selection pressure to "catch up" evolutionarily. This suggests that measuring the population sizes and traits during an invasion event may provide a misleading view of the eventual outcome of the process. For example, in panel (a) x_2 has adapted mean trait values that make it a strong competitor to x_1 by half-way through the simulation, but population levels that reflect its new competitive ability are not achieved until almost the end. If this aspect of the eco-evolutionary process were evident in real systems it would make empirical evaluation of the eco-evolutionary state of the system difficult to determine.

The periods of very low population levels of x_2 evident in Fig. 2(a and b) and of x_1 in Fig. 2(c) represent periods in which these populations are especially vulnerable to extinction. Whereas the model will always produce the outcome predicted by equation (8), it is more ecologically realistic to modify

these results by including a probability of extinction due to the population falling below levels at which it can reproduce, or falling victim to some random environmental perturbation that kills the remaining few members.

We can make a crude estimate of the relative likelihood of successful invasion and/or survival of the incumbent population of a particular invasion scenario using the period of time that each population is smaller than some arbitrary small level. We define the likelihood of extinction of a population ξ_{x_i} to be:

$$\xi_{x_i} = \frac{T_\epsilon}{T}, \quad (9)$$

where T_ϵ is the length of time the population x_i spends below an arbitrary population size ϵ and T is the invasion time scale. We set an arbitrary $\epsilon = 0.0005$ (1% of the initial invading population size), and used the simulation time as the invasion time scale $T = 200$ for the simulations in Fig. 2, to provide a relative measure of the susceptibility of the populations to extinction in each simulation. The results are shown in Table 4.

Table 2 Eco-evolutionary outcomes for the four non-evolutionary scenarios. The outcomes are described by the post-invasion equilibrium populations x_1^{**} and x_2^{**} , and the relative extinction likelihoods ξ_{x_1} and ξ_{x_2} .

SCENARIO	Non-evolutionary prediction	x_1^{**}	x_2^{**}	ξ_{x_1}	ξ_{x_2}
Competitive exclusion	x_2 cannot invade	0.33	0.42	0	0.76
R^* theory - x_1 wins	x_2 cannot invade	0.47	0.22	0	0.42
R^* theory - x_2 wins	x_2 invades - x_1 goes extinct	0.14	0.64	0.18	0
Coexistence	x_2 invades - x_1 dominates	0.27	0.33	0	0

The non-evolutionary approach competitive exclusion scenario (Fig. 1(a)) predicts that x_2 cannot invade, but the eco-evolutionary simulation (Fig. 2(a)) shows that x_2 goes through a long and restrictive evolutionary bottleneck during which its trait mean and variance slowly adapt in response to competition from x_1 . If it survives this long period of slow adaptation of a small population (the relative extinction likelihood indicator ξ_{x_2} suggests this is less likely for a single invasion event than other scenarios) then it eventually has adapted sufficiently to enable it to exponentially grow and dominate the system. The low population levels of x_2 prior to its rapid increase have not initiated any adaptation in the x_1 population - this only starts to occur after x_2 has taken over the system. However, Fig. 2(a) suggests that x_1 will survive and adapt and eventually reach the stable coexistence population predicted by equation (8).

The plots of trait variance in Fig. 2 (the bottom plot in each triptych) suggest that different trait variances will be evident in different types of invasions, and at different stages of the invasion process. In scenarios where the invasion is *a priori* "guaranteed" (Fig. 1(c and d)) the populations will still adapt and trait variance will reduce. Figs. 1 and 2(d) show that although the

initial trait properties in the invading and incumbent populations are such that they can coexist without any trait adaptation, the trait variances relatively slowly reduce as the populations stably coexist and optimise their interaction.

The simulation scenarios show that the invading population x_2 adapts more quickly than the incumbent population x_1 as it is subject to intense selection pressure by the much larger incumbent population. The deleterious effect of x_1 on x_2 very rapidly prunes that component of the x_2 population that has attributes that make them poor competitors with x_1 . As these individuals are deleted from the population, the mean trait value changes and the trait variance reduces. The x_2 population also reduces, and if it survives the reduction a population that can successfully compete with x_1 is selected for.

The rapid loss of trait diversity that occurs when the invading population is small for an extended time in Fig. 1(a and b), that is consistent with founder effects [11], is evident only in scenarios where non-eco-evolutionary theory would predict that the invading population would be unsuccessful. Founder effects are much less evident in the scenarios Fig. 1(c and d) where non-eco-evolutionary theory would predict that the invading population would be successful, although these populations will experience reductions in trait diversity after they have established in the system. Not all invading populations go through bottlenecks, but the reduction in trait diversity often associated with invasions [33] suggest that bottlenecks may have beneficial consequences for invading populations by "purging deleterious alleles" or "preserving highly adapted clonal lineages" in the population.

The results observed in the fourth scenario (Fig. 1(d)) in which the invading population already had attributes that would allow it to coexist with the incumbent population are consistent with genetic studies of aquatic species that suggest that not all invading populations go through genetic bottlenecks [33]. The invading population in Fig. 1(d) avoided a genetic bottleneck, invaded with its trait distribution virtually unchanged, and then slowly adapted to improve its competitive abilities with the incumbent population. This loss of trait diversity is not an attribute of the invasion, but rather an artefact of the large trait variance assigned to the populations due to their having never previously encountered each other, and our assumption that their interaction parameters are defined by attributes of their phenotypes that have arisen from their interactions with other populations and are essentially random.

A caveat on these results is that we have considered theoretical mathematical limits to adaptation rather than environmental, ecological or physiological limits. These practical limits would usually be more restrictive than the theoretical limits, which allow a_{12} and a_{21} to approach r_1 and r_2 infinitesimally closely. The eco-evolutionary outcomes we consider here are theoretical limits that in more realistic models would be modified by population and environmental constraints. The model results we present provide general principles for evaluating eco-evolutionary outcomes of population interactions associated with invasions. The predictions of K^* theory might be interpreted as limits that would be achieved by optimally-adapted populations.

5 Conclusions

The parameter relationships inherent in simple resource-limited ecosystem models reveal that the adaptation of average trait values in eco-evolutionary scenarios have natural bounds that arise from simple ecological axioms. The theoretical trait bounds suggest that the assumption of a non-normal, in this example a γ -distribution, is more appropriate for some traits than the assumption of a normal distribution. The trait variance is then dependent on the relative magnitudes of the trait mean and the trait bound, and adaptation is limited by fundamental properties of the populations and how they interact. We note that the bound for one trait may be defined in terms of the bound for a different trait. In long-term eco-evolutionary studies, where all traits are adapting, these bounds would not be fixed, but must retain a relationship about a moveable bound. The value of this bound is perhaps determined by physiological/environmental/ecological constraints not captured in simple population models.

We also note that while the adaptation timescale (here β_i/h_i^2) is in principle longer than the ecological timescale (here $1/r_i$), a large variance of a trait distribution can produce relatively rapid adaptation. Large variances of trait values may be expected for parameters describing how populations that have never met interact. This situation is commonly observed in invasion scenarios, where the interaction parameters are functions of the overall attributes of each population and how they have adapted to their previous environments, competitors, mutualists, and predators.

This eco-evolutionary study also provides some useful heuristics for empirical investigations of ecosystem invasions. First, the traits of the populations sampled during an invasion/adaptation process may not be consistent with the population states, suggesting that population dynamics observed early in an invasion may not be good predictors of long term outcomes. Our simulations reveal that while small populations may adapt rapidly, there may be a substantial time lag before the influence of the adapted traits is apparent in the ecosystem state. Second, in all cases the consequences of allowing the interactions between the populations to adapt to the competing presence of the other, is to facilitate the adaption of both the invading and invaded population for coexistence. This model study suggests that even when extinctions are strongly predicted by conventional ecological arguments, the populations co-adapt for stable coexistence if sufficient invaders/incumbents survive the evolutionary bottlenecks when these occur.

The adaptation of the population traits to enable coexistence is not of itself a surprising or novel result (see for example [40,23]), as this suggests that when populations encounter each other and compete for the first time, they will effectively partition the niche by reducing the level of direct competition. This is captured in equations (5), that reveal that the outcome of adaptation will be to reduce the values of the inter-population competition parameters. This is also seen in the simulations of Vasseur et al. [40], who

assumed normally-distributed traits with constant variances with "neighbor-dependent-selection".

The parameter constraints in equation (2), that reflect fundamental properties of the populations, suggest that the requirement for coexistence in Lotka-Volterra competition models, that intra-population competition exceeds inter-population competition, will generally be met in eco-evolutionary simulations [30,40,23]. However, we note that our optimally-adapted post-invasion populations stably coexist in contrast to the oscillating solutions of Merico et al. [30], Vasseur et al. [40] and Kremer and Klausmeier [23]. Simple observation of invasions in natural situations might determine whether steady or oscillating populations are the usual outcomes.

Further, our simulation results emphasise the role of bottlenecks in the eco-evolutionary process, so that intuitive numerical results might not always be achieved in nature. Bottlenecks in invasion/competition scenarios will determine whether Tilman's R^* theory [37,38] or our K^* theory (equation (8)) determines the outcome of the interaction. If an invading/competing population does not make it through the eco-evolutionary bottleneck, then R^* theory does a good job of predicting the outcome, especially in laboratory and/or experimental settings. However, if an invading/competing population does make it through the eco-evolutionary bottleneck, then we suggest that K^* theory will predict the outcome. This provides a testable hypothesis that may be evaluated in simple laboratory experiments, and then tested in real ecosystems, where like R^* theory, we might expect it to be reasonably effective provided populations are allowed sufficient time to fully adapt to each other.

The inclusion of an explicit, finite resource for every population, and the application of the simple axiom that populations require resources to grow, leads to a subtle refinement of a simple eco-evolutionary modelling framework that suggests that bounded trait distributions are a fundamental attribute of living systems. In many cases, these bounds represent relations between trait values (such as (2)) rather than absolute bounds, such as positivity, that often also apply. The trait bounds themselves may also be subject to eco-evolutionary processes, but constrained by environmental/physiological limits rather than ecological processes. The resource-limited eco-evolutionary approach has proved useful in the limited case of invasion scenarios considered here, but more complex eco-evolutionary problems, where many traits and trait bounds simultaneously co-evolve, await a more general specification of population fitness.

6 Authors' Contributions

Both authors contributed to the conception and design of the study, and the writing of the manuscript. RC did the numerical analysis and produced the figures and data.

7 Funding

RC thanks the Mathematical Institute of the University of Oxford for providing funding to support this research.

8 Acknowledgements

The authors thank two anonymous reviewers for their thoughtful and helpful comments that considerably improved this manuscript.

9 Appendix: Traits with Bounded Distributions

Many phenotypes have gamma distributions as they are constrained to be positive, negative, or greater or lesser than other parameters. Such constraints arise naturally in LVCN systems, and are fundamental to the system being ecologically valid. Here, where equation (1) represents competition between two populations, one incumbent and one potential invader, the parameter relations (2) are fundamental.

We follow the derivation of Lande [24] and consider the evolution of phenotypes based on an equation provided by Falconer [13] that describes the deterministic change in the average value of a phenotypic character \bar{z} in response to selection:

$$\begin{aligned}\Delta\bar{z}(t) &= \bar{z}(t+1) - \bar{z}(t), \\ &= [\bar{z}_w(t) - \bar{z}(t)]h^2,\end{aligned}\tag{10}$$

where $\bar{z}(t)$ is the mean value of the character in generation t before selection, $\bar{z}_w(t)$ is the mean value of the character after selection, but before reproduction, and h^2 is the realised heritability of the character. We denote the distribution of phenotypes z in the generation t before selection as $p(z, t)$, and then the average phenotype before selection is:

$$\bar{z}(t) = \int zp(z, t)dz,\tag{11}$$

the mean fitness of individuals in the population is:

$$\bar{W} = \int p(z, t)W(z)dz,\tag{12}$$

and the average phenotype after selection is:

$$\bar{z}_w(t) = \frac{1}{\bar{W}} \int zp(z, t)W(z)dz.\tag{13}$$

Then assuming that the phenotype has a γ -distribution:

$$\begin{aligned}
p(z, t) &= \frac{\beta^\alpha}{\Gamma(\alpha)} z^{\alpha-1} e^{-\beta z}, \\
&= \frac{\alpha^\alpha z^{\alpha-1}}{\Gamma(\alpha)} \bar{z}(t)^{-\alpha} e^{-\frac{\alpha z}{\bar{z}(t)}},
\end{aligned} \tag{14}$$

where we have used $\bar{z}(t) = \alpha/\beta$ to eliminate β . This gives the change in mean fitness of the population (\bar{W}) with respect to a change in the average phenotype ($\bar{z}(t)$) as:

$$\begin{aligned}
\frac{\partial \bar{W}}{\partial \bar{z}(t)} &= \int \frac{\partial p(z, t)}{\partial \bar{z}(t)} W(z) dz, \\
&= \int \frac{\alpha[z - \bar{z}(t)]}{\bar{z}(t)} p(z, t) W(z) dz, \\
&= \frac{\alpha \bar{W}}{\bar{z}(t)^2} [\bar{z}_w(t) - \bar{z}(t)].
\end{aligned} \tag{15}$$

Then combining (15) with (10) gives:

$$\begin{aligned}
\Delta \bar{z}(t) &= \frac{h^2 \bar{z}(t)^2}{\alpha \bar{W}} \frac{\partial \bar{W}}{\partial \bar{z}(t)}, \\
&= \frac{h^2 \bar{z}(t)}{\beta} \frac{\partial \ln \bar{W}}{\partial \bar{z}(t)}.
\end{aligned} \tag{16}$$

Note that $\bar{z}(t)/\beta$ is equivalent to the variance of the distribution, and represents the change in variance of the distribution as the mean approaches the lower bound (zero in the general case). As parameters in LVCN models may have lower bounds other than zero, for example a_{ij} in (1), we allow for a non-zero lower bound z_L in (16) and assume continuous trait variation:

$$\frac{d\bar{z}}{dt} = h^2 \left(\frac{\bar{z}(t) - z_L}{\beta} \right) \frac{\partial \ln \bar{W}}{\partial \bar{z}(t)}. \tag{17}$$

Equation (17) ensures that phenotypes with bounded distributions are not able to exceed their bounds during simulations.

The key attribute of traits that have gamma distributions for eco-evolutionary modelling is that the mean value of the trait is bounded and the variance is related to the mean trait value, so that as the mean of the trait approaches its bound the variance of the distribution of the trait reduces.

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