

Life history complementarity and the maintenance of biodiversity

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Kenneth Jops^{1,2} & James P. O'Dwyer^{1,2}

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Life history, the schedule of when and how fast organisms grow, die and reproduce, is a critical axis along which species differ from each other^{1–4}. In parallel, competition is a fundamental mechanism that determines the potential for species coexistence^{5–8}. Previous models of stochastic competition have demonstrated that large numbers of species can persist over long timescales, even when competing for a single common resource^{9–12}, but how life history differences between species increase or decrease the possibility of coexistence and, conversely, whether competition constrains what combinations of life history strategies complement each other remain open questions. Here we show that specific combinations of life history strategy optimize the persistence times of species competing for a single resource before one species overtakes its competitors. This suggests that co-occurring species would tend to have such complementary life history strategies, which we demonstrate using empirical data for perennial plants.

Neutral ecological models have provided a tractable approach to understanding competition among multiple species^{9–14}. These models assume that species are identical in their resource requirements and have shed light on patterns of species diversity and abundance observed in natural communities, particularly in cases where there seem to be relatively few ways for species to partition distinct resources^{11,15–18}. However, the very different traits observed among the species that populate natural communities have led to the question of how to build on neutral models by incorporating species differences and biological complexity^{12,19–21}, both to better explain patterns where neutral predictions break down^{14,22–25} and to put the basic theory on a more sound ecological footing. In short, the assumption that species are exactly identical seems to be untenable, but we lack a systematic path to understanding how species differences may change neutral predictions.

If hunger for resources sets the ecological scene, life history determines how and when that scene plays out. Life history is a description of the development, mortality and reproduction of an organism, and how the properties of these processes change throughout its lifespan. Some of the most obvious and consistent differences between species—what we often think of as defining characteristics of different species—fall under life history; for example their expected lifespan, time to reach maturity, fecundity and growth rate^{1–3,26–32}. This makes life history a natural axis along which to break the extreme symmetry of neutral ecology and introduce realistic species differences. Here we model competition among species that, like those in neutral models, have equal raw fitnesses—an assumption that we will later relax. This focus on equalizing mechanisms is motivated by the idea that there may be a limit to fitness³³ and that there may be multiple distinct strategies with this same optimal fitness. Previous models combining life history strategies and stochastic competition have then either allowed for complex life history variation but with the same life history strategy across all species^{34–36}, or have allowed for different life histories across

species but with life history variation assumed to collapse into just a single overall rate^{37,38}. Our new model and analysis considers groups of species with different, complex life history strategies (Fig. 1), and we show that a single critical parameter determines the persistence of these species in ecological communities.

Our model is detailed in Methods, ‘Competition simulation’, and simulates the dynamics of two species with different life history strategies competing over a limiting resource (such as light, space, water or nutrients). The life history strategy of each given species is then encoded in a matrix population model (MPM), in which mortality, growth and fecundity are recorded^{39,40}. Whatever parametrization is chosen, competitive dynamics arise from the combination of demographic stochasticity with the finite nature of that limiting resource. In support of these numerical results, we derive mathematical predictions drawing from two classic population genetics results. These results pertain to the year-to-year variance in abundance for a species with a given life history strategy, and fixation times for two competing alleles with different sensitivities to drift. The effective population size⁴¹ (N_y) for a stage or age-structured population^{42,43}, has an important role; N_y is quantified⁴³ by:

$$N_y = \frac{NT^2}{\sigma_L^2}. \quad (1)$$

Here, N is the number of new individuals born each year (correlated with the actual population size), T is the average age of a parent (a measure of generation time) and σ_L^2 is the lifetime variance in reproductive success of an individual—that is, taking into account the probability of survival to maturity, lifespan as a reproducing adult, and variance in fecundity across different ages or life stages^{44,45}. This result makes certain approximations for the structure of fluctuations around mean tendencies⁴³, which typically will hold to a good approximation, with the exception of extreme but

¹Department of Plant Biology, University of Illinois, Urbana, IL, USA. ²Carl R. Woese Institute for Genomic Biology, University of Illinois, Urbana, IL, USA. [✉]e-mail: kjops2@illinois.edu; jodwyer@illinois.edu

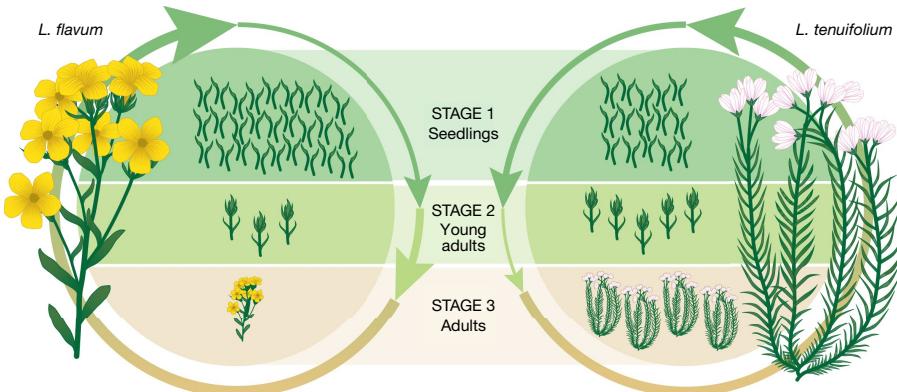


Fig. 1 | Life history differences among related, co-occurring species.

Linum flavum and *Linum tenuifolium* are two flaxes that co-occur across broad ranges in Europe and parts of Asia. Here we show some of the differences in birth, growth and mortality rates between these two species, as quantified in samples from the Czech republic⁶¹. Arrow thicknesses represent transition rates between life stages, whereas the abundance of individuals at seedling,

non-flowering adult and adult stages represent the approximate proportions of these abundances in the steady state for empirical populations. The name ‘flax’ etymologically shares a root with the word complexity, and these flaxes provide a motivating example for our study: why do their complex life history strategies differ in this way? We will seek to shed light on how and why those differences are constrained when both compete for similar resources.

unlikely life history strategies³⁶. Despite the name, the effective population size N_y has units of time, and is defined here in units of years (rather than the typical alternative of generations). In the context of population genetics for a single population, effective population size governs fixation times for novel alleles, and smaller values of N_y are generally associated with higher mutational load^{41,46,47}. Studies have identified broadly similar values for the effective population size across a range of taxonomic groups^{47,48}, albeit with some notable outliers⁴⁹.

Here, we will leverage the effective population size in a new context: understanding the outcomes of competition between species with different life history and the consequences for communities. Using a classic result for fixation of neutral alleles in haploid populations^{50,51}, we can derive the probability that one species with a given life history strategy will ultimately outcompete and exclude the other. For example, the probability that species 1 excludes species 2 is:

$$w_1 = \frac{N_{y1} p_1}{N_{y1} p_1 + N_{y2} (1 - p_1)} \quad (2)$$

where N_{yi} is the effective population size of species i and p_i is the initial fraction of space occupied by species i , with $p_1 + p_2 = 1$. Drawing from the same theoretical basis, we derive (in Methods, ‘Analytical derivation’) a normalized, dimensionless timescale for one of these two to exclude the other:

$$\langle t \rangle_{\text{normalized}} = \frac{2 N_{y1} N_{y2}}{(N_{y1} + N_{y2})(N_{y1} p_1 + N_{y2} p_2)}. \quad (3)$$

In Fig. 2a we compare these theoretical predictions with numerical simulations of competition, described above and in Methods. In summary, each of these species has an equal chance of winning this competition when the equation

$$N_{y1} p_1 = N_{y2} p_2. \quad (4)$$

holds true, and in cases where typical population sizes of two populations are similar so that $p_1 = p_2$, we should further expect that $N_{y1} \approx N_{y2}$, so that in effect the two species’ per capita effective population sizes (that is, their effective population size divided by actual population size) are equal or very close to being equal. We term the situation in which these life history quantities match ‘complementary’. Complementarity thus generalizes the idea of neutrality, since any pair of complementary species maximizes the persistence time relative to other possible

combinations of life history strategies, and any pair of truly neutral species matches this persistence time.

We next examine the consequences of this theory for diverse, natural communities. We predict that all other things being equal, we should see combinations of complementary life history strategies co-occurring, since these will persist longer than non-complementary combinations. Of course, all other things are not equal. Many factors act in concert to determine biodiversity maintenance. For example, in any model with stochasticity there is the possibility of local or global extinction of a given species. In neutral models, this is balanced by the introduction of novelty, via immigration or speciation, which combines with extinction timescales to determine the level of diversity maintained at a given spatial scale. These spatial and evolutionary processes are therefore important in predicting diversity, even when equalizing mechanisms are dominant. Moreover, coexistence theory also allows stabilizing mechanisms and niche differences to maintain diversity^{52–54}. In summary, the interplay of stochasticity, life history, dispersal and resource partitioning⁵⁴, as well as various types of mutualistic interaction^{55–57}, are all likely to have important roles in many communities. Conversely, if equalizing mechanisms do have a dominant role in the maintenance of biodiversity^{58–60}, our theory of complementarity predicts that as long as there is scope for sufficient trait variation, the per capita effective population sizes should vary less among co-occurring pairs of species than among species drawn from an appropriate null expectation.

We explore the outcome of life history complementarity at three different scales of organization. First, we consider specific, empirical population data to identify whether co-occurring pairs of species do have complementary life history strategies, as predicted by our theory. To test this idea, we draw from COMPADRE, an extensive database for life history strategies across species and groups^{61,62}. Our theory tells us that competition gives co-occurring pairs of species a reason to have similar effective population sizes, whereas groups of species with non-overlapping ranges are not constrained in the same way, and we show precisely this in Fig. 2b. For eight pairs of herbaceous, perennial plant species drawn from COMPADRE, filtered by the condition that their life history is documented in the same study, and that they are found at the same location, we find that persistence times are atypically high when compared with a suitable null group of herbaceous perennials. Put another way, the effective population sizes among these pairs are atypically similar, as our theory would predict.

Our second set of analyses is for communities of perennial plant species. We have shown in our theoretical derivations that pairs of complementary species persist for as long as pairs of neutral species.

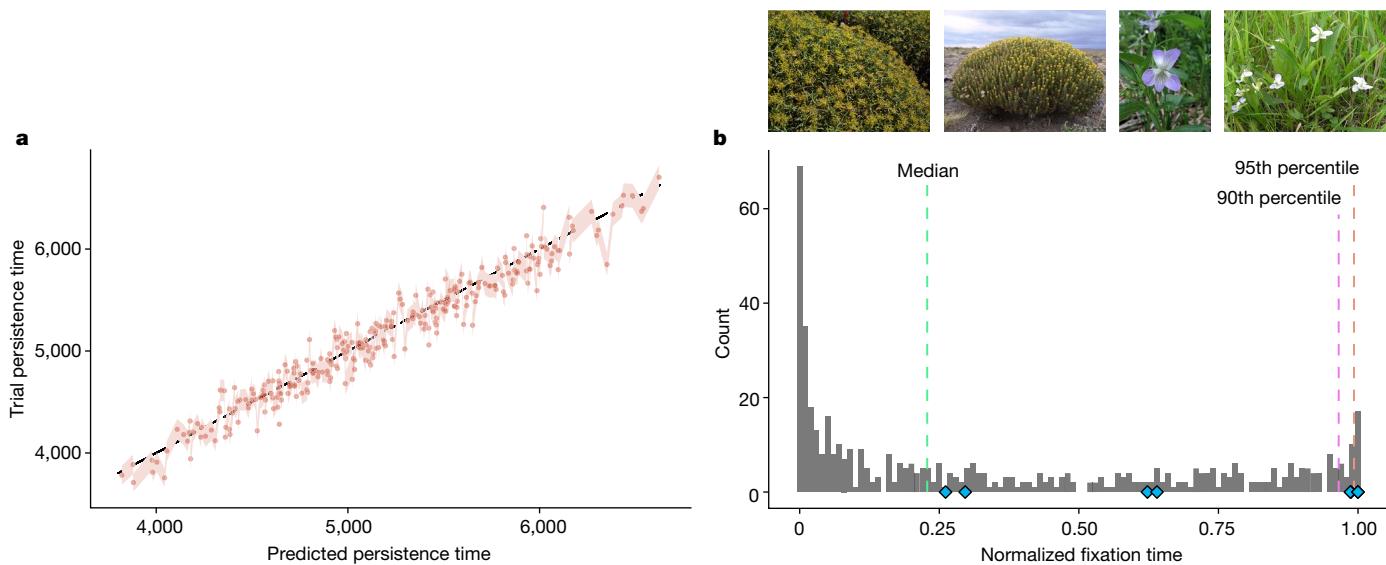


Fig. 2 | Simulation supports theory, and data support importance of life history for species pairs. **a**, Pairwise competition between pairs of life history strategies with two stages, generated synthetically, as described in Methods. The plot compares the predicted persistence time given by equation (3) with simulated persistence times for pairwise competition in a finite landscape, demonstrating that equation (3) captures the dependence of timescale on life history in competitive outcomes. Each data point represents the mean result over 500 model iterations, while the ribbons around points represent standard errors. **b**, Quantification of the complementarity of pairs of species drawn from the COMADRE database⁶¹, filtered by the condition that their life history is documented in the same study, they share a species type (such as herbaceous

perennial, shrub or tree (pictured)) and that they are found at the same location. Eight such pairs were discovered in eight locations and we plot the predicted, normalized persistence time of each pair. On this scale, a pair of species with complementary life history would have a persistence time of 1, the same as a truly neutral pair of species. We compare the persistence times of each of the eight empirical pairs of co-occurring species (blue dots on the x-axis) with an ensemble of pairs drawn from all species of matching types within the COMADRE database (grey bars). We find that the co-occurring pairs have atypically high normalized persistence times (equation (25)). All eight pairs exceeded the median (green line) of the set of random pairs, consistent with a P value of $\left(\frac{1}{2}\right)^8 = 0.0039$ in a one-tailed test on the relevant medians.

In neutral theory, high levels of biodiversity then follow from these long persistence times. This diversity is maintained in combination with a given level of immigration from an outside, regional source pool (or at larger scales, via speciation). Life history complementarity predicts two outcomes for diversity in these larger communities (Fig. 3). We

simulate a system with immigration events from a regional source pool occurring at a constant rate, and first show that when the source pool of life history strategies encompasses a narrow range of effective population sizes, local diversity is higher—consistent with the expectation that life history complementarity extends local persistence times, but

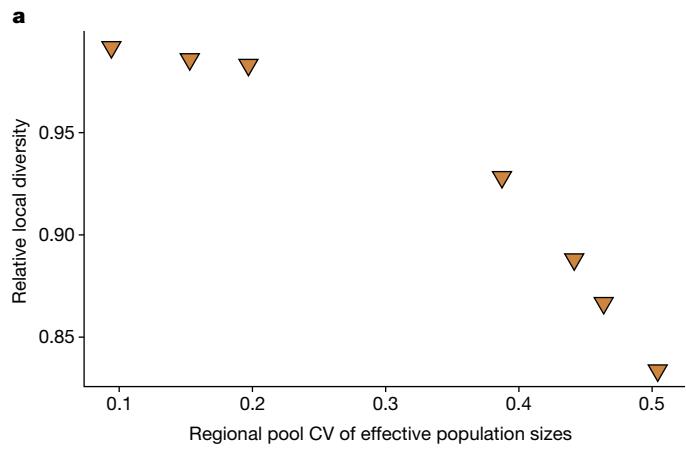


Fig. 3 | Complementarity boosts diversity, and competition filters effective population size. In neutral models, long persistence times of species in a local community—when combined with the introduction of novelty from outside—can maintain high levels of diversity. The set of regional pools that we used is described in Methods. **a**, The local diversity maintained in the steady state in a local community, when local extirpation is balanced by immigration from a regional pool. On the x-axis, we vary the degree of complementarity in this source pool from an essentially neutral source pool to a regional community with considerable variation in the per capita effective population size of its species. We see that local diversity is at its highest (shown here normalized by the fixed regional pool diversity) when the coefficient of variation (CV) of

effective population sizes in the regional pool is at its lowest. This dependence indicates that life history complementarity at a regional scale boosts diversity at a local scale. **b**, Local competition filters the variability in effective population sizes in a given regional pool. This numerical analysis complements our analytical predictions for pairs of species. Here we see that when a source pool of species contains a broad range of effective population sizes, the local community will filter this pool down to a more clustered group of effective population sizes. That is, groups of locally co-occurring species will tend to have more similar effective population sizes than those in the regional pool they draw from. Each data point represents the mean result over 500 model iterations.

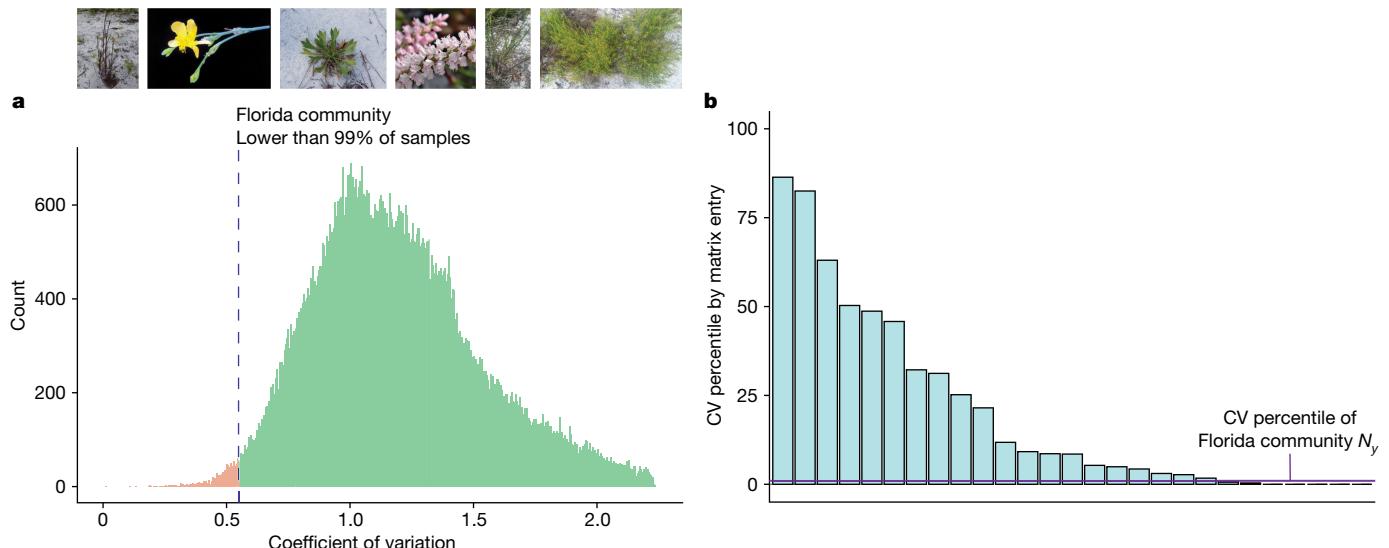


Fig. 4 | Life history strategies in a plant community are complementary, but not neutral. **a**, Analysis of a group of herbaceous perennials that co-occur in Florida. To identify whether their life history strategies are more complementary than by chance alone, we quantify the coefficient of variation in N_y values using a simple permutation test of 100,000 random samples of size 6. These samples are drawn from a set of 213 herbaceous perennials with documented life history strategies⁶¹, and individual species' effective population sizes were calculated as the mean of 500 model iterations. Across 100,000 samples (without replacement), the Florida group had a lower coefficient of variation than all but 975 random samples, and the P value was thus 0.00975 in a one-tailed comparison. Quantified in terms of index of dispersion (variance divided by mean), the Florida group had a lower value than all but four samples, with a P value of 4×10^{-6} . The six species are shown in photographs (from left to right, *Polygonella basiramia*, *Hypericum cumulicola*, *Eryngium cuneifolium*, *Polygonella robusta*, *Lechea cernua* and *Lechea deckertii*). **b**, Although the

strategies of these species are complementary, they are not neutral. Thirty-one of the entries of the Florida species' demographic matrices are non-zero for at least one species, thus allowing the coefficient of variation to be defined for that trait across these six species. We compare the Florida coefficient of variation values to the coefficient of variation for the corresponding trait (that is, the same matrix entry) across groups of six randomly drawn perennials, and plot the percentile for each Florida coefficient of variation relative to this null distribution. From **a**, the percentile for coefficient of variation for effective population size indicates that the Florida effective population sizes are clustered, relative to those of six species drawn from the null group. This is shown as a purple line in **b**. By contrast, the vast majority of traits have a larger percentile for their coefficient of variation relative to this null group, indicating that most demographic traits are not particularly clustered among the Florida species relative to effective population size.

now for larger groups of species. Thus, life history complementarity at a regional scale boosts diversity at a local scale, similarly to true neutrality. Second, even when the source pool of species contains a broad range of effective population sizes, the local community will filter this pool down to a relatively clustered group of effective population sizes, extending our analytical result above from pairs to larger groups of species—that is, groups of locally co-occurring species will tend to have more similar effective population sizes than their regional pool. This generalizes the idea that complementarity implies exactly the same values of N_y , to a more general expectation of tightly clustered values of effective population sizes. To explore this community-level prediction, we identified one co-occurring group of six perennials, documented in Florida, with life history strategies quantified in COMPADRE^{61,63–65}. This community was selected as the largest group of species in a single location of the same general species type (herbaceous perennials) with overlapping sampling years, the same matrix dimension, recorded by a small number of authors to control for methodology, and meeting the criteria listed in Methods, 'Identifying complementarity for pairs of co-occurring species'. We show in Fig. 4a that the coefficient of variation among the effective population sizes of these species is extremely (and significantly) unlikely to be as small by chance alone.

This provides further empirical evidence in support of our theory, but there is an important caveat: in cases where we identify similar effective population sizes among co-occurring species, we could just be rediscovering neutrality. That is, if the co-occurring species happen to be extremely similar in all their life history traits, we would expect this small amount of variation in traits to propagate through to a small amount of variation in effective population size. This would still be a case of complementary life history, but would be a trivial, neutral

version of it. In Fig. 4b, we provide evidence to the contrary: the Florida group of species are complementary, but not close to neutral. Specifically, they exhibit much smaller variation in their effective population sizes than we would expect from the raw variation in their life history traits. To explore this, we note that the Florida species' demographic matrices contain 36 possible traits that might vary. Thirty-one of these traits are non-zero for at least one of the six species, meaning that we can compute the coefficient of variation for that trait across this group, as we did for effective population size. Our methodology for understanding whether these species are close to neutral is then based around a comparison of how variable each trait is relative to variation in the same trait among an appropriate null group of species. For each Florida trait coefficient of variation, we compare its value to the distribution of coefficient of variations for the same trait, for groups of six perennials randomly drawn from COMPADRE. In Fig. 4b, we demonstrate that the majority of traits are much less tightly clustered relative to this null group than was effective population size. This suggests either that traits are varying only if they happen to have little effect on effective population size, or are varying in such a way that trade-offs between different traits effectively cancel their impact on effective population size. Either way, most demographic traits are highly variable across this group, whereas effective population size is highly clustered.

In our final exploration of the implications of complementarity, we identify predictions for the scaling of different life history traits at large scales using a simple, two-stage model. Individuals of a given species are divided into juveniles and adults, and the dynamics play out year by year. Juveniles can age into adults, with a mean age of maturity T_{mat} , and can also die with pre-reproductive mortality rate μ_1 . Adults can die with mortality rate μ_2 , but they also produce f new individuals per

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year. We consider multiple species with different values for these life history traits, and where each species has a typical population density J . If all species in a given community have complementary life history strategies, each species will be constrained by the relationship

$$\frac{(T_{\text{mat}}\mu_2 + 1)^2 J}{(1 + f T_{\text{mat}})\mu_2} = c \quad (5)$$

for a constant value c that may vary from ecosystem to ecosystem. We note that this bears a strong resemblance to documented empirical relationships between life history variables^{4,30}. Notably, this constraint can incorporate both fast and slow strategies, as long as the resulting combination incorporates negative correlations both between species fecundity and species age at maturity, and between species population density and species lifespan. The relationship between species fecundity and species age at maturity is documented for a broad range of taxonomic groups^{4,31,62}, whereas species population density and species lifespan have been proposed to depend strongly on organism size at maturity, but in opposite directions⁶⁶. In summary, broad, empirical relationships commonly observed between life history traits are compatible with our complementarity constraint for competing species.

We arrived at the prediction of life history complementarity by assuming that two or more species compete within the same niche, with the same deterministic fitnesses. We next examine how our prediction of life history complementarity changes when species have different fitnesses or partition resources differently. We demonstrate that the prediction of life history complementarity is robust to small variations in the fitnesses and niches of two competing species, whereas for large differences in either, we would indeed expect to see departures from life history complementarity (Supplementary Information and Extended Data Fig. 1a,b). First, suppose that two species compete for space but have different mean growth rates (λ_1 and λ_2) when rare. Naturally, we would expect to see the species with the higher growth rate outcompete the other; this would be the case if the world was purely deterministic. In a stochastic world, however, fitness differences of this type can be compensated for by differences in the two species' effective population sizes, N_{y1} and N_{y2} . We show in Extended Data Fig. 1a and Supplementary Information that the appropriate generalization of equation (14) indicates that this compensation will occur approximately when

$$\frac{1}{N_{y1}} - \log \lambda_1 \approx \frac{1}{N_{y2}} - \log \lambda_2. \quad (6)$$

Thus we might expect that groups of species with similar mean growth rates will have correspondingly similar—although not necessarily identical—effective population sizes. When fitness differences vary substantially but species still compete within the same niche, we predict this more general relationship between fitness and life history.

While we have focused on equalizing mechanisms, there is an ongoing debate over the prevalence of equalizing mechanisms versus stabilizing mechanisms in maintaining plant community diversity^{33,52,59}. Stabilizing mechanisms are also likely to have an important role⁵⁴—for example, arising from the partitioning of distinct resources. When species do differ in their resource requirements, but not by very much, they can still exhibit neutral patterns and dynamics^{20,21}. This suggests that our theory of complementarity among co-occurring species may still apply when species partition resources. We demonstrate this for two species competing for space but among two different soil types, and with species-specific growth rates in each soil type. For intermediate degrees of resource partitioning, we show that persistence time for two species remains peaked around the point where their life history strategies are complementary (Extended Data Fig. 1b, with the model described in Supplementary Information). In a third analysis, we combine fitness and niche differences (Extended Data Fig. 2 and Supplementary Information) and demonstrate that the schedule of birth,

growth and death matters for predicting persistence time, even when fitness and niche differences are taken into account. Thus, for stochastic competition, life history strategy should be considered alongside growth rate differences and resource partitioning in understanding what maintains biodiversity.

There is a long history in ecology of seeking simplifying theories, with notable examples in modelling the maintenance of diversity and in understanding life history traits. But in many cases these models oversimplify. Neutral ecology and its striking assumption of equalizing mechanisms looms large when we think of simplified models for species coexistence. However, its assumption that species are identical does not ring true for most ecologists, and it is difficult to know how to gradually introduce meaningful complexity. Life history theory also has a long history of simplified models, with r–K selection theory⁶⁷ and related, taxon-specific approaches such as Grime's Competitor-Stress tolerator-Ruderal theory⁶⁸. That idea that one of a handful of quantities will tend to be optimized in life history has been enriched by a focus on the multiple demographic differences in species across life stages encapsulated by the MPMs that we study here—and the consensus has perhaps converged on the idea that there may be no single, simplifying rule for life history⁶⁹. Our approach puts these complex demographic differences together with stochastic competition, and what emerges is a new understanding of both. On the life history side, we find evidence for the optimization of a new life history quantity—not r or K, but effective population size, N_y . On the competition side, we already knew that neutral, equally fit species can persist for extremely long timescales before one species excludes the others. Incorporating life history differences between species could a priori have led to the collapse of such communities, or it could have been that so long as fitnesses are equalized, life history strategy makes no further difference at all. The third possibility and actual outcome is somewhere in between, with effective population size picked out as the key life history variable that both constrains and is constrained by competition.

Putting these predictions together, we have a powerful new incentive to extend efforts to quantify life history strategies for entire communities. In addition to predictions for persistence and coexistence, our approach may also inform our understanding of spatial distributions and evolutionary changes in life history strategy. Certain life history strategies clearly confer a competitive advantage, but this advantage may play out over long timescales and interact with dispersal limitation to produce the distributions in life history strategy that we observe across space and time. Finally, our model also has implications for broader, applied ecological questions. These include our understanding of how life history influences the displacement of one species by others during successional processes⁷⁰, the invasibility of resident communities⁷¹, and perhaps even in seeking life history traits that are important for ecological restoration and management^{72,73}.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-023-06154-w>.

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Article

Methods

Matrix population models

The primary metric of a species' life history strategy in this study is the set of demographic indicators, broken down by ages or stages, as seen in a matrix population model (MPM). These indicators represent survival and fecundity at each age or stage as well as the probability of transition between two stages. We will present only stage-structured MPMs rather than age-structured, or Leslie matrix, models as the latter can be formulated as a case of the former. In an MPM the parameters are arranged in a matrix so that they can be multiplied by a column vector n_t of n_i values at some time t , each representing the number of individuals in that stage, to give the stage-structured population at the next time step, $t + 1$:

$$n_{t+1} = \begin{pmatrix} s_1 & t_{12} + f_1 & \dots \\ t_{21} & s_2 & \dots \\ t_{31} & t_{32} & \dots \\ \vdots & \vdots & \ddots \end{pmatrix} \times \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \end{pmatrix} \quad (7)$$

Where the fecundity terms, denoted by f_i , represent the mean number of offspring produced by an individual of stage i , the transition terms t_{ji} are the probability of an individual in stage i transitioning to stage j , and the survival terms s_i are the probability of a stage i individual remaining in that stage over a given time step^{39,40}. We consider only annual time steps in this study, but present our methods such that other time steps can be used.

Several useful statistics can be extracted from these matrices, and many will be referenced in the description of modelling methods below.

For a stage-dependent mortality rate over one time step, one can subtract the column sums of the survival matrix (defined as the matrix with its fecundity terms subtracted out) from 1 to define vector μ (letting U be the survival matrix in question):

$$\mu = 1 - \text{colSums}(U) \quad (8)$$

The solution to the vector equation:

$$A \times v^0 = \lambda v^0 \quad (9)$$

normalized such that $|v^0| = 1$ gives a vector of steady proportions between stages for an MPM defined by matrix A . This vector has an associated largest eigenvector λ which takes a real value and describes a long-term exponential growth rate for a population in steady proportion. A population in such proportion is not expected to change in total size between time steps³⁹ if the eigenvalue λ is also normalized to 1.

Competition simulations using MPMs

Model construction. We developed a model to simulate the interactions of multiple species with different life history strategies competing over a common resource or set of resources. The demographic parameters associated with each species are given by an empirically measured or synthetically constructed MPM. To begin, set a matrix of initial population values broken up by stage and species, P^0 , and a cap on the total population size such that $\sum(P^0) \leq \text{cap}$. Typically, trials begin with species in proportion to their steady state and to avoid biases from rounding (individuals must be in discrete numbers whereas v^0 is a continuous vector) the proportions are adjusted by multiplying by a normal distribution with mean 1 and s.d. 0.01 and then rounded.

Transitions between stages and deaths are then tallied. Each individual has transition probabilities as defined in the relevant MPM. Thus if an individual has probability μ_i of dying, s_i of remaining in stage i and

t_{ij} of transitioning to some other stage j (letting stages run from 1 to k), its stage at the next time step is given by a multinomial distribution with one trial and probabilities given by

$$\mu_i + s_i + \sum_{j=1}^k t_{ij} = 1 \quad (10)$$

To scale the process up to n_i individuals of stage i , a multinomial of n_i trials and the probabilities given above is used.

After the number of individuals in each stage following transitions is set, the number of new offspring for this time step is calculated. Individuals in reproductive stage i have an associated f_i from the MPM which determines the mean number of offspring produced in a time step. Each individual in stage i then produces a number of potential offspring given by a Poisson distribution with mean f_i and all recruits of that species are assumed to be stage 1. If the number of recruits produced exceeds the cap on total individuals in the system, the recruits are instead tallied and then drawn randomly so that the total population is equal to the cap. Note that reproduction is the only process in this model that can increase the total number of individuals (the transition stage can only reduce it), so the cap is relevant only at this step.

This process is repeated until one species has 0 individuals left in the system or the model exceeds a certain maximum number of time steps. A 'winner' is defined as the species that remains, and the years to monodominance of this trial is given by the number of time steps completed, assuming a distinct winner emerges, or set to the maximum number if both species persist throughout the trial. Given the highly variable nature of this stochastic simulation, 500 trials were performed for each combination of species and the mean number of time steps completed or aggregate number of wins per species are presented.

Analytical derivation of persistence times and complementarity condition

Species in a neutral community will not coexist indefinitely. For example, one of two neutral species competing will eventually exclude the other, characterized by a mean persistence time⁷⁴:

$$\langle t \rangle_{\text{neutral}} = 2N_y \left((1-p)\log\left[\frac{1}{1-p}\right] + p\log\left[\frac{1}{p}\right] \right), \quad (11)$$

where one species starts with frequency p and the other with $1-p$, and N_y is the yearly effective population size. How does this outcome change when two species with equal fitness, but different life history strategies, compete for space? We draw on a formulation of this question in terms of two competing alleles with different levels of drift⁵⁰, where the latter is characterized by variances in year-to-year changes in the respective populations, σ_1^2 and σ_2^2 . In this model, one has a system where population sizes fluctuate independently over time, but with the total sum of individuals periodically 'reset' to equal the carrying capacity of system⁵¹, K . Under these assumptions, the probability $P(p, t)$ that species 1 has frequency p at time t satisfies:

$$\frac{dP}{dt} = -\frac{\partial}{\partial p} (M(p)P) + \frac{1}{2} \frac{\partial^2}{\partial p^2} (V(p)P) \quad (12)$$

where

$$M(p) = \frac{p(1-p)}{K} (\sigma_2^2 - \sigma_1^2) \quad (13)$$

$$V(p) = \frac{p(1-p)}{K} (\sigma_2^2 p + \sigma_1^2 (1-p)) \quad (14)$$

If species 1 has initial frequency p_1 (and consequently species 2 has initial frequency $p_2 = (1 - p_1)$), the probability that species 1 ultimately excludes species 2 is given by⁵⁰

$$w_1 = \frac{\sigma_2^2 p_1}{\sigma_2^2 p_1 + \sigma_1^2 (1 - p_1)}$$

as stated in the main text. In certain limits, it is straightforward to derive the mean time for either species to exclude the other. The probability $Q(t, p_1)$ that species 1 excludes species 2 after a time t , conditioned on that eventual outcome, satisfies the backwards Kolmogorov equation⁷⁵:

$$\frac{1}{2} V(p_1) \frac{\partial^2 Q}{\partial p_1^2} + M^*(p_1) \frac{\partial Q}{\partial p_1} = \frac{\partial Q}{\partial t}, \quad (15)$$

where

$$M^*(p_1) = M(p_1) + \frac{V(p_1)}{w_1(p_1)} \frac{dw_1}{dp_1}. \quad (16)$$

The Laplace transform $g(s, p_1) = \int_0^\infty e^{-st} Q(t, p_1) dt$ of this distribution satisfies

$$\frac{1}{2} V(p_1) \frac{\partial^2 g}{\partial p_1^2} + M^*(p_1) \frac{\partial g}{\partial p_1} - sg = 0. \quad (17)$$

The mean time for species 1 to exclude species 2, conditioned on that event happening, can be expressed in terms of this Laplace transform as follows. We first note that by definition:

$$\partial_s g(s, p_1) = \int_0^\infty te^{-st} Q(t, p_1) dt \quad (18)$$

and so our quantity of interest is given by:

$$\langle t(p_1) \rangle_1 = \int_0^\infty t Q(t, p_1) dt = -\partial_s g(s, p_1)|_{s=0}. \quad (19)$$

From this we can deduce that by taking the derivative of equation (17) with respect to s , and then setting $s = 0$ we will have:

$$\begin{aligned} 0 &= \frac{1}{2} V(p_1) \frac{\partial^2 \langle t \rangle_1}{\partial p_1^2} + M^*(p_1) \frac{\partial \langle t \rangle_1}{\partial p_1} + g(0, p_1) - 0 \times \langle t(p_1) \rangle_1 \\ &= \frac{1}{2} V(p_1) \frac{\partial^2 \langle t \rangle_1}{\partial p_1^2} + M^*(p_1) \frac{\partial \langle t \rangle_1}{\partial p_1} + 1. \end{aligned} \quad (20)$$

When $\sigma_2^2 \gg \sigma_1^2$, so that $M^*(p) \approx \frac{p(1-p)\sigma_2^2}{K}$ and $V(p) \approx \frac{p^2(1-p)\sigma_2^2}{K}$, this differential equation for $\langle t(p_1) \rangle_1$ has the following closed-form solution

$$\langle t(p_1) \rangle_1 \approx \frac{2K}{\sigma_2^2} \left(\frac{1-p_1}{p_1} \log \left[\frac{1}{1-p_1} \right] + \log \left[\frac{1}{p_1} \right] \right). \quad (21)$$

which can be checked via direct substitution of equation (21) into equation (20) (and taking the limits above for $M^*(p)$ and $V(p)$).

Using equation (2) to supply the appropriate probabilities, we can then convert expected times $\langle t(p_1) \rangle_i$ conditional on a particular species ($i = 1$ or $i = 2$) excluding the other, into an expected time for either species to exclude the other. That is, the mean persistence time for which the two species will co-occur, as a function of the initial frequency of species 1:

$$\begin{aligned} \langle t(p_1) \rangle &= w_1 \langle t(p_1) \rangle_1 + (1 - w_1) \langle t(p_1) \rangle_2 \\ &\approx \frac{2K}{\sigma_2^2 p_1 + \sigma_1^2 (1 - p_1)} \left((1 - p_1) \log \left[\frac{1}{1 - p_1} \right] + p_1 \log \left[\frac{1}{p_1} \right] \right). \end{aligned} \quad (22)$$

Effective population size N_{y_i} in effect allows us to eliminate both of the σ_i^2 , as they are defined via $N_{y_i} = \frac{K}{\sigma_i^2}$. Replacing each instance of σ_i^2 by the corresponding expression in terms of effective population size, we therefore arrive at:

$$\langle t(p_1) \rangle = \frac{2N_{y_1}N_{y_2}}{N_{y_1}p_1 + N_{y_2}(1-p_1)} \left(p_1 \log \left[\frac{1}{p_1} \right] + (1 - p_1) \log \left[\frac{1}{1 - p_1} \right] \right). \quad (23)$$

In the special case where initial population sizes of both species are the same (the condition in which model results were obtained), this expression collapses to:

$$\langle t(1/2) \rangle = 2 \log[2] \frac{2N_{y_1}N_{y_2}}{N_{y_1} + N_{y_2}}. \quad (24)$$

Which is equal to the harmonic mean of the neutral fixation time of each species given in equation (6).

Finally, we note that, as per equation (11), there is a characteristic persistence time for either of these species if they were competing against an exact copy of themselves. This means that some species pairs will tend to persist for a long time primarily because one of them is associated with a long persistence time, independent of the other. To normalize for this effect, we now divide by the mean neutral persistence time for each species competing against a copy of itself from equation (11), averaged across the two species. Doing so, we arrive at equation (3) in the main text:

$$\langle t \rangle_{\text{normalized}} = \frac{2N_{y_1}N_{y_2}}{(N_{y_1} + N_{y_2})(N_{y_1}p_1 + N_{y_2}p_2)}. \quad (25)$$

Testing theoretical predictions for persistence using competition simulations

We now link the MPMs and competition simulations described in 'Matrix population models' and 'Competition simulations using matrix population models' to the analytical results derived in 'Analytical derivation of persistence times and complementarity condition'. The result provides the basis for the test of the theoretical predictions shown in Fig. 2a of the main text. We first describe how to extract the effective population size N_y for a given MPM via simulation, and then describe the specific MPMs that we compete against each other to generate Fig. 2a.

Computing effective population size for a given MPM. Though we do not present here a generalized analytical method for the effective population size (N_y) of a species or arbitrary matrix dimension, this quantity can be inferred from the simulation described in 'Competition simulations using matrix population models'. This is done by running simulated trials to find the neutral fixation time of the species, using two identical copies of the species starting at equal abundances. These trials are run just as trials between different species are, recording the number of annual time steps until one copy reaches an abundance of 0. This value, averaged across trials, is thus a numerical approximation of the value derived in equation (21). In this case, since both species are identical, $N_{y_1} = N_{y_2}$ and equation (21) collapses to:

$$\langle t(1/2) \rangle = 2 \log[2] \frac{2N_{y_1}^2}{2N_{y_1}} = 2 \log[2] N_{y_1} \quad (26)$$

and thus the effective population size of a species is simply a linear factor of its own neutral fixation time.

Synthetic matrix construction. Synthetic matrices used for trials in this study were generated through non-linear optimization using the R package nloptr and the improved stochastic ranking evolution strategy algorithm^{76,77}. Initial conditions were generated randomly by

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picking values between 0 and 1 for each of the three survival and transition terms in the matrix. The fecundity entry (the fourth entry in the matrix) is fixed by these three values along with a constraint on the leading eigenvalue of the matrix. The characteristic polynomial for the matrix with constraint $\lambda = 1$ was solved along with additional constraints to make the matrices feasible for analysis. These included ensuring that column sums were less than 1 to ensure positive mortality rates, lower and upper bounds on transition rates (between 0 and 1), and often additional constraints on the properties of the matrix. The set of matrices demonstrated in Fig. 2a were generated by solving for a range of predicted N_y values across the set of 25 matrices with a fixed starting population size. To achieve this, the objective function of the optimization was set to solve $N_y = \frac{T^2 N}{\sigma^2}$ for a given value of N_y from the matrix entries as detailed in 'Two-stage, juvenile–adult model'. The matrices used in Fig. 3a,b were constructed using the same method, generating a larger set of 130 matrices with predicted N_y such that each value was 100 higher than the last. The matrix with the median N_y was run neutrally with 12 copies for comparison. For each set of trials, 12 matrices were selected such that their mean N_y varied as little as possible (the set with the furthest mean from the neutral set was less than 3% lower than the median comparison matrix) but their variance in N_y varied. The set with the highest variance had variance 28 times higher than that with the lowest, corresponding to the roughly five-fold increase in the coefficient of variation shown on the x-axes of Fig. 3a,b.

Identifying complementarity for pairs of co-occurring species

As described in the main text, we leveraged the COMPADRE database⁶¹ to provide a selection of pairs of co-occurring perennial plant species with quantified life history strategies. We hypothesize that if equalizing mechanisms underly the persistence of these co-occurring pairs, then their life history strategies will be such that they will persist longer before one species excludes the other, in comparison to an appropriate null model of pairs of competing species.

For both the observed co-occurring pairs, and the null pairs, we compute a theoretical persistence time by competing the corresponding MPMs for the two species in the competition algorithm described in 'Competition simulations using matrix population models'. Figure 2b in the main text then summarizes the outcome for persistence times among co-occurring species, and how this contrasts with the typical persistence time for a randomly drawn pair from the comparison group. Here we describe the process by which we selected species from COMPADRE.

Selection of matrices from COMPADRE. We included matrices based on the following criteria. First, only matrices marked as 'Unmanipulated' and 'Divisible' in their metadata were included. The unmanipulated designation excludes matrices resulting from studies on the effects of treatments in various experiments (such as burning, grazing, chemical treatment, etc.). Divisibility refers to the separation of matrices into total, survival, fecundity, and clonal reproduction components. This was to ensure that species' fecundity was distinguishable from transitions into their first stage (this distinction is not apparent when looking only at the full matrix). Species with clonal reproduction were not sampled, though changes to our modelling framework could allow for clonal reproduction in future studies. The maximum dimensionality of matrices was limited to 15 to optimize running time for the large number of trials necessary.

The pairs of co-occurring species analysed in Fig. 2b were chosen such that each pair came from the same study and same location as indicated in their metadata in the COMPADRE database⁶¹. These pairs are: *Mulinum spinosum* and *Senecio filaginoides*⁷⁸, *Viola elatior* and *Viola pumila*⁷⁹, *Neobuxbaumia macrocephala* and *Neobuxbaumia mezcalensis*⁸⁰, *Minuartia obtusiloba* and *Paronychia pulvinata*⁸¹, *Eremospatha macrocarpa* and *Laccosperma secundiflorum*⁸², *Tillandsia macdougallii* and *Tillandsia violacea*⁸³, *Broughtonia cubensis* and *Dendrophylax lindenii*⁸⁴, and *Coespeletia spicata* and *Coespeletia timotensis*⁸⁵.

For the comparison group for these pairs of co-occurring species, 291 species were subset from COMPADRE, representing all species satisfying the criteria above, viable for normalization as detailed in the next section, and filtered only to shrubs, perennials, palms, succulents and epiphytes (the five architectural types represented in the eight coexisting pairs listed above). For each of the 500 comparison pairs, one species was chosen randomly out of the 291 and the second was chosen randomly among species of the same type to avoid comparing species with substantially different morphologies.

Normalization. For both the eight pairs of co-occurring species, and the comparison group of pairs drawn from COMPADRE, we wanted to isolate the effects of life history, as opposed to short-term transient changes in population sizes. Hence, each matrix was normalized such that its leading eigenvalue (and thus long-term, intrinsic growth rate) was 1—we did this because departures from $\lambda = 1$ likely represent stochastic fluctuations over the specific timeframe observed, or transient deterministic growth or decline. The following process was used to convert matrices from raw data in COMPADRE into matrices with $\lambda = 1$ while preserving as much of the life history strategy as possible: first, all reproduction into stages past the first was converted to reproduction into stage 1. This is to preserve a definition of 'seedling' within the model as best as possible, though exceptions may occur for species with seed banks. This exception was rare and no matrices in the communities or pairs studied here had species with substantial reproduction of this type. Then, each matrix was multiplied entrywise by the inverse of its leading eigenvalue. This, if successful, linearly scales all terms such that the leading eigenvalue is one. This is not, however, guaranteed to work for all matrices as some matrices converted by this method then had column sums that exceeded 1 for some stages. This would imply negative mortality and make the matrix unfeasible. If this was the case an algorithm was used to scale fecundity alone until the matrix had $\lambda = 1$. Small adjustments were made to all fecundity terms for up to 10,000 iterations until the matrix had $|1 - \lambda| < 10^{-6}$. If this failed, and another matrix entry was available in COMPADRE for the same species, that entry was tried instead. If neither of the two available matrices was scalable in this manner then that species was not analysed.

Identifying complementarity for larger groups of co-occurring species

In the case of competing pairs of species, our analytical results in 'Analytical derivation of persistence times and complementarity condition' provide a clear prediction for persistence time. We do not have a corresponding analytical prediction for larger groups of co-occurring species, but our simulation analysis shown in Fig. 3 of the main text strongly suggests that the effective population sizes of a group of co-occurring species are likely to be more clustered than the regional pool from which these species are drawn. We hypothesize that if equalizing mechanisms underly the persistence of a co-occurring group, then the life history strategies will be more clustered in comparison to an appropriate null model of groups of competing species, as quantified by variance in effective population sizes or a related measure of variability.

Our pipeline for identifying whether complementarity holds for a group of co-occurring species is therefore based on whether effective population sizes for the group are more or less clustered than an appropriate null comparison, where clustering is quantified using the coefficient of variation in effective population sizes (alongside the variance, and the dispersion index, to check that our conclusions are robust to different ways of characterizing the spread of N_y).

We do not have a broad range of larger communities for which life history strategies have been quantified using a consistent methodology. However, again using COMPADRE, we were able to identify a group of six species sourced from studies in the COMPADRE database at the same site near Archbold Biological Station⁶¹. The species (illustrated in order from left to right in Fig. 4a of the main text) are: *Polygonella*

basiramia, *Hypericum cumulicola*, *Eryngium cuneifolium*, *Polygonella robusta*, *Lechea cernua* and *Lechea deckertii*^{63–65}. For each of these six species, we normalized the MPM to ensure that $\lambda = 1$ as described above, and we were able to quantify its effective population size by competing that species neutrally against itself, as described earlier (in ‘Analytical derivation of persistence times and complementarity condition’) for synthetic MPMs. We recorded the mean of the neutral fixation time for each species across these 500 trials for each herbaceous perennial, keeping the system cap and starting population constant for each trial.

To generate a comparison group to test the clustering of effective population sizes we used 213 herbaceous perennials drawn from COMPADRE that satisfy the criteria described in ‘Identifying complementarity for pairs of co-occurring species’. We determined their per capita effective population size by again simulating truly neutral competition for two variants of the same of the species in a finite landscape as detailed in ‘Testing theoretical predictions for persistence using competition simulations’. We then drew 100,000 random samples with replacement of 6 species from this overall set of 213 species. For each group of six, we computed the coefficient of variation, along with the variance and dispersion index. The comparison of the Florida group to this null set of 100,000 synthetic communities is shown in Fig. 4a.

Two-stage, juvenile–adult model

We now consider an MPM with two stages, and with only the second stage reproductive. This gives a matrix M of the form:

$$M = \begin{pmatrix} 1 - \mu_1 - g & f \\ g & 1 - \mu_2 \end{pmatrix}. \quad (27)$$

The constraint that the leading eigenvalue for the discrete dynamical system is $\lambda = 1$, so that no species experiences net growth. Since all eigenvalues of M must satisfy:

$$(1 - \mu_1 - g - \lambda)(1 - \mu_2 - \lambda) - gf = 0. \quad (28)$$

having an eigenvalue such that $\lambda = 1$ provides one constraint on these four parameters:

$$fg = (\mu_1 + g)\mu_2. \quad (29)$$

We now compute the annual effective population size for a species with life history defined by the above system. First, the lifetime variance in reproductive output is

$$\sigma^2 = (1 - P_{\text{rep}}) + P_{\text{rep}} \int dT \mu_2 e^{-\mu_2 T} \left(\frac{\mu_2 T}{P_{\text{rep}}} - 1 \right)^2 \quad (30)$$

$$\approx \frac{2}{P_{\text{rep}}} = \frac{2f}{\mu_2}$$

where $P_{\text{rep}} = \frac{\mu_2}{f} = \frac{g}{\mu_1 + g}$ is the probability that a new juvenile will eventually become reproductive. Next, the number of new individuals per generation (once the proportion of juveniles vs adults has reached its steady-state) is equal to the number of deaths per year, which depends on the steady state total system size J , μ , and the leading eigenvector of M .

$$N = J\mu \cdot v^0. \quad (31)$$

That leading eigenvector v^0 is (when normalized)

$$v^0 = \begin{pmatrix} \frac{f}{f + \mu_1 + g} \\ \frac{\mu_1 + g}{\mu_1 + g + f} \end{pmatrix} \quad (32)$$

so that

$$N = J \frac{\mu_1 f + \mu_2(\mu_1 + g)}{\mu_1 + g + f}. \quad (33)$$

Finally, the expected age of a parent, T , which is often interpreted as a measure of generation time, is

$$T = \frac{1}{\mu_1 + g} + \frac{1}{\mu_2} = T_{\text{mat}} + \frac{1}{\mu_2}. \quad (34)$$

Putting this together, the annual effective population size is

$$N_{\text{year}} = T^2 N / \sigma^2 = J \frac{\mu_1 f + \mu_2(\mu_1 + g)}{\mu_1 + g + f} \left(T_{\text{mat}} + \frac{1}{\mu_2} \right)^2 \frac{\mu_2}{2f} \quad (35)$$

We have three degrees of freedom here (taking into account the eigenvalue constraint).

The complementary life history condition from the main text adds a further constraint relating those three remaining variables. Essentially that

$$\frac{\mu_1 f + \mu_2(\mu_1 + g)}{\mu_1 + g + f} \left(T_{\text{mat}} + \frac{1}{\mu_2} \right)^2 \frac{\mu_2}{f} J = c \quad (36)$$

among a group of similar species, with no difference in competitive ability, for some value of c that may differ from community to community. We now rewrite this in terms of three variables that are commonly considered in life history theory: expected age of maturity (T_{mat}), expected lifespan of adults (T above), and fecundity (f above). Note that from first principles

$$T_{\text{mat}} = \frac{1}{\mu_1 + g} \quad (37)$$

So we can eliminate $(\mu_1 + g)$ and then

$$\mu_1 = 1/T_{\text{mat}} - g. \quad (38)$$

Then

$$\frac{\frac{f}{T_{\text{mat}}}}{1/T_{\text{mat}} + f} \frac{(T_{\text{mat}}\mu_2 + 1)^2}{f\mu_2} J = c \quad (39)$$

or

$$\frac{(T_{\text{mat}}\mu_2 + 1)^2}{(1 + f T_{\text{mat}})\mu_2} J = c \quad (40)$$

as stated in the main text.

Statistics

The ribbons around points in Fig. 2a represent s.e., assessed from 500 simulation trials for each synthetic pair of competing species. The tests of significance in Figs. 2b and 4a are one-tailed tests, as we specify the directionality of the tests. Exact P values are presented in the figure captions. Our methodology and criteria for sampling species’ empirical life history strategies from COMPADRE is explained in ‘Testing theoretical predictions for persistence using competition simulations’, above.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Article

Data availability

Data needed to generate Figs. 2b and 4 are available in the publicly accessible COMPADRE database⁶¹. Synthetic matrices used to generate Figs. 2a and 3 have been uploaded to the Zenodo repository⁸⁶.

Code availability

Code samples of both a pairwise competition model and the meta-community model used to generate Fig. 3 are provided via the Zenodo repository⁸⁶ as R scripts (R version 4.2.2 using reshape2 version 1.4.4, dplyr version 1.0.10, and tidyverse version 1.2.1.). This upload also contains annotations to help viewers run the code and sample sets of properly formatted matrices.

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Author contributions K.J. and J.P.O. designed the project. K.J. and J.P.O. developed the simulation and analytical results, and K.J. analysed COMPADRE data. K.J. and J.P.O. interpreted the analyses and wrote the manuscript.

Competing interests The authors declare no competing interests.

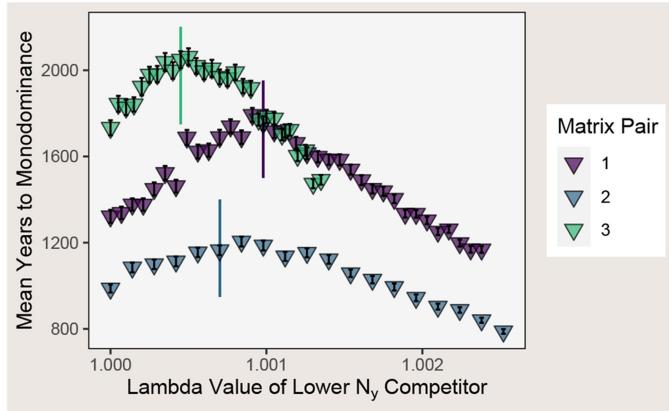
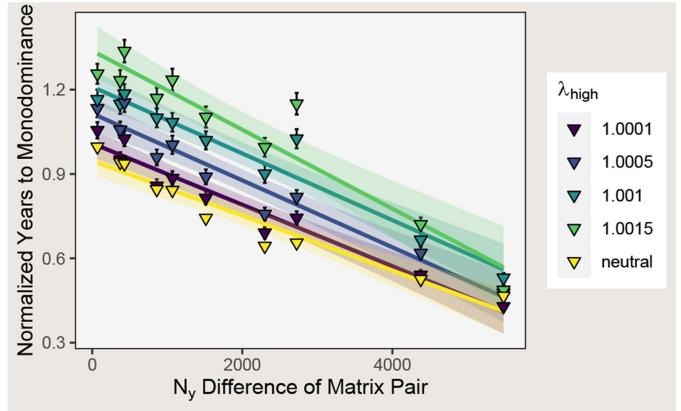
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-023-06154-w>.

Correspondence and requests for materials should be addressed to Kenneth Jops or James P. O'Dwyer.

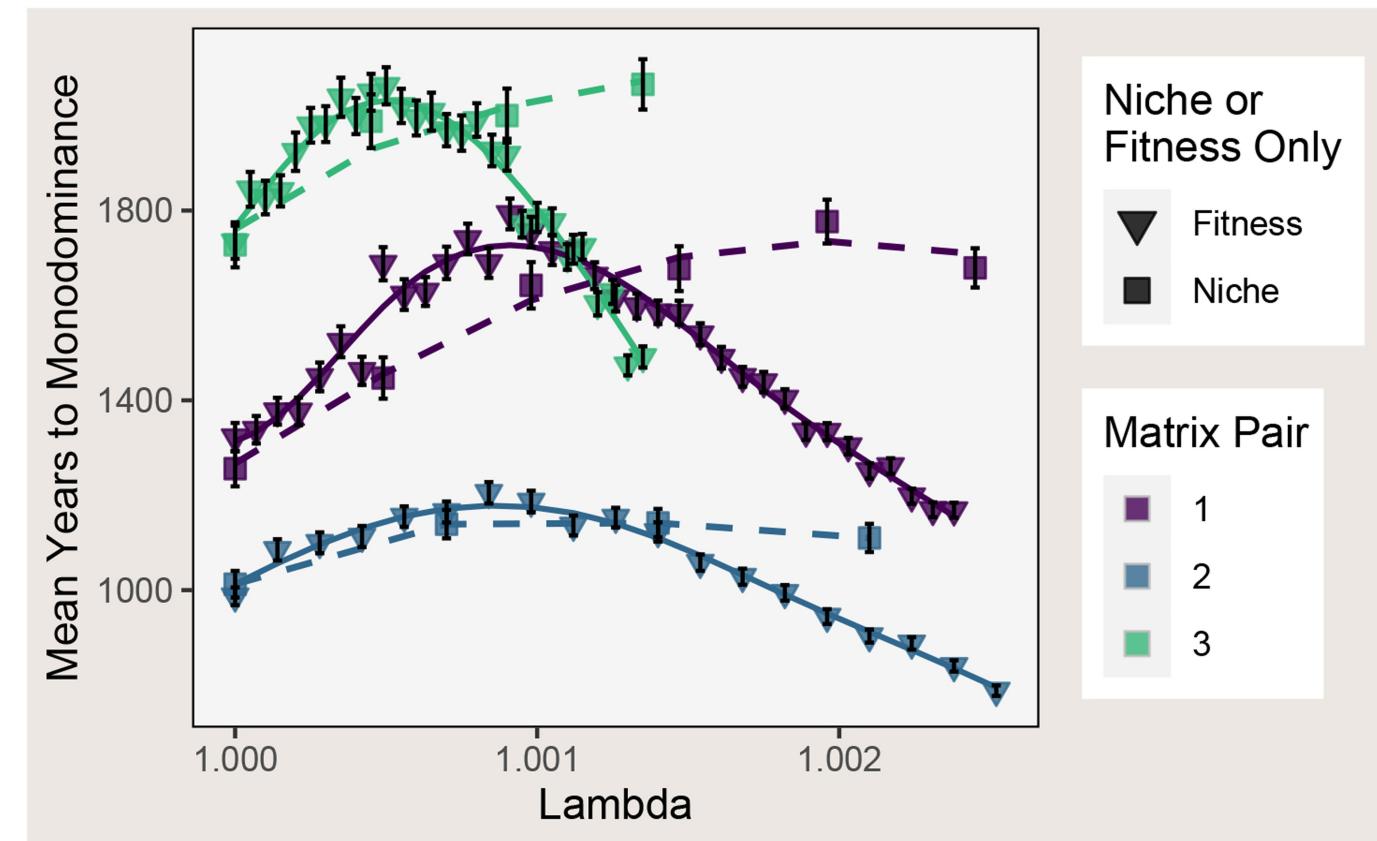
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a**b**

Extended Data Fig. 1 | Life History Complementarity, Fitness Differences, and Niche Differences. In **Panel A**, we show the combined effects of fitness differences and life history strategy on pairwise competition. We take 3 pairs of species and vary the long-term growth rate λ of the competitor with the lower N_y value. The colors denote the set of species and the vertical lines show the predicted optimal value of λ to maximize persistence. The persistence time when $\lambda = 1$ is the same as that in the trials shown in the main text. This time increases as we approach the optimum identified in Supplementary Information Eq.(1) before decreasing for larger values of λ . Here we see that a) life history variation still affects persistence time when we relax the assumption of equal fitness and b) that a new persistence optimum is introduced by varying fitness between species in a community. **Panel B** demonstrates the interplay between niche differences and life history. Here we construct our model

according to Supplementary Information Section 1.2 and vary λ_{high} across 10 pairs of matrices with varying levels of difference in their N_y values. As λ_{high} and thus our degree of niche differentiation increases, persistence times increase in tandem—i.e. niche differentiation boosts persistence, as expected. Across all of these trials, however, differences in N_y still influence persistence times, and optimal persistence is achieved when species have the closest values of N_y —our definition of life history complementarity. The “neutral” points represent trials where $\lambda_{high} = \lambda_{low}$, analogous to the trials in the main text. The solid lines represent linear regressions for each λ_{high} value and the shaded regions represent 95% confidence intervals for these regressions. Error bars in both Panel A and Panel B show standard error across 500 numerical trials, centered on the mean across those trials.



Extended Data Fig. 2 | Life History, Fitness, and Niche Differences. In Extended Data Fig. 2 we compare the model results of Extended Data Fig. 1A with the results of a combined fitness, niche, and life history differences model. Triangular points show the same data as ED Fig. 1A and square points show the results of trials where λ_{high} is set to the same λ value as the lower N_y , competitor's fitness in the trials from 1A. The matrix pairs are the same for the two sets of trials. The solid and dashed lines are approximate spline fits to the data points and serve to guide the viewer to the overall trend. Partitioning the community into niches results

in a higher persistence time optimum of λ_{high} and a slower approach to this optimum. Peak persistence times are similar across both implementations, shown by the y-axis maxima for each matrix pair. Most importantly, the signature of life history differences is clear—the broad comparisons of the pairs of curves of each color show that differences in effective population size significantly impact persistence times even in the presence of both fitness and niche differences. Error bars show standard error, centered at the mean, across 500 trials.

Reporting Summary

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- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
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Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection No software was used for data collection

Data analysis We used custom code to simulate community dynamics as described in the text, we provide annotated and functional samples of this code at the following link via the Zenodo Repository: <https://doi.org/10.5281/zenodo.7596014>. These scripts were run in R version 4.2.2 with packages reshape2 version 1.4.4, dplyr version 1.0.10, and tidyr version 1.2.1.

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We have included the publicly-available COMPADRE database in our reference list.

Field-specific reporting

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Study description

We developed code to model the dynamics of multiple species according to their demographic parameters encoded in Matrix Population Models. These models were sourced either through the COMPADRE database or generated via algorithm.

Research sample

We sampled matrices from the COMPADRE database with the following restrictions: matrices must be marked "Unmanipulated" to exclude artificial treatments from the original studies, the sampling interval for matrices must be annual, no matrices with clonal reproduction were considered (due to modeling constraints), matrices must be divided into survival and fecundity to determine total reproduction, and matrices with dimension above 15 were not considered to conserve computer memory.

Sampling strategy

The above conditions were applied to each entry in the database and if more than one matrix for a species was present, a random matrix was chosen. An algorithm then attempted to linearly scale the matrix such that the species had a long term growth rate of 1. If this failed or caused infeasible distortions in the matrix, the algorithm attempted to scale fecundity terms such that the growth rate condition was satisfied. If both methods failed, another random matrix for that species was selected if available. If this second matrix could not be scaled the species was skipped.

Data collection

Data for matrices came from a variety of field studies, those explicitly considered are cited as references.

Timing and spatial scale

Timing for sampling in original studies queried via COMPADRE was variable. The nature of our specific goals in using this data made the sampling schedule largely irrelevant, though in direct comparisons we made efforts to limit this variability by sourcing data from the same authors and studies when possible.

Data exclusions

See "Sampling Strategy"

Reproducibility

Code for an iteration of the model will be made publicly available.

Randomization

For analyses requiring randomization, this was done via computer random number generation in R.

Blinding

As we did not collect the data used in this study, blinding was largely irrelevant to our work. To the extent that it would be possible to manipulate the results of comparisons across large sets of species, this was precluded by using computer randomness in selection.

Did the study involve field work? Yes No

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We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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Methods

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