Robustness vs productivity during evolutionary community assembly: short-term synergies and long-term trade-offs

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Abstract

The realization that evolutionary feedbacks need to be considered to fully grasp ecological dynamics has sparked recent interest in the effect of evolution on community properties like coexistence and productivity. However, modern coexistence theory being limited to pairwise interactions, little is known about coevolution and diversification in rich communities. We leverage the recent multidimensional coexistence theory metrics, together with a structural community robustness metric, to study such properties in a general trait-based model of competition on a niche axis. We show that the effects of coevolution on coexistence are two-fold. In the short-term our results show synergies emerging between increasing productivity and reinforcing coexistence, while in the long-term, diversification and niche-packing destabilize communities, thus inducing a long-term trade-off between productivity and coexistence. In light of classical and recent work, our findings help advance understanding of evolutionary effects in high-dimensional systems. We illustrate how our theoretical predictions echo in observed empirical patterns. Finally, we discuss their implications and provide testable hypotheses.

Keywords: Eco-evolutionary dynamics, evolutionary stable communities, diversification, coexistence theory, structural stability, niche difference, fitness difference, productivity, Pareto optimality

1 Introduction

While ecology and evolutionary biology have long developed as separate disciplines (Lewontin, 2003), recent years have seen an effort to better grasp the feedbacks that link variations in the biotic environment (inter- and intraspecific interactions) and evolutionary trajectories (McPeek, 2017). The realization that evolutionary changes can happen over relatively short time-scales (Lankau and Strauss, 2007; Fussmann et al., 2007; Yoshida et al., 2003; Hairston Jr et al., 2005) fostered a renewed interest in the interface between ecology and evolution, an area of research now named eco-evolutionary dynamics (Hendry, 2009). The feedback loop between ecological interactions and evolutionary change in characters can give rise to complex dynamics beyond the simple optimization of growth rates, such as disruptive selection and evolutionary branching (Geritz et al., 1998).

Understanding the effects of evolution on the maintenance of species diversity remains an open question. At the single species level, evolutionary adaptation may save species from extinction under specific conditions, a phenomenon named evolutionary rescue (Bell and Gonzalez, 2009). But accounting for density- or frequency-dependent selection can open up scenarios where a species evolve towards self-extinction (Matsuda and Abrams, 1994), a case dubbed evolutionary suicide in the adaptive dynamics literature (Ferriere and Legendre, 2013). In a two species scenarios, there can be both evolution towards stronger niche differentiation (Lankau, 2009) or one species can push the other to extinction (Dercole et al., 2006). Recently, Pastore et al. (2021) studied the effect of co-evolution of niche positions in a model of two competing species in the framework of Chesson's coexistence theory (Chesson, 2000; Barabás et al., 2018*a*). Their work shows that evolution tends to have a negative effect on coexistence by increasing competitive imbalance, an outcome matching the experimental results of Hart et al. (2019).

In communities, we have no reason to expect that evolution, which is driven by differences in individual fitness, will lead to optimization of emergent properties at a larger organizational scale (here, communities) (Metz et al., 2008). Brännström et al. (2012)

highlighted the dual nature of evolution in rich competitive communities, which can lead to the increase of diversity at different levels through generation of polymorphism and speciation but also to competitive exclusion and evolutionary murder. Classical ecological theory also predicts that stability in arbitrary large systems may be difficult: in randomly interacting communities local dynamical stability decreased with richness (May, 1972), but adding non-random interactions such as adaptive foraging or eco-evo dynamics can counter this effect (Kondoh, 2003). Loeuille (2010) showed that evolution stabilizes moderately rich communities but destabilizes more species-rich systems.

Importantly, dynamical stability - the return to equilibrium after a state perturbation - is only half the picture (Rohr et al., 2014), the other half being feasibility - the existence of an equilibrium state where all species have positive abundances. The structural framework developed by Saavedra et al. (2017) allows us to quantify the tolerance to perturbations in the parameter space (such as changes in growth rates due to environmental factors). The study of feasibility of competing species on a niche axis is tightly linked to what classical theory calls species packing, a concept which dates back to Hutchinson's work on species niches (Hutchinson, 1957, 1979) and was mathematically formalized by MacArthur (1969). In their paper, they studied the limit in similarity between species, i.e., how close species can be on the niche axis while still coexisting. Case (1981) extended this approach by including coevolutionary forces, and studied limiting similarity under the constraint imposed by evolution. To our knowledge, a study of the evolutionary effect on structural stability has never been proposed to this day.

If species interactions are important drivers of evolutionary change we expect that communities arising from co-evolution, for which Edwards et al. (2018) suggested the term Evolutionary Stable Communities (ESCs), should comprise a highly non-random subset of all possible combinations of species. This has been advocated already by Rummel and Roughgarden (1983), which analyzed island communities modeled through coevolution processes versus random colonization. More recently, Aubree et al. (2020) showed that coevolved communities were generally more productive, more stable, more resistant to invasion than collections which were randomly assembled from the species pool.

Here, we aim to study how evolution and the emergence of polymorphism interplay with coexistence and productivity constraints. Using the structural stability approach to coexistence theory (Saavedra et al., 2017), we expand on previous approaches based on species pairs and dynamical stability, to focus on multispecies co-evolutionary communities. Our aim is to go beyond previous works by 1) explicitly linking eco-evolutionary dynamics and structural coexistence metrics; 2) discussing how these links vary in contrasting ways depending on the time scale that is considered; 3) Uncovering and explaining the emergence of positive or negative correlations among various community properties, particularly diversity, productivity and coexistence, along evolutionary trajectories.

To do so, we follow the structural indicators of niche and fitness difference. For a given niche difference, small fitness differences increase robustness through equalizing effects; similarly, for a given fitness difference, niche differences increase robustness due to stabilizing effects. However, as is widely recognized, these two metrics do not exist independently (Barabás et al., 2018*b*; Song et al., 2019), and we find they are insufficient to paint a complete picture of extinction risks. Therefore, we make use of a structural metric which quantifies the community robustness in the face of perturbations that would cause loss of one or more of its constituent species (Medeiros et al., 2021). We track all three metrics along evolutionary trajectories. Finally, we consider changes in total community productivity, and contrast it with measures of coexistence.

We expect evolution to cause character displacement along the resource axis (Macarthur and Levins, 1967; Dieckmann and Doebeli, 1999; Grant and Grant, 2006), which should first result in an increase of niche differentiation. At the same time, divergence of niche positions ultimately results in a decrease in the growth rate of phenotypes situated further from the resource optimum, and in a larger imbalance of growth rates in the community and greater fitness differences. We therefore expect that effects of evolution on coexistence and productivity may vary depending on the scale (environmental width) and timeframe considered.

2 Materials and methods

2.1 Ecological dynamics

We study a niche-based model of competition based on generalized Lotka-Volterra dynamics (Volterra, 1931), following the α-r parametrization (Mallet, 2012). Each phenotype is defined by its position μ_i on a niche axis representing resources. Position on the niche axis affects both the intrinsic growth rates $r(\mu_i)$ and the strength $\alpha(\mu_i, \mu_j)$ of density-dependent competition interactions between types. This kind of model has been commonly used to model competition on a niche axis (MacArthur, 1972), and has been shown to readily lead to the evolutionary emergence of polymorphism (Dieckmann and Doebeli, 1999). We use this behavior to explore the conditions of coexistence throughout the diversification process. Population dynamics of a type i then follow:

$$\frac{dN_i}{dt} = N_i \cdot \left(r(\mu_i) - \sum_{j=1}^{S} \alpha(\mu_i, \mu_j) \cdot N_j \right) \qquad i = 1, \dots, S. \tag{1}$$

We assume a Gaussian function for $r(\mu_i)$, with fecundity decreasing with distance from a resource optimum μ_R, while including a small density-independent intrinsic mortality m to prevent phenotypes with unreasonably large or small trait values from persisting at virtually nil abundances:

$$r(\mu_i) = f_{\max}\, e^{-\frac{(\mu_i - \mu_R)^2}{2\sigma_R^2}} - m. \tag{2}$$

The parameter $f_{\max}$ represents the maximum fecundity rate at the resource optimum, while σ_R depicts the width of resources availability on the niche axis.

In line with previous works (Macarthur and Levins, 1967), we suppose that competition strength is defined by the similarity among types. It then follows a Gaussian function centered in μ_i, so that $\alpha(\mu_i, \mu_j) = \alpha(\mu_j, \mu_i)$, and interaction strength reaches its maximum $\alpha_{\max}$ for $\mu_i = \mu_j$:

$$\alpha(\mu_i, \mu_j) = \alpha_{\max}\, e^{-\frac{(\mu_i - \mu_j)^2}{2\sigma_\alpha^2}}. \tag{3}$$

The parameter σ_α controls the width of the niche. This model is conceptually a size S

extension of the model used by Taper and Case (1992); Dieckmann and Doebeli (1999); Doebeli and Dieckmann (2000). The form of the competition function presents the agreeable property of being dissipative *sensu* Volterra (Volterra, 1931; Logofet, 1994). This implies that ecological dynamics possess one and only one globally stable equilibrium point. Moreover, if there exists a feasible equilibrium, i.e., $N_i^* > 0$ for all i, all ecological dynamics will converge to it regardless of initial abundances. Note that a feasible equilibrium must fulfill $r(\mu_i) = \sum_{j=1}^{S} \alpha(\mu_i, \mu_j) \cdot N_j^*$ for each i.

2.2 Evolutionary dynamics

We study evolution within the adaptive dynamics framework (Metz et al., 1995; Brännström et al., 2013), thereby accounting for both frequency- and density-dependent selection. The adaptive dynamics framework assumes clonal reproduction where mutations are infinitesimally small and rare, and a separation of timescales where ecology is assumed faster than evolution. This implies that advantageous mutations always go to fixation. The evolution of a quantitative trait is determined by the invasion fitness function, defined as the *per capita* growth rate of a rare mutant of traits μ_i' in a resident population of S phenotypes with traits $\mu_1, \ldots, \mu_S$ at their ecological equilibrium (Metz et al., 1992):

$$\omega_i(\mu_i'|\mu_1, \ldots, \mu_S) = r(\mu_i') - \sum_{j=1}^{S} \alpha(\mu_i', \mu_j) \cdot N_j^*. \tag{4}$$

Note, that each phenotype i has its invasion fitness function ω_i.

The evolution over time of niche positions is determined by the canonical equation of adaptive dynamics (Dieckmann and Law, 1996):

$$\frac{d\mu_i}{dt} = c \cdot N_i^* \cdot \left.\frac{\partial \omega_i(\mu_i'|\mu_1, \ldots, \mu_S)}{\partial \mu_i'}\right|_{\mu_i'=\mu_i} \qquad i = 1, \ldots, S. \tag{5}$$

The partial derivatives

$$\left.\frac{\partial \omega_i(\mu_i'|\mu_1, \ldots, \mu_S)}{\partial \mu_i'}\right|_{\mu_i'=\mu_i} \qquad i = 1, \ldots, S \tag{6}$$

correspond to selection gradients, and they determine the direction of co-evolution of the

S niche positions. The coefficient c incorporates the mutation rate and the mutational variance, which we assume to be equal for all phenotypes. Without loss of generality, we can set $c = 1$ by rescaling the time axis. We integrate the canonical equation (Equ. 5) numerically until an evolutionary singular strategy is reached, i.e, a set of traits $\mu_1^*, \ldots, \mu_S^*$, at which all selection gradients vanish

$$\left.\frac{\partial \omega_i(\mu_i' | \mu_1, \ldots, \mu_S)}{\partial \mu_i'}\right|_{\mu_i'=\mu_i=\mu_i^*} = 0 \qquad i = 1, \ldots, S. \tag{7}$$

We start with a single monomorphic population and once we reach an evolutionary singular strategy, we evaluate the evolutionary stability condition (invasibility of the strategy) for each phenotype (Brännström et al., 2013; Metz et al., 1995). Invasibility happens when the second derivative of the invasion fitness function (Equ. 4) with the mutant trait is positive at the singular strategy (Dieckmann and Law, 1996; Geritz et al., 1998). Evolutionary branching ensues, and we introduce a new phenotype at a small distance of the singularity, thereby augmenting the dimensionality of the system. We continue the simulation until all strategies are evolutionary stable, thereby forming an Evolutionary Stable Community (ESC) *sensu* Edwards et al. (2018). The algorithm is detailed in the Supplementary Materials S1.

2.3 *Classical coexistence metrics*

Along co-evolutionary trajectories where $S > 2$, we assess coexistence metrics. Within the structural approach, coexistence is quantified by structural niche differences Ω and structural fitness differences θ. These two metrics are extensions to species-rich systems of the stabilizing niche difference and the fitness ratio, defined within the modern coexistence theory framework (Chesson, 2000), and were introduced in their multispecies form by Saavedra et al. (2017). The niche difference Ω quantifies the possibility of coexistence and is mathematically defined as the solid angle of the domain of intrinsic growth rates leading to coexistence given the interaction strength $\alpha(\mu_i, \mu_j)$, defining the feasibility domain (Figure 1). In turn, the fitness difference θ quantifies the deviation from neutrality, i.e., to what extent a phenotype dominates the system. The fitness difference θ depends on both the intrinsic growth rates vector $\mathbf{r}(\mu_i)$ and the competition strength $\alpha(\mu_i, \mu_j)$. To compare values of niche difference across communities of different sizes S, we consider the standardized niche difference $\hat{\Omega} = \sqrt[s]{\Omega}$ (Song et al., 2018).

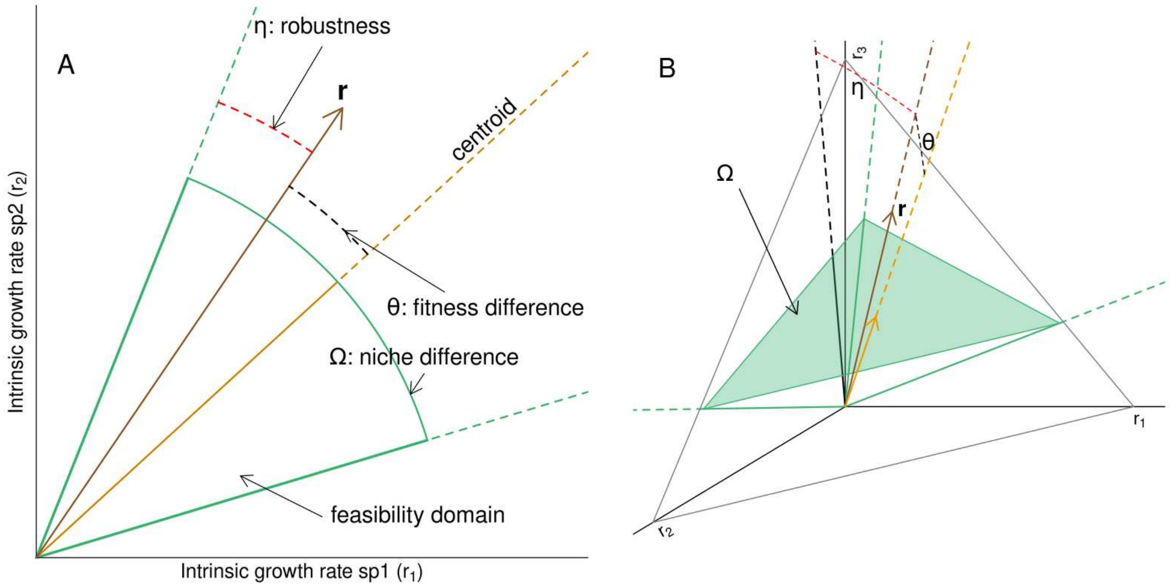

Figure 1: Geometric representation of the structural coexistence metrics for a 2-species system (panel A) and a 3-species system (panel B). On both panels, the green cone, called domain of feasibility, determines the set of intrinsic growth rates leading to a positive equilibrium for each species, i.e., to coexistence. The niche difference Ω is given by the amplitude of this cone, while the fitness difference θ measures the deviation of the vector of intrinsic growth rates ($\mathbf{r}$) from the centroid of the cone. Finally, η – structural measure of robustness – is given by the smallest angle between the vector of intrinsic growth rates and the border of the feasibility domain. It gives an indication of the fragility of the community with respect to perturbations on $\mathbf{r}$. Note that we illustrated the structural metrics for $S = 2$ and $S = 3$, but they are effectively defined and computed for S-rich systems (though they become hard to represent).

2.4 Structural robustness metric

While the classical metrics allow for partitioning coexistence effects, they do not give a clear indication of the absolute strength of coexistence. For example, if both Ω and θ increase, we do not know whether coexistence is favored or weakened. Hence, we utilize a complementary measure which we call η, the smallest angle between the vector of intrinsic growth rates $\mathbf{r}$ and the border of the feasibility domain. This angle, which we call "robustness", gives an indication of the fragility of the community with respect to perturbations on $\mathbf{r}$, i.e., how close the community is to losing of one or more of its components. Figure 1 provides a representation of Ω, θ, and η in a system of $S = 2$. It is worth noting that a version of this metric was used in Medeiros et al. (2021), where it is called "full resistance".The mathematics of how η is computed are detailed in the Supplementary Materials S2.

2.5 Productivity metrics

Besides coexistence metrics, we also measure the evolution of productivity using the proxy of total community biomass (or abundance) $N_{\text{tot}} = \sum_i N_i^*$ is (Tilman et al., 1997). Biomass diversity effects (overyielding of polymorphic communities compared to monocultures) can be due to complementarity in resource use, as well as selection for high-yield phenotypes (high carrying capacity $K_i = r_i/\alpha_{ii}$). Both of these mechanisms can be easily captured under our model, and are expected to vary along coevolutionary time. Furthermore, we follow relative yield $Y_{\text{tot}} = (\sum_i N_i^*/K_i)$, another common currency of biodiversity-productivity studies Vandermeer (1989); Loreau and Hector (2001).

2.6 Randomizations

We follow the coexistence metrics and productivity along co-evolutionary trajectories and branching points. However, this does not tell us whether those properties are maximized by evolution. To this end, we generate between 4'000 and 128'000 (depending on S) communities for each singular strategy (branching point or stable strategy) of each simulation, by sampling uniformly sets of niche positions μ_i, conditioned on the resulting community being feasible ($N_i^* > 0$ for all $i = 1, ..., S$). We then compare the metrics (niche and fitness difference and total biomass) of the sampled communities with the eco-evolutionary trajectories. We use two different rules to define the range of niche positions from which we sample. For the first rule, we sample communities within the range of niche positions observed at the ESC (restricted range), which tells us if the evolutionary community is unique within this bracket of niche positions. For the second rule (full range), the range of sampled μ_i covers all niche positions leading to positive intrinsic growth rate $r(\mu_i) > 0$. Such bounds are given by $\mu_R \pm \sqrt{2\sigma_R^2(\log f_{\max} - \log m)}$ and allow us to compare strategies with respect to the whole trait space.

2.7 Choice of parameter values

To reduce the number of free parameters, we first transform the dynamical system into a nondimensional form. That is, we freely chose the time unit, the abundance unit, and the scale of the niche axis. Regarding the abundance and time unit, we can set without loss of generality $\alpha_{\max} = 1$, $f_{\max} = 1$. The latter defines the ecological timescale, but adaptive dynamics assumes that ecological equilibrium is reached before the next mutation occurs. The combination of both determines the scale of species abundance and can arbitrarily be rescaled. The additional mortality rate m remains, and thus cannot be freely chosen. Regarding the niche axis, we can rescale, without loss of generality, its origin to $\mu_R = 0$. Then we can also choose its scale by setting arbitrarily the resource width $\sigma_R = 1$ and explore the effect of the niche width σ_α, or alternatively, we can also set arbitrarily the niche width $\sigma_\alpha = 1$ and explore the effect of the resource width σ_R.

For simplicity, in the main text we show the results for one specific parametrization, set to $m = 0.01$ and $\sigma_\alpha 1 =$, and $\sigma_R = 1.7$. In the Supplementary Material S6 and S7, we show that our findings are robust relative to different choices of environmental niche width σ_R and mortality m.

3 Results

3.1 Co-evolutionary trajectories and branching events

Figure (2.A) shows a co-evolutionary trajectory, which undergoes diversification events until it reaches a stable and convergent community (ESC). After each branching, we observe a divergence in the niche positions, which leads to a decrease in the level of interspecific competition. The evolutionary endpoint for the monomorphic situation (i.e., before the first branching) can be determined analytically. It converges to an evolutionary singular strategy that is always located at the resource optimum $\mu^* = \mu_R$. Its invasibility depends on the width of the competition function (σ_α), the width of the resources (σ_R), the maximum fecundity rate ($f_{\max}$), and the mortality rate (m). We show that branching occurs if and only if $\sigma_R^2 \cdot (f_{\max} - m) > \sigma_\alpha^2 \cdot f_{\max}$ (Supplementary Materials S3). Branching will therefore occur if the resource range is wide enough (as defined by σ_R) and/or limiting similarity strong enough (small σ_α). This formula is alike the one derived by Dieckmann and Doebeli (1999); Doebeli and Dieckmann (2000) but generalized to an additional mortality term, which has an evolutionary stabilizing effect through reducing the resident abundance at equilibrium. As expected by niche packing theory Macarthur and Levins (1967); MacArthur (1969), the number of subsequent branching, and therefore, the number of species at the ESC, increases with the resource availability (σ_R) and decreases with the competition width (σ_α), see Supplementary Material S4.

Figure 2B shows the evolution of the niche difference $\hat{\Omega}$. Between each branching point, the niche difference increases. This can be expected from panel A showing that niche positions diverge, which implies an increase in the niche difference and relaxed competition among phenotypes. But at the branching points, the addition of a new phenotype very close to an existing one causes the average niche difference to abruptly decrease. Hence, for a period, coexistence is driven by more neutral (fitness-equivalent) mechanisms, rather than by strong niche separation. More specifically, branching points are the only contiguous trait regions where indefinitely close phenotypes can coexist, creat-

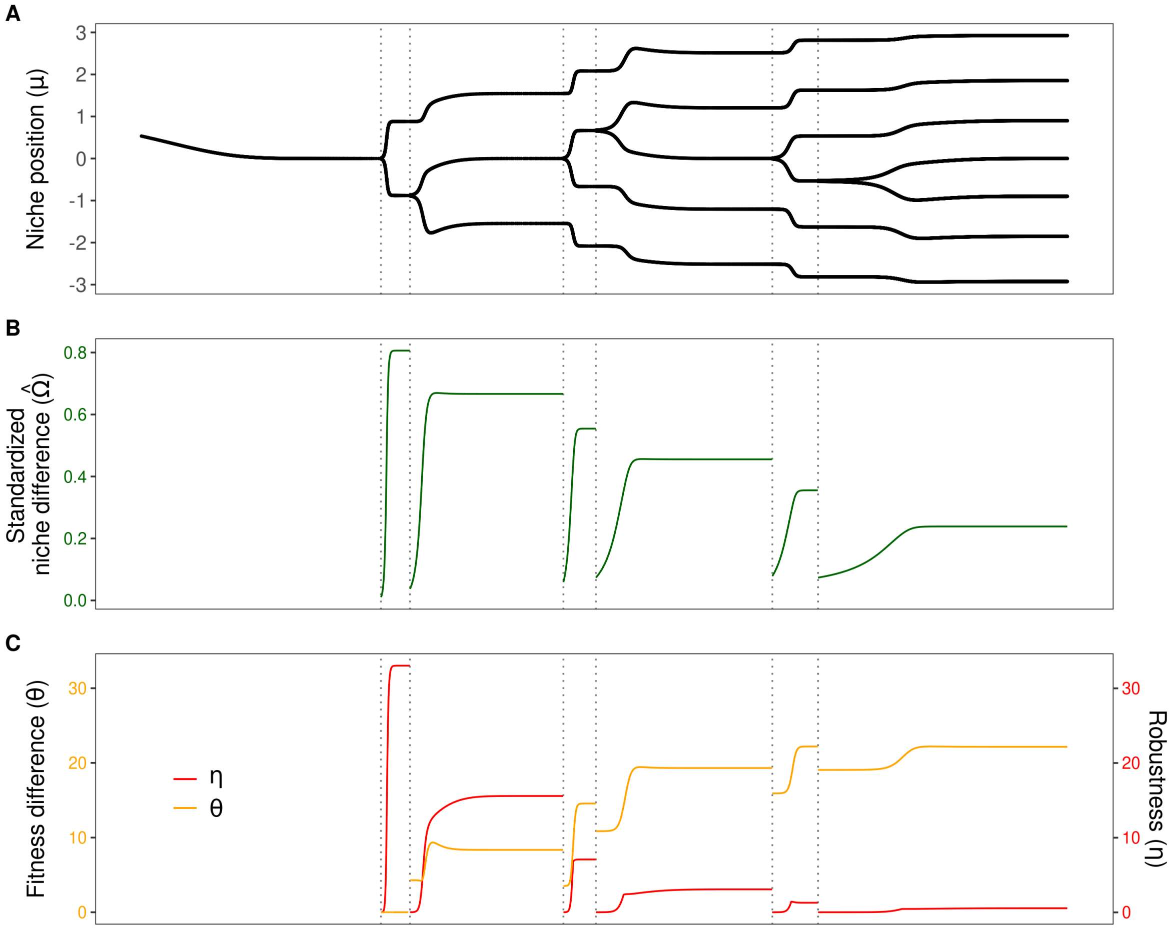

Figure 2: **Evolutionary trajectory**. Panel **A** shows the evolutionary trajectory of the niche positions μ_i. The vertical dotted lines indicate evolutionary branching. Panel **B** shows the evolution of the niche difference $(\hat{\Omega})$. Panel **C** shows the evolution of fitness difference (θ) and the robustness (η). For this figure, the resource width has been set to $\sigma_R = 1.7$, the niche width to $\sigma_\alpha = 1$, and the mortality term to $m = 0.1$.

ing a niche-neutrality continuum *sensu* Song et al. (2019). Conversely, fitness differences θ increase all along evolutionary trajectories, which undermines community robustness (Fig. 2C). Fitness differences θ are initially zero when only two types coexist, as their trait positions are symmetric around the resource center. They later tend to increase for $S > 2$ as phenotypes start differing in their intrinsic growth rates, reflecting imbalances between strong and weak competitors. Note that because evolution here increases both niche differences (stabilizing effect) and fitness differences (unequalizing effect) between branching points, its overall effect on coexistence is not obvious. We therefore use the robustness indicator – the angle η – to assess the evolution of the distance to the border to the feasibility domain. Figure 2C shows that the robustness η tends to increase between the branching points, so that the overall effect of a simultaneous increase in both fitness and niche difference ultimately results in more robust communities. As logically expected, η decreases at each branching point. Moreover, as S increases and the community becomes saturated, the value of η becomes very small. Once maximum phenotype packing is achieved (at ESC), small perturbations in $\mathbf{r}$ suffice to lead to non-feasibility, and the community is structurally more fragile than an undersaturated one (fewer phenotypes than at the ESC).

Supplementary Materials S6 and S7 show that these results are consistent when varying the resource width σ_R and the mortality rate m.

3.2 Projection into coexistence space

Figure 3 illustrates how coexistence metrics $\hat{\Omega}$ and θ change along the evolutionary trajectory of figure 2 when $S \geq 2$. Remember that large niche differences $\hat{\Omega}$ and small fitness differences θ enhance persistence. In the background, we show the coexistence metrics of randomized communities that were produced according to the two rules presented in the Methods.

Considering all randomized communities, it appears that communities that have small fitness differences most often also have small niche differences. This is due to both

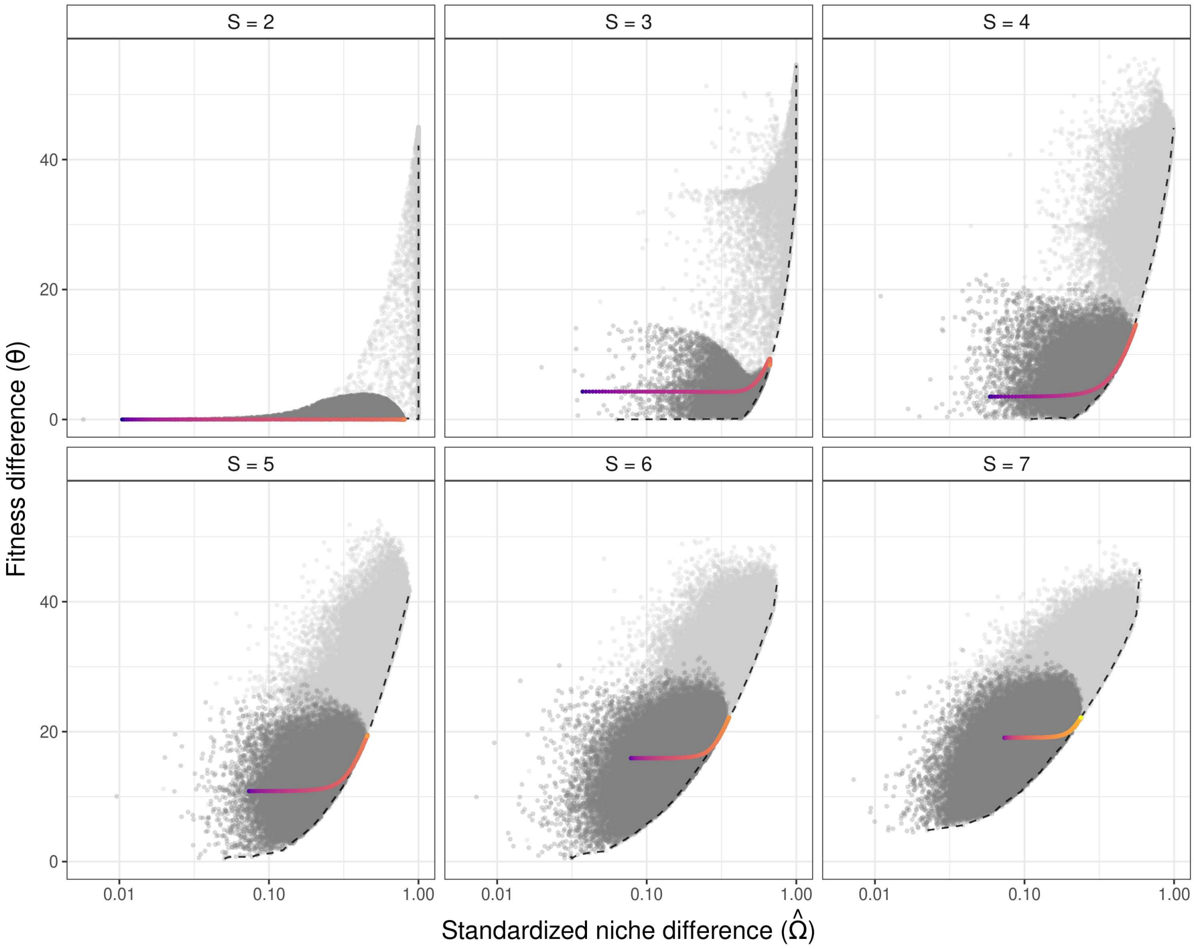

Figure 3: **Variations of coexistence metrics along evolutionary trajectories.** The figure is split into six panels according to the number of phenotypes S. Each panel therefore represents a slice (in between two branching points) of the trajectory presented in figure 2. The colored line represents the projection of the evolutionary trajectory of figure 2 into the space of coexistence metrics for a given S, variations of color from purple to orange indicating evolutionary time. The X-axis represents the standardized niche difference ($\hat{\Omega}$), while the Y-axis stands for the fitness difference (θ). Gray points represent randomized feasible communities, with niche position value sampled from the restricted range explored by evolution (1st rule; dark gray) or the full range leading to positive intrinsic growth rates (2nd rule; light gray). Pareto fronts among randomized communities are shown using dashed lines.

selecting for feasible communities, but also to ecological constraints under this model, which generate a global trade-off at the community level between the two coexistence metrics. Points that optimize one of the two properties relative to the other lie on a Pareto front. Figure 3 shows that evolution leads to this Pareto-optimality, and more specifically to the point on this front that also maximizes the standardized niche difference within the restricted range (first randomization rule). More extreme niche positions would also allow larger niche differences, but this decrease in competition would come at the cost of decreasing intrinsic growth rates for the phenotypes further from the resource optimum, thereby increasing fitness differences θ.

Regarding community robustness (η), figure 4 indicates that evolution optimizes it within the range of niche positions explored by evolution (first randomization rule), but greater robustness could (rarely) be reached for the second randomization rules. However, among the niche positions explored by evolution and for a given number of phenotypes, evolution converges to more robust communities, by optimizing the niche difference Ω and the robustness η.

Supplementary Materials S6 and S7 show that these results are consistent when varying the resource width σ_R and the mortality rate m.

3.3 Evolution of productivity

In general, co-evolutionary dynamics increase productivity. While strict optimization can be proven in the monomorphic situation (Supplementary Materials S3), productivity increase also happens throughout diversification, as illustrated by figure 5. For the total abundance (panel A), the co-evolutionary trajectory, though not strictly optimal, is among the most productive communities. This holds for the two randomization rules. We have seen on figure 3, that within the restricted range of randomization, co-evolution tends to maximize niche differentiation, and thus to decrease interspecific competition. Given a fuller range of randomization, however, communities with larger niche differentiation can be sampled. Results for the relative yield metric are presented in the

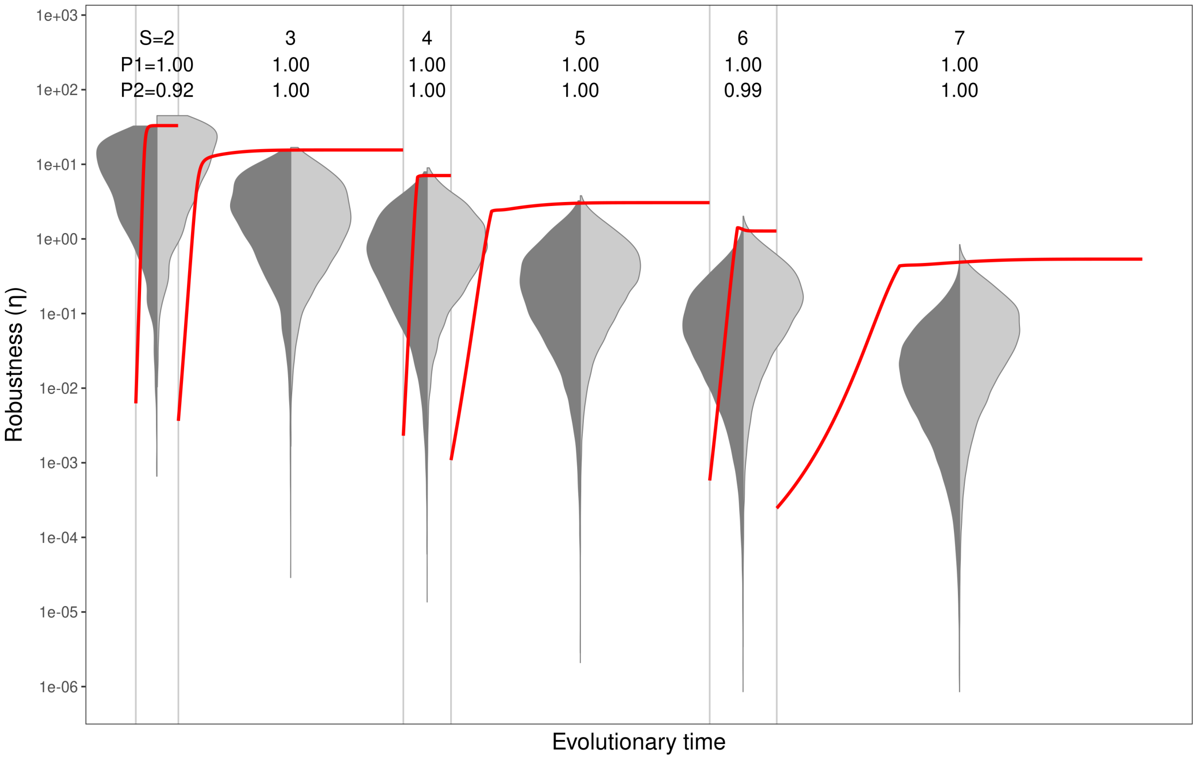

Figure 4: **Evolution of community robustness.** The red line shows the evolution of η. Gray points represent randomized feasible communities, with niche position value sampled from the restricted range explored by evolution (1st rule; dark gray) or the full range leading to positive intrinsic growth rates (2nd rule; light gray). At the singular strategy, the evolved community reaches a value of η greater or equal to than a proportion $P1$ and $P2$ of randomized communities according to the first and second randomization rules, respectively.

309 Supplementary Materials S5.

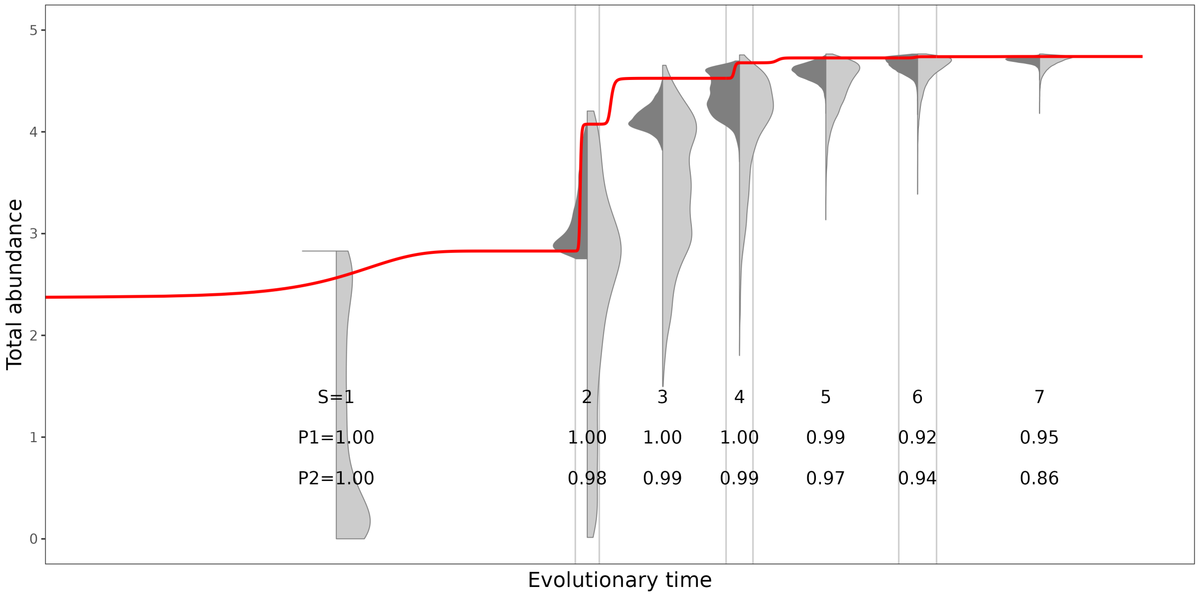

Figure 5: **Productivity along evolutionary trajectories.** Evolution of productivity. Here the numbers $P1$ and $P2$ in the second row of text indicate the percentage of randomized communities that are less productive than the ESC. For S=1, biomass production is optimized at the ESC. For S=6, the ESC is in the 80th percentile of the most productive communities. Point clouds represent randomization in the narrow (1st rule; dark gray) or the full range (2nd rule; light gray).

4 Discussion

In light of global changes, understanding the way evolution shapes and affects community robustness is paramount. Communities are currently reshuffled by the arrival of non-native species and by range shifts (Alexander et al., 2016). How these novel, evolutionary non-equilibrium communities differ from ESCs is unclear. We also need to assess under which conditions and how quickly evolution may prevent species from going extinct following environmental change, considering not only population-level processes (as in evolutionary rescue) but also larger spatial or organizational scales (Urban, 2016). Previous studies showed that mechanisms such as adaptive foraging, which can be evolutionary in nature, can stabilize complex systems (Kondoh, 2003; Valdovinos et al., 2013). Recently a handful of studies, both theoretical and experimental, have explored this question for pairs of coevolving species within the framework of modern coexistence theory Pastore et al. (2021); Hart et al. (2019). Here we go further by employing recent theoretical advances to investigate the question for species-rich systems ($S > 2$) where diversity arises through subsequent branching events. We show that evolution of coexistence properties follows two distinct trends on two different timescales, while productivity systematically increases along evolutionary trajectories.

The short-term trend, in-between branching events, allows for increased efficiency in resource partitioning and decreased competition. On this timescale, evolution promotes niche differentiation ($\hat{\Omega}$), but this effect is counterbalanced by a simultaneous increase in fitness difference (θ) (Fig. 2). Hence, coexistence is enhanced by favoring niche partitioning, rather than by neutral mechanisms. Since we observe both an increase in the stabilizing mechanisms (increase in niche differences) and a reduction of the equalizing mechanism (in fitness differences), as in (Pastore et al., 2021), we use the measure of robustness η introduced earlier to show that between branching communities, evolution selects less fragile communities with respect to environmental perturbations that impact growth rates $\mathbf{r}$ (Saavedra et al., 2017). The fact that coexistence metrics are usually not independent is already appreciated (Barabás et al., 2018*a*; Song et al., 2019), but we here show how they are readily coupled throughout evolutionary dynamics. This link is made obvious in our trait-based model (Fig. 3), where niche position affects both growth rates and competition strength, and in turn Ω and θ. This interdependence makes it impossible to minimize simultaneously niche overlap and fitness differences (Fig. 3). Still, evolution leads to communities that are not strict optima of Ω nor minima of θ but rather lie on a Pareto front, an optimal compromise that is reached between niche increasing differentiation and restricting fitness imbalances. In a rare direct empirical test of this short term effect, Hart et al. (2019) find an increase in fitness difference after evolution, but not one in niche difference, which they explain may have been prevented by competition for a single discrete, non-substitutable resource. Still, evidence of (evolutionary) niche differentiation measured as character displacement abounds in other natural and experimental settings (Grant and Grant, 2006; Dayan and Simberloff, 2005), hence confirming that we should also expect evolution to increase both metrics in nature.

Our results suggest that costs in terms of community robustness may happen on a longer timescale, where evolution leads to diversification along with evolutionary niche packing. Branching points, by virtue of addition of one more phenotype, whose trait value and fitness are initially very close to an existing one, have a simultaneously equalizing and destabilizing effect. As the community size increases, robustness and niche differences peak at increasingly lower levels. This is a consequence of trying to pack a greater amount of phenotypes in the same resource width σ_R (Fig. 2). Classical theory shows that the number of phenotypes that can be packed on a resource axis is a function of resource width σ_R relative to the niche width of species (Macarthur and Levins, 1967). But when evolution is allowed in the community, the richness at the ESC is lower than under strict maximum (non-evolutionary) packing. In fact, ESCs are by definition uninvadable, because the fitness landscape for any possible invading trait value μ_m is zero at the resident trait values $\mu_1, ..., \mu_S$ and negative everywhere else; however, richer, feasible non-evolutionary configurations do exist for a given environment. This result has been shown to be consistent across a range of models, for both continuous and discrete resources (e.g., Case (1981); Rummel and Roughgarden (1983); Shoresh et al. (2008)). It is worth pointing out that the answer to whether evolution helps or hinders coexistence is context-dependent: when the community is undersaturated (fewer members than at the ESC), evolution drives an increase in robustness η. Conversely, by starting with feasible but supersaturated communities (more diversity than allowed at the ESC), η will repeatedly drop to zero and we observe a sequence of extinction events until the ESC is reached. For example, Shoresh et al. (2008) found that evolution destabilizes communities, which can be explained by the fact that they started with supersaturated communities. This also helps explain why (Loeuille, 2010) found evolution to be usually stabilizing for small communities (likely undersaturated), while its effect is reversed for rich communities (likely oversaturated). Empirical evidence for the longer term effects of evolution on community properties is difficult to acquire, but could be found in phylogenetic patterns of niche conservatism (Mayfield and Levine, 2010). For example, Yguel et al. (2016) report patterns consistent with increased productivity along time due to niche diversification and filling.

Ultimately, the evolutionary process results in ESCs that are highly non-random with respect to their structure and properties. Coevolved communities also show more evenly-spaced trait distributions than non-evolutionary communities in the model of Barabás and D'Andrea (2016) (but see Bennett et al. (2013)). Our results show that they are also more structurally robust. This has important implications in the context of global change: if coevolved communities are more robust to environmental stresses (changes in temperature, water, nutrients levels), this could have important consequences in terms of managing global changes that may need to be considered when guiding conservation efforts. Indeed, studies on the effects of global change often focus on single-species responses, but many have argued that community-level responses should be given more attention (Walther, 2010; Alexander et al., 2016; Gilman et al., 2010). Because community composition and interactions are modified by climate change and invasive species, leading to new assemblages that likely depart from coevolved structures (David et al., 2017; Blowes et al., 2019), our results suggest that the robustness of these new communities may be relatively poor. Further experimental testing of community-level responses to environmental stress in co-evolved versus randomized assemblages should prove an exciting and critically needed avenue of research, and the structural approach provides a useful theoretical framework to tackle the question. Experimental testing could for instance be undertaken using systems that rapidly diversify (e.g., the *Pseudomonas* system in Rainey and Travisano (1998)).

Regarding productivity, rich randomized communities tend to be more productive on average than poor ones (Fig. 5). By requiring randomized communities to be feasible, we however introduce a selection bias: in this sense, the positive slope between richness and productivity is indeed a byproduct of coexistence (Pillai and Gouhier, 2019), since the conditions that promote coexistence (namely niche differences), are also those that promote complementarity and greater productivity. Thus, we observe the emergence of trade-offs between community properties: higher total biomass values are possible among randomized communities, but these tend to have larger fitness imbalance and/or lower community robustness. This finding echoes results of Rohr et al. (2016) showing that very productive communities have low evenness, while those with lower deviation from the feasibility domain center (θ) have intermediate levels of biomass production. In agreement with Aubree et al. (2020), our results also show that evolutionary communities are often more productive on average than randomized ones, especially when species richness is low. Total abundance increases monotonically along evolutionary trajectories, first because of selection for higher intrinsic growth rates in the monomorphic case (selection effect), then due to a better use of the resource space by the diversifying phenotypes (complementarity effect) (Fig. 2). This is consistent with the expectation that increased diversification within and across species should lead to occupation of vacant niche spaces, leading to increased niche complementarity and utilization, and ultimately increased abundances at the consumer level (a hypothesis supported by Yguel et al. (2016)). For instance, some of the largest biodiversity ecosystem-functioning experiments have consistently reported an increase in the net effect of biodiversity on biomass production and of niche complementarity across a decade (Fargione et al. (2007); Marquard et al. (2009); Cardinale et al. (2007)). Similarly, Stefan et al. (2022) showed that plant-plant interactions shifted towards increased complementarity and yield over just a few generations of coexistence, while van Moorsel et al. (2018) report higher productivity in polycultures with an 8-year co-evolution history compared to identical-composition, but evolutionary naive plant communities. This evidence strongly supports the idea that the complementarity effect often observed in biodiversity-ecosystem functioning experiments is expected from an evolutionary point of view, and likely reinforcing along evolutionary trajectories. A consequence of this result is that many BEF studies may have underestimated the productivity gains due to biodiversity, by assembling *de-novo* communities, instead of coevolved ones. Conversely, relative yield measures might have been overestimated (Supplementary Material S5).

It is, however, possible to find more productive combinations among the random communities. Indeed, strict evolutionary optimization of total biomass at equilibrium only arises for the monomorphic case in this class of model and is lost in higher-dimensional systems (Rohr and Loeuille, 2022). Mathematically, this is because for $S = 1$, the selection gradient coincides with the gradient of $r(\mu)$ (Supplementary Materials S3). In polymorphic systems, maximizing biomass productivity would require further niche differentiation, at the expense of increasing fitness imbalance, which is not achieved under the Pareto-optimality engendered by evolution. This runs contrary to a widespread belief that evolution begets optimality: while growth rate optimization might be the norm in simple systems with weak or no interactions, this assumption does not generally hold true if we introduce realistic eco-evolutionary feedback loops (see also Lion and Metz (2018) for a treatment in epidemiological models and Metz and Geritz (2016) for a discussion on optimization principles).

Several questions remain open for investigation. We considered only competitive interactions and a single resource axis, so that packing more than two species with the same amount of niche overlap between all of them is impossible Macarthur and Levins (1967). If phenotypes were arranged in a multidimensional trait space, neutral configurations with multiple species would be possible. In addition, we considered only evolving niche positions in our model, but niche width could also evolve, leading to possible diversification between generalists and specialists species. Nevertheless, the theoretical predictions of our study need to be further experimentally tested. Although there is empirical support in biodiversity ecosystem-functioning studies regarding the increase in niche complementarity and biomass production over time, it remains unclear whether those predictions would hold in co-evolved communities emerging from diversification. Experimentally, comparison of properties of ESCs to non-evolutionary communities is complicated by the fact that ESCs are conceptually useful, but whether they are frequent in nature, and how to go about identifying them, is unclear (Edwards et al., 2018). Despite these hurdles, experimental tests of our theoretical results could provide timely evidence that would contribute to our understanding of evolution of communities properties and their interplay in rich systems. Such experiments could be undertaken in microbial systems, where rapidly evolving communities could be compared to control treatments of non-coevolved assemblages (Rainey and Travisano, 1998; Altermatt et al., 2015).

Data and code

Numerical simulations of eco-evolutionary trajectories were performed in Julia 1.5.1 (Bezanson, Edelman, Karpinski, and Shah, 2017), while computation of metrics of coexistence and plotting of results were done in R 4.0.3 (R Core Team, 2020). Code to reproduce the analyses will be made available on github.

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