Biodiversity is enhanced by sequential resource utilization and environmental fluctuations via emergent temporal niches

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Natural communities are incredibly diverse, and explaining how this biodiversity is even possible remains a central question in ecology. Resource competition is thought to play an important role in community interactions, but understanding diverse communities using resource competition is limited by the competitive exclusion principle: the prediction that only as many species as resources should coexist. Here, we demonstrate that sequential resource utilization, also known as diauxie, under periodic growth and death cycles allows for many more coexisting species than resources, violating the competitive exclusion principle. These violations become possible when fluctuations produce variations in the resource depletion order on each growth cycle. The depletion order varying allows the community to experience different sequences of temporal niches on each growth cycle, with temporal niches being the increasingly depleted environments produced by sequential resource depletions. While community-driven fluctuations and competitive-exclusion violations are rare under constant environmental conditions, we find that with even small environmental fluctuations most communities violate competitive exclusion, with several times as many survivors as resources in some simulations. We explore the competitive interactions within these communities and show that survivors are accurately predicted by temporal niches. We thus demonstrate highly diverse communities as a likely outcome of resource competition with a competitive structure based on ordered resource preferences.

Introduction

From coral reef fishes and grassland plants to ocean plankton and gut microbiota, natural communities display remarkable biodiversity. Yet, how this species diversity is stably maintained has long puzzled researchers[1–4]. As all organisms must consume resources to grow and survive, resource competition is often assumed to be a dominant interspecies interaction. However, current understanding of resource competition predicts a "competitive exclusion principle" that there should not be more surviving species than resources to compete for[5]. Amongst mechanisms such as tradeoffs between growth at high and low resource availability and interactions other than resource competition, temporal dynamics were an early suggestion for resolving the paradox and are still widely assumed to be a central part of the puzzle[2,4,6–15], in additional to broader experimental and theoretical interest in how temporal dynamics alter community

assembly[16–21]. However, how competitive exclusion violations become possible, whether these violations are biologically likely, and what niche structure arises remain largely unresolved.

Various dynamics in resource competition are known to produce competitive exclusion violations but typically do so only in narrow parameter regions, limiting their likelihood of occurring and of scaling to explain highly diverse communities. For example, tightly obeyed tradeoffs between growth rates and other parameters such as Monod constants, yields, and various forms of lag can allow two species to coexist on a single resource[12,14,22,23], with infinitely precise metabolic tradeoffs allowing infinitely many species to coexist on just one or a couple resources[22–25]. Yet, how to scale these simple mechanisms to support many more species than resources in multi-resource environments without relying on implausibly precise tradeoffs remains unclear. By leveraging dynamics specific to multi-resource competition, Huisman and Weissing 1999 demonstrated the stable coexistence of six species competing for three resources and twelve competing for five due to community-driven oscillations and chaos[8], but these competitive-exclusion violations occurred only in narrow parameter regions and the resulting communities were vulnerable to invasion and collapse[26,27]. Thus, a framework for exploring and understanding how resource competition can robustly lead to highly diverse communities remains lacking.

Previous consideration of resource competition has typically assumed that species simultaneously utilize all resources available to them. However, in nature sequential utilization of resources, also known as diauxie in case of microbial growth, is a ubiquitous phenomenon[14,28–34]. For example, a microbe might consume glucose first, lactose only after glucose depletion, and acetate last when all three are initially available. Even in complex environments microbes initially consume only a subset of the available resources and consume the remaining resources only after the first set has been depleted[31]. While sequential resource utilization is less commonly associated with macroscopic species, its essential elements appear across scales, such as when foraging animals display sequential utilization of resources by searching for lower preference resources only when others are unavailable[33–35]. And these sequential utilizations can lead to ecological consequences. Recent work has used diauxie as a lens for understanding and predicting microbial community assembly[14], including how the resource preferences of coexisting species relate to each other[36]. On macroscopic scales, seasonal changes in the niche overlap of foraging birds as resources become more or less available have been observed and connected to their ecology[34]. Together, these examples illustrate the importance of diauxic growth and the sequential depletion of resources to ecological community dynamics across scales.

Here, we use a simple model of diauxic growth to demonstrate the survival of many more species than resources due to temporal fluctuations. We first consider community-driven oscillations under constant environmental conditions and then consider a stochastically fluctuating environment. Community-driven oscillations are rare, but when they do occur exponentially many species as resources can coexist. This

enhanced coexistence is possible because fluctuating population sizes drive variations in the resource depletion order and therefore variations in which "temporal niches", or intermediately depleted environments, occur on each growth cycle, with exponentially many temporal niches as resources possible. We then introduce extrinsic environmental fluctuations in the form of a fluctuating resource supply and observe that with even small fluctuations the vast majority of communities violate the competitive exclusion principle. We show that the same temporal niche structure applies to both community-driven oscillations and environmental fluctuations and use our understanding of temporal niches to accurately predict which species survive. Our work builds upon previous understandings of highly diverse communities by elucidating the temporal niches that define their competitive structure and demonstrate how such rich biodiversity can arise from resource competition alone.

Results

Competitive exclusion can be violated under diauxic resource competition when oscillations or chaos occur. We wanted to better understand how temporal fluctuations lead to highly diverse communities, whether resource

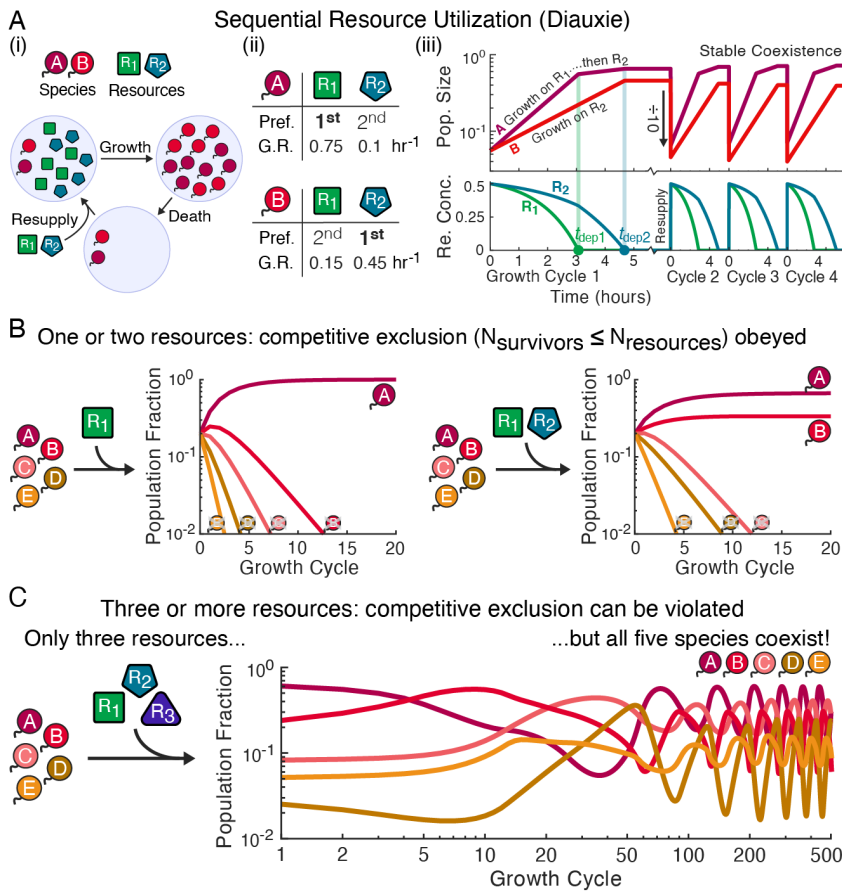

Figure 1. Diauxic resource competition can violate the competitive exclusion principle due to community-driven oscillations. (**A**) Definition of our model of resource competition with sequential utilization, also known as diauxie. (i) We assume a model of boom-and-bust cycles. Throughout all figures, circles with tails represent species and polygons represent resources. Species are inoculated into a well-mixed environment with finite quantities of resources available and fully deplete those resources as their populations grow. Species then experience a mortality before an instantaneous influx of resources and the start of the next growth cycle (Methods). (ii) Species are defined by their resource preferences orders (Pref.) and growth rates (G.R.) for each resources (Methods), as is illustrated for two example species. (iii) Simulated growth (top) and resource consumption (bottom) dynamics for those two species over four growth cycles. The resources depletion times determine each species' overall growth on each cycle and are indicated with vertical lines. Species A and B coexist because, while A initially outpaces B, after R_1 is depleted A's growth slows while B continues growing at its maximum growth rate. (**B**) When species compete for only one or two resources, the competitive exclusion principle, which predicts that only as many species as resources can survive, is obeyed. Species' population fractions at the end of each growth cycle for two example communities are shown (Appendix §1.1 for parameters). (**C**) However, when three resources are supplied, diauxie can produce community-driven oscillations and competitive exclusion violations. Shown is an example of five species competing for three resources with all five stably coexisting (Appendix §1.1 for parameters and Figure 2 for exploration of this example).

competition is sufficient for this diversity to be a likely outcome, and what structure highly diverse communities should have. Toward this goal, we began by developing a simple model of diauxie based on exponential growth and a periodic pulsed resource supply, capturing, for example, seasonal resource availability or the serial dilution experiments often performed experimentally. We assumed the period of the supply pulses was long enough that species completely depleted one pulse of resources before the next, creating a series of discrete growth cycles. In the case of a single resource, species grow at constant exponential rates until the resource is depleted, at which point the population sizes are divided by 10 (representing death or emigration during the starvation period), the resource concentration is returned to its supply value, and another growth cycle begins (Fig 1A, Methods). Because species have a single, constant growth rate with only one resource, the same species will always be the fast-grower and will outcompete all other species (Fig 1B). Thus, only a single species survives on a single resource.

With two or more resources, new dynamics arise because species now have ordered resource preferences that can vary between species and growth rates for each resource (Methods). Figure 1A illustrates an example in which species A prefers resource R_1 over R_2 while species B prefers R_2 over R_1. Species A is the initial fast-grower because its top-preference growth rate is faster than B's. However, A's faster growth means R_1 is depleted before R_2 and A needs to switch to R_2. In the example, A's R_2 growth rate is much slower than B's, and B is able to catch back up to A before R_2 is also depleted (Fig 1A). Feedback between the resource depletion times and species' population sizes allows the two species to stably coexist, converging towards a fixed point with constant population sizes from one growth cycle to the next (Fig 1A-B, Appendix §2.1). In the Appendix we show that when competing for two resources a fixed point is always reached (Appendix §3.1) and, with any number of resources, if a fixed point is reached there can be no more stably coexisting species than resources (Appendix §2.2). Thus, with one or two resources, at most one species per resource can stably coexist, obeying the "competitive exclusion principle" (Fig 1B).

However, when we proceeded to study diauxic competition for three or more resources, we discovered communities that did not reach fixed points but instead oscillated and had more surviving species than resources (Fig 1C). These examples were rare when sampling random communities (Appendix §3.2), but we were able to construct plentiful examples by choosing species likely to oscillate, confirming those oscillations, and then adding additional species that could coexist with the original species (Appendix §3.5). The example in Figures 1C and 2 has "anomalous" resource preferences that do not correlate to a species' growth rate order, but these are not necessary for oscillations to occur (Appendix §3.3). In addition to periodic oscillations, chaos was also observed (Appendix §3.4), with chaotic communities also able to violate competitive exclusion. Such rich dynamics and large increases in diversity were intriguing and suggested a valuable opportunity for studying and understanding highly diverse, resource competition-driven communities.

Temporal niches explain how fluctuations increase diversity and predict exponentially many species as resources could coexist. Having demonstrated competitive exclusion violations were possible, we proceeded to study the niche structure of the resulting highly diverse, fluctuating communities. Fluctuating population sizes should cause resource depletion times to also fluctuate, and, as these depletion times are fundamental to all interspecies interactions (Appendix §2.1), we began by looking at how they varied during oscillations. Focusing on the community of five species on three resources originally presented in Figure 1C (Fig 2A), we explored the growth and resource consumption dynamics on different growth cycles (Fig 2B).

We immediately noted that not only did the depletion times fluctuate, but the fluctuations were large enough that the order in which resources were depleted varied between cycles (Fig 2B). This varying depletion order has important consequences. On each growth cycle species grow in an increasingly depleted environment, first with all three resources present, then with all but one, and eventually on a

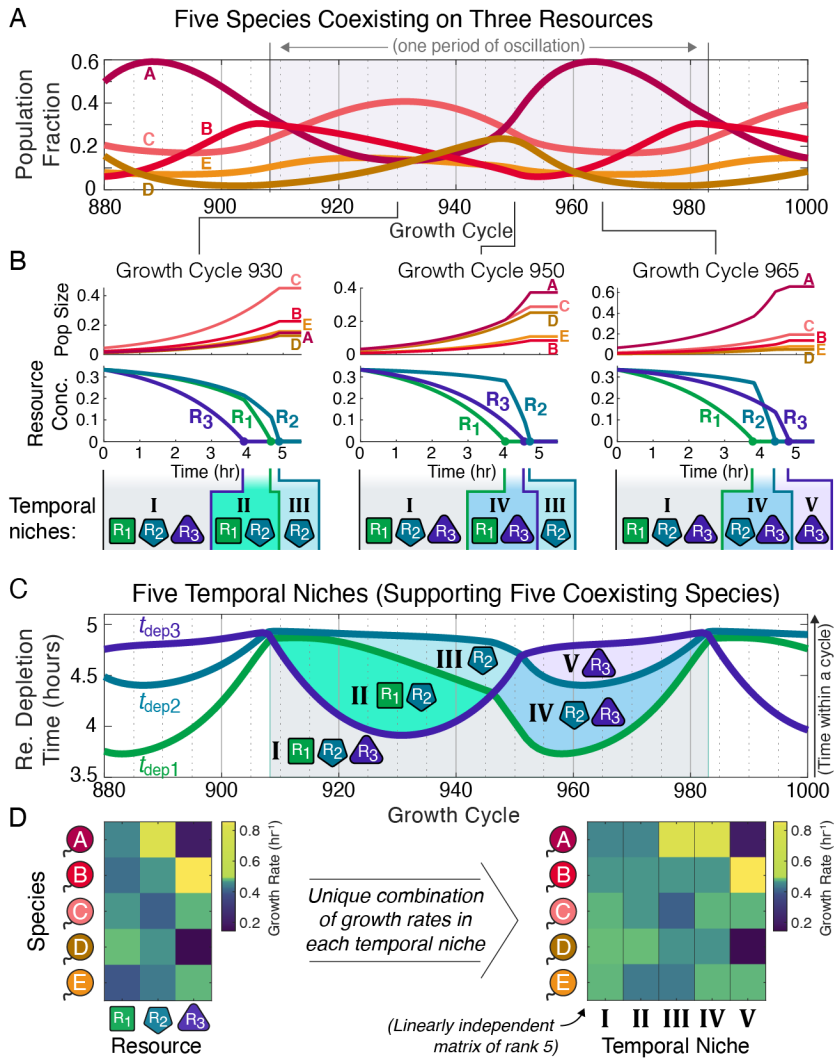

Figure 2. Oscillations allow for competitive exclusion violations due to an emergent temporal-niche structure with more niches than resources. (**A**) Population fractions at the end of each growth cycle for the example of five species coexisting on three resources presented in Figure 1C (Appendix §1.1 for parameters). (**B**) Growth and resource-consumption dynamics on three different growth cycles. Top row shows population growth over the course of each growth cycle, while middle row shows decaying resource concentrations. Because each resource is depleted at a different time, species grow first in the three-resource environment, then in a two-resource environment, and finally in a single-resource environment. These sequentially realized environments are "temporal niches". Fluctuating population sizes cause resources to be depleted in different orders on different growth cycles, so which temporal niches occur also varies, as is highlighted in the bottom row. (**C**) Resource depletion times (with $t_{\mathrm{dep}\,i}$ being the time spent in a cycle until resource R_i is depleted) across the entire period of the oscillation show a total of five temporal niches. Lines show the resource depletion times and shaded regions highlight the temporal niches. (**D**) Species' growth rates by resource (left) and in each temporal niche (right). Species only have one growth rate per resource, but their differing resource preferences produce different combinations of growth rates in each temporal niche such that each niche becomes a distinct growth phase with independent dynamics.

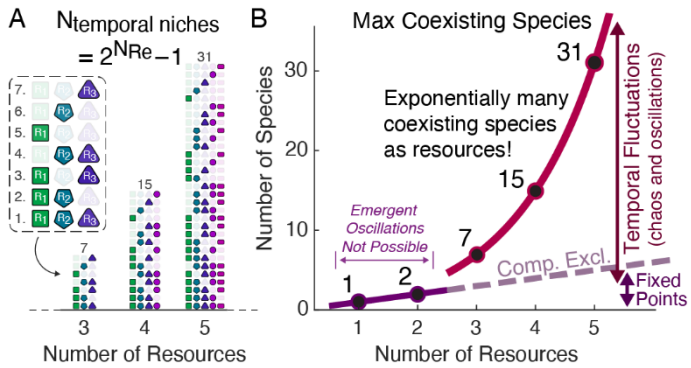

Figure 3. The maximum number of coexisting species scales exponentially with the number of resources. (**A**) The number of possible temporal niches is the number of binary combinations of whether or not each resource is still present ($2^{N_{\text{resources}}}$) minus the combination corresponding to all resources being depleted. Shown are all the possible temporal niches for the cases of three, four, and five resources. (**B**) There can be at most one surviving species for each temporal niche, creating an upper bound on the maximum number of coexisting species that rises exponentially with the number of resources, as shown here in red. For comparison, the competitive exclusion principle is shown as a dashed gray line. Oscillations or chaos are necessary for competitive exclusion violations and require at least three species and three resources (Appendix §3.1), so competitive exclusion applies if there are only one or two resources (blue line).

single resource (Fig 1B and 2B). We refer to these sequential environments as "temporal niches". In an oscillation with a variable resource depletion order, different sets of temporal niches occur on each growth cycle (Fig 2B). In the Figure 2 example, on Cycle 930 of the simulation species grow first in the all-resource niche then in the R_1-and-R_2 niche and finally in the R_2-only niche (Fig 2B). However, by Cycle 950, R_1 is depleted before R_3 (Fig 2B) due to the rising population fraction of species A, which prefers R_1, and declining fraction C, which prefers R_3 (Appendix §1.1). Because R_1 is now depleted before R_3, the two-resource temporal niche is now the R_2-and-R_3 niche (Fig 2B). Considering the resource depletion times across the entire oscillation, we tallied five temporal niches (Fig 2B and 2C) – five niches allowing five species to coexist on only three resources.

Although species have fixed growth rates for each resource and only consume one resource at a time, each temporal niche has distinct dynamics: species' growth rates are distributed across the temporal niches according to their resource preference orders such that no temporal niches share the same combination of species' growth rates (Fig 2D and Appendix §2.3). Thus, the environmental mediation of community interactions has enough degrees of freedom that conditions exist in which as many species as temporal niches can exactly match the periodic mortality and therefore coexist (Appendix §2.3). Differing resource preferences also create rich patterns in when and how often species are direct competitors and to which depletion times each species contributes on each growth cycle, allowing for the necessary independent degrees of interaction to stabilize multi-way coexistence (Appendix §2.3). Temporal niches thus explain how highly diverse communities can arise from resource competition when temporal fluctuations occur.

There can be one coexisting species for each temporal niche, and the maximum number of temporal niches is the number of combinations of whether each resource has been depleted yet, excluding the case of all resources being depleted (Fig 3A). This sets $N_{\text{species}} \leq 2^{N_{\text{resources}}} - 1$ as an upper bound on the number of coexisting species, and suggests that exponentially many species as resources may be able to coexist when oscillations or chaos occur (Fig 3B; Appendix §2.3). We are not aware of a proof that this bound is achievable for arbitrary numbers of

resources, but we leveraged our knowledge of the temporal niche structure (Appendix §2.3) to construct and simulate communities in which 7 species coexisted on 3 resources and 15 coexisted on 4 resources, which each saturated the upper bound, as well as examples of 23 species on 5 resources, which saturated 74% of the upper bound (Appendix §3.5), although increasing equilibration times to definitively demonstrate community stability made finding larger communities impractical. It therefore appears likely that exponentially many species as resources can coexist under diauxic resource competition when community-driven oscillations or chaos occur.

Competitive exclusion is usually violated in the presence of environmental fluctuations. Having established competitive exclusion violations were possible with a constant resource supply, we proceeded to consider the more realistic case of fluctuating environmental conditions as well as the frequency with which competitive exclusion is violated by random communities. When constructing examples with a constant resource supply, we had noted that community-driven oscillations, and therefore competitive exclusion violations, were rare (Appendix §3.1). Other mechanisms for violating competitive exclusion have been shown to have limited robustness to perturbations[26], so one might expect competitive exclusive violations under diauxic growth to become even less likely in the presence of environmental fluctuations. However, the competitive-exclusion violations we have demonstrated depend primarily on the resource depletion order varying, and environmental fluctuations would drive depletion-time fluctuations, so we speculated that the frequency of competitive exclusion violations and community diversity actually increase in the presence of environmental fluctuations.

To test whether environmental fluctuations would indeed increase the frequency of competitive exclusion violations, we defined sampling distributions for resource supply on each growth cycle as a function of the environmental fluctuation magnitude σ_{RS} (Fig 4A-B, Methods). The fluctuation magnitude varied from a constant resource supply at $\sigma_{\mathrm{RS}} = 0$ to a uniform-random supply at $\sigma_{\mathrm{RS}} = 0.236$ (Fig 4B). We generate 100 communities each containing 5000 random species with the metabolic constraint that the L2-norm of each species' growth rates equaled 1 hr^{-1} (i.e. $\sum_i g_{\mu i}^2 = 1\ \mathrm{hr}^{-2}$ where $g_{\mu i}$ is the growth rate of species μ on resource R_i), simulated these communities at each of 9 environmental fluctuation magnitudes, and tallied the survivors (Fig 4A-C, Methods). Without environmental fluctuations, all 100 communities saturated but never exceeded competitive exclusion (Fig 4C). However, with even small fluctuations of $\sigma_{\mathrm{RS}} = 0.09$ (Fig 4B for illustration), 74/100 random communities violated the competitive exclusion principle (Fig 4C). For fluctuations between $\sigma_{\mathrm{RS}} = 0.09$ and $\sigma_{\mathrm{RS}} = 0.236$ diversity remained high, with 64/100 to 83/100 communities violating competitive exclusion and an average of 4.21 +/- 0.04 coexisting survivors (on just the three resources). Thus, with even small to moderate magnitudes of environmental fluctuation, the majority of random communities violated the competitive exclusion principle.

Having shown competitive exclusion violations to be the most likely outcome with a fluctuating three-resource supply, we also

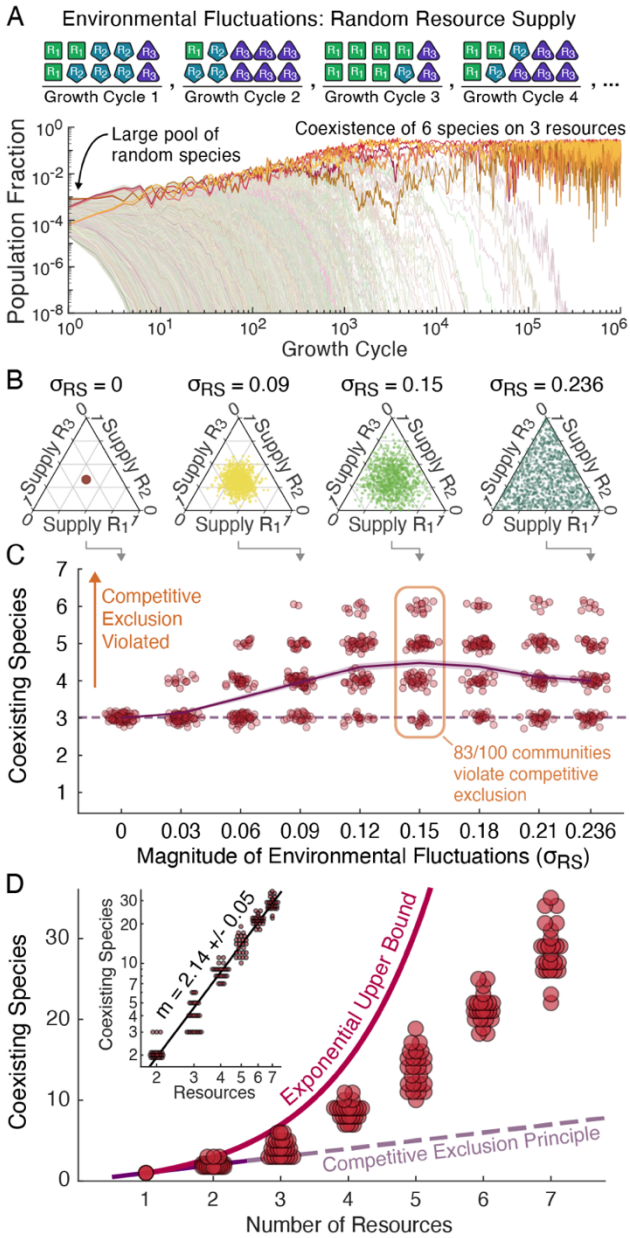

Figure 4. With environmental fluctuations, communities of random species frequently violate competitive exclusion. (**A**) Top row illustrates our implementation of extrinsic environmental fluctuations by randomly sampling the resource supply fractions on each growth cycle while keeping total supply constant (Methods). Plot shows population fractions at the end of each growth cycle for an example in which 5,000 random species were inoculated and simulated for 10^6 growth cycles with a uniform-randomly sampled resource supply on each day (σ_{RS} = 0.236). (**B**) Illustration of our resource supply sampling distributions as a function of the fluctuation magnitude σ_{RS} on simplex diagrams in which an equal supply of all resources maps to the middle of the triangle and a single resource being supplied maps to a corner (Appendix §1.2, Methods). For σ_{RS} = 0.09, 0.15, and 0.236, one thousand randomly sampled resource supplies are shown. (**C**) We sampled 100 communities of 5000 species competing for three resources with the metabolic constraint that the L2-norm of species' growth rates equal 1 hr^{-1}, simulated these communities at 9 different fluctuation magnitudes, and tallied the survivors (Methods). Points represent the number of coexisting species for each community at each fluctuation magnitude, the dashed line shows the competitive exclusion principle (one species for each of the three resources), and the solid line and shaded region provide the mean number of survivors and standard error. With even the smallest level of fluctuation 13/100 of communities violated competitive exclusion, and with fluctuations of σ_{RS} = 0.09 or larger competitive exclusion was usually violated, with a peak frequency of violations of 83/100 at σ_{RS} = 0.15. (**D**) We next simulated 25 random species pools for each of two through seven resources using a uniform-random resource supply (Methods). Points represent the number of survivors in the simulations. Shown for comparison are the competitive exclusion principle (one species per resource) and the exponential upper bound (Fig 3B). Inset shows the same data on a log-log scale with a monomial best fit. The monomial was a better fit than both linear and exponential models (Appendix §1.3).

investigated community diversity with more than three resources available. We sampled random growth rates for large species pools growing on two through seven resources (Methods) and simulated these communities with a uniform-random resource supply (σ_{RS} = 0.236 in the three-resource case). For four or more resources, all random communities violated the competitive exclusion principle with up to several times as many species as resources coexisting (Fig 4D). For example, with seven resources we saw an average of 28.2 +/- 0.6 survivors or four stably coexisting species for every resource (Fig 4B). However, while the expected number of survivors increased rapidly with the number of resources, it did not grow exponentially as our previously derived upper bound suggested it might. Instead, the best fit through our data grew slightly faster than

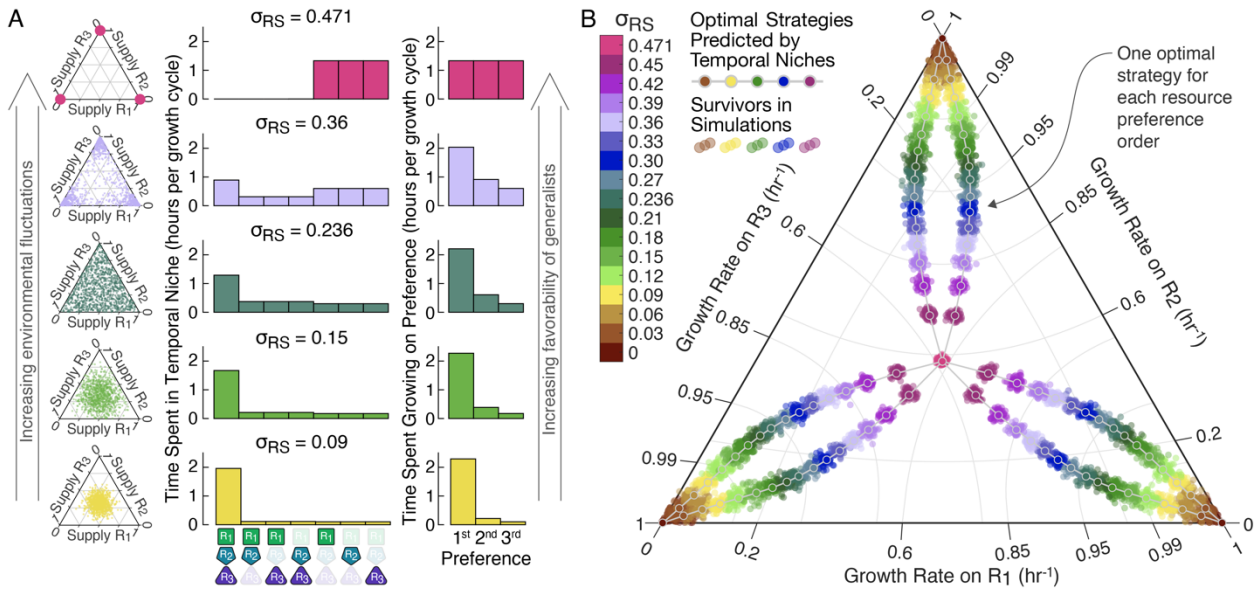

Figure 5. Temporal niches explain the composition of highly diverse communities in fluctuating environments. (**A**) We extended the resource supply sampling distributions to now have a maximum value $\sigma_{RS} = 0.471$, corresponding to a single randomly supplied resource on each growth cycle. Resource supply distributions are shown in the left column on the same simplex diagrams as in Figure 4B. We then simulated the 100 random communities of 5000 species from Figure 4 at 8 additional magnitudes for 17 total fluctuation magnitudes from $\sigma_{RS} = 0$ to $\sigma_{RS} = 0.471$. To develop a prediction of optimal strategies, we began by looking at the time spent in each temporal niche (middle column) and the time species spent growing on each of their resource preferences (right column). As the environmental fluctuation magnitude increased so did the time species spent growing on their second and third preferences, which would favor resource generalists. (**B**) Because species had been sampled with a metabolic constraint on their growth rates ($\sum_i g_{\mu i}^2 = 1\text{hr}^{-2}$), we could predict the optimal strategies (Appendix §2.4). We compared these optimal strategies against the survivors in simulations using a simplex plot which is nonlinear in $g_{\mu i}$ but in which complete specialization on a single resource still maps to the corners and equal investment in all resources still maps to the center (Methods, Appendix §1.2). At all fluctuation magnitudes, survivor growth rates are tightly clustered around the predicted optimal strategies.

quadratically, specifically $N_{\text{survivors}} = 0.44 * N_{\text{resources}}{}^{2.14}$ (Fig 4D). This growth in the number of coexisting species nevertheless scales to explain massively diverse communities, for example predicting over 100 species should stably coexist on 13 resources and over 1000 on 38. That not just some but all random communities would violate competitive exclusion and do so to such a high degree indicated that resource competition can be fully sufficient to explain highly diverse communities.

Temporal niches explain how environmental fluctuations reshape community composition With highly diverse communities shown to be a likely outcome of diauxic resource competition, we proceeded to explore whether our understanding of temporal niches could be used to predict the survivors and structure of these communities. To do this, we returned to the 100 random communities of 5000 species competing for 3 resources (Fig 4C), extended our definition of environmental fluctuations to allow for magnitudes up to $\sigma_{\text{RS}} = 0.471$, which corresponded to a single randomly selected resource being supplied each growth cycle (Fig 5A, Methods), and simulated the communities at eight additional fluctuation

magnitudes from $\sigma_{\mathrm{RS}} = 0.27$ to $\sigma_{\mathrm{RS}} = 0.471$.

We then considered the average time spent growing in each temporal niche and average time species spent growing on each preference (Fig 5A). Without fluctuations, all resources were depleted at nearly the same time, as found in previous reports[36]. This nearly simultaneous depletion meant essentially all growth occurred in the all-resources niche with all species growing on their top preferences, favoring specialists entirely invested in their top preference. By contrast, with only a single random resource supplied on each growth cycle at the maximum magnitude of environmental fluctuation, species spent equal time growing on each resource, favoring generalists equally invested in all resources (Fig 5A, top row). At intermediate levels of environmental fluctuations, the fluctuating depletion times meant all temporal niches occurred and that species grew on each resource but with more time spent on top preferences, favoring intermediate strategies in which species had some investment in all resources but greater investment on higher preferences (Fig 5A middle and bottom rows).

From the expected time on each preference and the metabolic constraint species had been sampled with ($\sum_i g_{\mu i}^2 = 1\mathrm{hr}^{-2}$), we calculated the optimal allocation of a species' growth rate allowance amongst its first, second, and third preferences at each fluctuation magnitude (Fig 5B, Methods). This optimal allocation could be applied to each of the possible resource preference orders to predict a set of six optimal strategies that would together form an uninvadable "supersaturated" community (Fig 5B, Appendix §2.4). We then compared the predicted optimal strategies to the growth rates of the species that had survived in simulation. At all fluctuation magnitudes the observed survivors had growth rates tightly clustered around the optimal strategies (Fig 5B). Our understanding of temporal niches thus led to intuitive and accurate predictions of the survivors in highly diverse communities, highlighting the potential for temporal niches as a lens for understanding the competitive structure of highly diverse communities.

Discussion

In this paper, we used a model of sequential resource utilization to show competitive exclusion violations first due to community-driven oscillations under constant environmental conditions (Fig 1-3) and then due to extrinsic environmental fluctuations in the form of a fluctuating resource supply (Fig 4-5). We used the case of community-driven oscillations to derive a temporal niche structure capable of supporting exponentially many species as resources (Fig 2-3). We then demonstrated that with environmental fluctuations most random communities competing for three resource and essentially all communities competing for four or more resources will violate the competitive exclusion principle with up to several times as many coexisting species as resources in our simulations (Fig 4). The temporal niche structure derived from the case of community-driven oscillations accurately predicted which species would survive in the case of environmental fluctuations (Fig 5). Our results thus demonstrate that resource competition is sufficient for environmental fluctuations to reliably produce highly diverse communities and that the structure of these

communities can be accurately predicted by the temporal niche structure we developed.

While we considered the simplest model of diauxic growth, numerous variations could be explored. For example, we did not incorporate diauxic lags, which are periods of little to no growth as species switch resources and which have been shown to be a source of coexistence[14,36]. With temporal fluctuations, if a species sometimes but not always finishes its lag in time to grow in a specific temporal niche, this sometimes-missed niche would be effectively split into two distinct niches, potentially greatly increasing the expected and maximum diversity. Similarly, Monod growth dynamics might increase diversity in our multi-resource model by having some species perform best early in a temporal niche while others perform best later in that niche. Additionally, microbial growth typically displays a mix of sequential and simultaneous utilization, consuming multiple but not all resources at a time[14,29–31]. If species' simultaneous utilization granted independent growth rates in each niche then communities that saturate the exponential upper bound on diversity could become a common occurrence due to potentially having a different species be the fastest grower in each niche. Incorporating each of these growth phenomena into the diauxie model could therefore yield even more greatly enhanced diversity and could each be an interesting subject of future research.

The metabolic constraint with which we sampled species could also be modified or even eliminated. When considering simultaneous utilization of multiple resources, metabolic constraints are an intuitive property of microbes as producing the enzymes to consume one resource leads to less capacity to produce the enzymes for others. With diauxie, however, microbes invest entirely in one resource at a time, so the origin of a tradeoff becomes unclear, although it still seems unlikely to have best-at-everything competitors. Macroscopic organisms, by contrast, cannot rapidly retool to the same extent microbes can and would therefore more likely be constrained by competitive tradeoffs. Nevertheless, to confirm that the metabolic constraint wasn't a prerequisite for our results, we ran additional simulations without any sampling constraints and saw that competitive exclusion violations were still a likely outcome (Appendix §4.1). Similarly acknowledging that in nature all resources are not equal, we ran simulations in which some resources were supplied in greater average amounts and in which some resources supported faster growth rates and again saw competitive exclusion violations remain likely (Appendix §4.2). These simulations thus confirm that highly diverse communities enabled by temporal niches are a likely outcome even without metabolic constraints or exact equality of resources.

Our findings about temporal niches suggest several phenomenon and properties which should be relevant across natural ecosystems at both microbial and macroscopic scales. The fundamental elements of diauxie are present whenever an ecosystem experiences boom and bust cycles or periodically available resources. For example, gut microbiomes breaking down food when their hosts have a meal, foragers feasting when foliage blooms, and predators whose prey is most available after a new generation is born would all experience sudden resource influxes and eventual depletions. In all these cases, some

resources will inevitably be depleted before others and a temporal niche structure will be created. Variability in relative resource influxes readily creates variability in relative resource depletion rates, which makes not just how a species responds to a depleting environment but how its response depends on which resources are being depleted most rapidly an important and consequential property. As we have shown in this paper, small changes in initial resource availability can create fundamentally different temporal niches as the environment becomes depleted.

Temporal niches supporting increased diversity can also be framed as a mechanistic basis for realizing the storage effect. The nonlinearity created when depletion orders change and the huge number of temporal niches created by even just a few resources explain how a large number of species could each have the potential for sufficiently beneficial conditions on particular growth cycles to recover and avoid extinction. Ecologist should consider whether a species that appears to lack the fitness necessary to coexist with its competitors benefits when specific temporal niches are created. Our work highlights how these temporal niches can explain highly diverse communities in a wide range of ecosystems. We hope this work can be a useful guide for other researchers exploring highly diverse communities, particularly those that appear to be driven by the competition for a relatively small number of resources.

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Methods

Diauxie Model

For clarity, we have used Greek letters (μ, ν, etc.) whenever indexing over species and Latin letters (i, j, etc.) whenever indexing over resources. Units are dimensionless except for time.

Species have population size $n_\mu(t)$ and growth rates $g_{\mu i}$. Resources have concentrations $c_i(t)$. Species grow exponentially on whichever resource is their highest remaining preference and consume one dimensionless unit of resource for each dimensionless unit of biomass gained (i.e. all yields equal 1). This produces dynamical equations

$$\begin{cases} \dot{n}_\mu(t) = g_{\mu\, r_\mu(\{c_i(t)\})} n_\mu(t) \\ \dot{c}_i(t) = -\sum_{\mu \text{ eating } R_i} g_{\mu i} n_\mu(t) \end{cases}$$

where the notation $r_\mu(\{c_i(t)\})$ indicates the index of the resource species μ is eating given the current resource concentrations (i.e. which resource ins its top remaining preference).

Growth rates and population sizes are always positive, so $\dot{c}_i(t) \leq 0$ and eventually $c_i(t) = 0$ is reached for each resource. We label the time when $c_i(t) = 0$ is reached for a particular resource as its depletion time $t_{\text{dep}i}$. When all resources have been depleted, the resource concentrations are reset to $c_i \to s_i$ where $\{s_i\}$ are the supply concentrations and all population sizes experience a mortality $n_\mu \to \frac{1}{10} n_\mu$. We refer to the time between consecutive resets as one growth cycle.

In all our simulations $\sum_i s_i = 1$, so at the end of a growth cycle $\sum_\mu n_\mu = \frac{10}{9}$ after accounting for day-to-day carryover. Reported population fractions are always at the end of growth cycle and therefore equal to $f_\mu = \frac{9}{10} n_\mu$.

Numerical Simulations

Simulations were performed in MATLAB. Because all growth is exponential, calculation of resource depletion times and species' growth on each cycle could be achieved by solving a sum of exponentials equations, eliminating the need for integrating dynamical equations. Species were declared extinct and removed from simulations when their population fractions dropped below 10^{-12}. Code needed to reproduce the basic results of the paper will be made available at the time of final publication.

Sampling Species in Environmental Fluctuation Simulations

Species were uniform-randomly sampled from the surface defined by $\sum_i g_{\mu i}^2 = 1\ \text{hr}^{-2}$ (where i indexes over a species' growth rates on different resources) by sampling from a symmetric multi-dimensional normal distribution, taking the absolute value of each component, and normalizing growth rate vector lengths to $1\ \text{hr}^{-1}$.

For the simulations with three resources and a varying fluctuation magnitude, 5000 species were sampled with independent growth rates and resource preferences, allowing so-called "anomalous" species. The same 100 pools of 5000 species per pool were used at all fluctuation magnitudes.

For the simulations with a variable number of resources, growth rates were randomly sampled and resource preferences were then set as matching the each species' growth rate order (thus disallowing "anomalous" species). To adjust for sampling species from a larger parameter space as the number of resources was increased, we held $\sqrt[\dim]{\rho_{\mathrm{Sp}}} = \text{const.}$, where $\dim = N_{\mathrm{Re}} - 1$ was the dimension of the space species were being sampled from and ρ_{Sp} was the density of species, and adjusted the number of species accordingly. The constant value of $\sqrt[\dim]{\rho_{\mathrm{Sp}}}$ was set such that the three-resource case used pools of 500 species.

Fluctuating Resource Supply Probability Distributions

In simulations in which the resource supply was not fluctuating, all resources were supplied in equal amounts.

When there were environmental fluctuations, resource supplies on each growth cycle were sampled from maximum entropy distributions under the constraint that on each growth cycle $\sum_i s_i = 1$ where s_i is the supply of resource R_i and that averaged across growth cycles the fluctuation magnitude,

$$\sigma_{\mathrm{RS}} = \sqrt{\langle \left(s_i - \frac{1}{3}\right)^2 \rangle},$$

had the desired value. These sampling distributions had the functional form of a normal distribution that was centered on an equal supply of all resources, was clipped by the boundary $s_i > 0$, and gained a negative variance at large fluctuation magnitudes. At small values the environmental fluctuation magnitude and the variance of the normal distribution were equal, but as clipping by the boundary $s_i > 0$ became significant the variance of the normal distribution grew faster than the fluctuation magnitude.

For the analysis of how diversity increased with increasing fluctuation magnitude (Fig 4), values of $\sigma_{\mathrm{RS}} > 0.236$ were excluded. The value $\sigma_{\mathrm{RS}} = \sqrt{1/18} \approx 0.236$ corresponds to a uniform-random sampling of $\{s_i\}$ so within the region $0.236 < \sigma_{\mathrm{RS}} \leq 0.471$ the entropy of the sampling distribution declines with increasing σ_{RS}. (For example, the limiting case of a single resource on each day at $\sigma_{\mathrm{RS}} = 0.471$ is arguably a less random resource supply than the uniform-random sampling at $\sigma_{\mathrm{RS}} = 0.236$ despite having a larger fluctuation magnitude as defined.) This unnecessarily complicated the interpretation of $\sigma_{\mathrm{RS}} > 0.236$, so this region was excluded from the analysis of how diversity increased with increasing fluctuation magnitude (Fig 4C). The full range $0 \leq \sigma_{\mathrm{RS}} \leq 0.471$ was, however, used for the analysis of how optimal strategies changed with increasing fluctuation magnitude (Fig 5) in order to highlight how an absolute generalist strategy eventually becomes favorable at $\sigma_{\mathrm{RS}} = 0.471$

For the simulations involving a variable number of resources (Fig 4D), the resource supply was always sampled uniform-randomly.

Numerically Sampling Resource Supply Distributions

For three resources, numerical sampling was implemented at small fluctuation magnitudes by sampling from normal distributions (using a lookup table to determine the correct variance after accounting for clipping by $s_i > 0$) and rejecting and resampling values outside $s_i > 0$. For three resource and intermediate to large fluctuation magnitudes ($\sigma_{\mathrm{RS}} \geq 0.21$), it proved faster to use a rejection-based sampling in which we uniform-randomly sampled s_1 through s_2, calculated $s_3 = 1 - s_1 - s_2$, rejected and resampled if $s_3 < 0$, and then randomly rejected and resampled at probability

$$\mathrm{P}_{\text{reject and resample}}(\{s_1, s_2, s_3\}) = 1 - p(\{s_1, s_2, s_3\})/\max\left[p\left(\left\{\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right\}\right), p(\{1,0,0\})\right].$$

Repetition of Simulations with Fluctuating Resource Supplies

For the simulations with three resources and a varying fluctuation magnitude, simulations were repeated five times in case species that could have coexisted with the other survivors experienced early stochastic extinctions. In many cases it appeared that one species would survive only if another experienced an early extinction. To determine which of these species was fitter, we then repeated simulations another three times, now giving any species that had survived in any of the first five simulations a head start (with population sizes $\sim 10^3$x higher) over the species that had been consistently excluded. This also served to test whether the final communities were vulnerable to invasion. The reported survivors are those that survived in at least two out of the last three repetition of the simulations. Time traces were then visually inspected to remove any species that were clearly trending towards but not quite reaching the extinction threshold (a population fraction of 10^{-12}).

Simplex Diagrams

For a visual explanation of simplex diagrams (used in Figures 4B and 5) see Appendix §1.2 and Appendix Figure S1.

Best Fit for Number of Species vs Number of Resources

We test two-parameter linear, monomial, and exponential fits. The monomial fit was the best fit as measured by either R^2 or mean square error:

	Functional Form	$\boldsymbol{b_1}$ **Fit**	$\boldsymbol{b_2}$ **Fit**	$\mathbf{R^2}$ **Stat**	**RMS Error**
Linear	$N_{\mathrm{Sp}} \sim b_1 + b_2 * N_{\mathrm{Re}}$	−11.1 ± 0.6	5.35 ± 0.12	0.935	2.43
Monomial	$N_{\mathrm{Sp}} \sim b_1 * (N_{\mathrm{Re}})^{b_2}$	0.444 ± 0.041	2.14 ± 0.05	0.963	1.83
Exponential	$N_{\mathrm{Sp}} \sim b_1 * \exp(b_2 * N_{Re})$	1.62 ± 0.11	0.414 ± 0.011	0.945	2.24

However, the monomial being the better fit was not statistically significant as measured by a F statistic: $p \approx 0.36$ for monomial vs linear and $p \approx 0.40$ for monomial vs exponential.

Down-Sampling in Figure 4A Plot

Due to computer memory limitations, we could not plot the full trajectories (including all 10^6 timesteps for all 5000 species), so for generating the plot shown in Figure 4A data were down-sampled. Population fractions after each of the first ten growth cycles are all shown. Populations fractions are then shown for every 2nd growth cycle for cycles 10 through 50. Then every 5th cycle for cycles 50 through 200. Then every 10th for cycles 200 through 1000. Every 20th for 1,000 through 2,000. Every 50th for 2,000 through 4,000. Every 100th for 4,000 through 7,000. Every 200th for 7,000 through 10,000. And every 500th for 10,000 through 1,000,000.