

Higher-order interactions stabilize dynamics in competitive network models

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Ecologists have long sought a way to explain how the remarkable biodiversity observed in nature is maintained. On the one hand, simple models of interacting competitors cannot produce the stable persistence of very large ecological communities^{1–5}. On the other hand, neutral models^{6–9}, in which species do not interact and diversity is maintained by immigration and speciation, yield unrealistically small fluctuations in population abundance¹⁰, and a strong positive correlation between a species' abundance and its age¹¹, contrary to empirical evidence. Models allowing for the robust persistence of large communities of interacting competitors are lacking. Here we show that very diverse communities could persist thanks to the stabilizing role of higher-order interactions^{12,13}, in which the presence of a species influences the interaction between other species. Although higher-order interactions have been studied for decades^{14–16}, their role in shaping ecological communities is still unclear⁵. The inclusion of higher-order interactions in competitive network models stabilizes dynamics, making species coexistence robust to the perturbation of both population abundance and parameter values. We show that higher-order interactions have strong effects in models of closed ecological communities, as well as of open communities in which new species are constantly introduced. In our framework, higher-order interactions are completely defined by pairwise interactions, facilitating empirical parameterization and validation of our models.

We studied deterministic models describing communities in which the number of individuals is large and the system is isolated (for example, bacterial strain competition in laboratory conditions¹⁷); in Supplementary Information section S4 we examine the case in which the dynamics are stochastic, which best describe communities in which the number of individuals is finite. Finally, we allow new species to be introduced at a given rate, allowing for a comparison with neutral models (Supplementary Information section S5).

Although our results hold for a wide class of systems, to exemplify our findings we consider the dynamics of a forest in which there is a fixed, large number of trees, so that we can simply track $x_i(t)$, the proportion of trees of species i at time t , with $\sum_i x_i(t) = 1$. At each step, a randomly selected tree dies, opening a gap in the canopy (that is, we initially assume identical per capita death rates for all species). This event ignites competition among seedlings to fill the gap. Suppose that all individuals produce the same number of seedlings, and that we pick two seedlings at random, with the winner of the competition filling the gap (Supplementary Fig. 1). The matrix H encodes the dominance relationships among the species: H_{ij} is the probability that the first seedling, belonging to species i , wins against the second seedling, belonging to species j . Clearly, $H_{ii} = 1/2$ for all i , and $H_{ij} + H_{ji} = 1$ for all i and j . If all $H_{ij} = 1/2$, we recover a neutral model. At the other extreme lies a model in which each pair (H_{ij}, H_{ji}) is either $(1, 0)$ or $(0, 1)$ (that is, species i always wins or always loses against j), in which case H is called a 'tournament matrix'¹⁸. A number of results have been derived for this case¹⁹, showing that coexistence is possible when species form

'intransitive cycles' of competitive dominance, such as in the rock-paper-scissors game²⁰. Here we extend these previous findings¹⁹ to the most general case in which interactions range from neutral to complete dominance.

We can approximate the dynamics of the n species as (see Methods):

$$\frac{dx_i(t)}{dt} = x_i(t) \left(2 \sum_j H_{ij} x_j(t) - 1 \right) \quad (1)$$

Where $-x_i(t)$ models the death process, and $x_i(t) 2 \sum_j H_{ij} x_j(t)$ is the probability of picking two seedlings of species i and j , with i winning the competition. The factor 2 arises from the fact that we could pick i first and j second, or vice versa, with the same outcome.

Simple manipulations (Supplementary Information section S1) show that these equations are equivalent to the system:

$$\frac{dx_i(t)}{dt} = x_i(t) \sum_j P_{ij} x_j(t) \quad (2)$$

which is the celebrated replicator equation^{21,22} for a zero-sum, symmetric matrix game with two players and payoffs encoded in the skew-symmetric matrix $P = H - H^T$. This equation is at the core of evolutionary game theory, with applications spanning multiple fields^{23,24}.

Thanks to this equivalence, we are able to characterize the dynamics. Unless specified, we assume H to be of full rank, that is, all of its eigenvalues are non-zero. We show in the Supplementary Information that violations of this assumption are unbiological, amounting to degenerate cases in which slightly altering the parameters dramatically changes the outcome. Suppose that we start with n species and initial conditions $x_i(0) > 0$, and that we let the dynamics unfold. Once the transient dynamics have elapsed, we find $k \leq n$ coexisting species, with k being odd. The $n - k$ species that go extinct do so irrespective of initial conditions, and the k coexisting species cycle neutrally around a unique equilibrium point x^* (Fig. 1, Supplementary Information section S1).

How large is k when we build the matrix H at random? When drawing H_{ij} (with $i < j$) from the uniform distribution $U[0, 1]$ and setting the corresponding $H_{ji} = 1 - H_{ij}$, we find that the probability of having k species coexisting when starting with n species, $p(k|n) = 0$ when k is even, and $p(k|n) = \binom{n}{k} 2^{1-n}$ when k is odd²⁵ (Supplementary Fig. 2). This matches what is found for tournament games^{18,19,26}, in which dominance is complete: we expect half of the initial species to coexist, irrespective of the choice of n ; moreover, monodominance is extremely rare, and about as rare as the coexistence of all species. Thus, this theory generates high biodiversity without the need to fine-tune parameters.

This model can generate any species-abundance distribution: for any choice of x^* , we can build infinitely many matrices H such that equations (1) and (2) have x^* as an equilibrium (Supplementary Information section S1). We note that this is true irrespective of the fact that x^* contains an even or odd number of species (Fig. 1)—but the case

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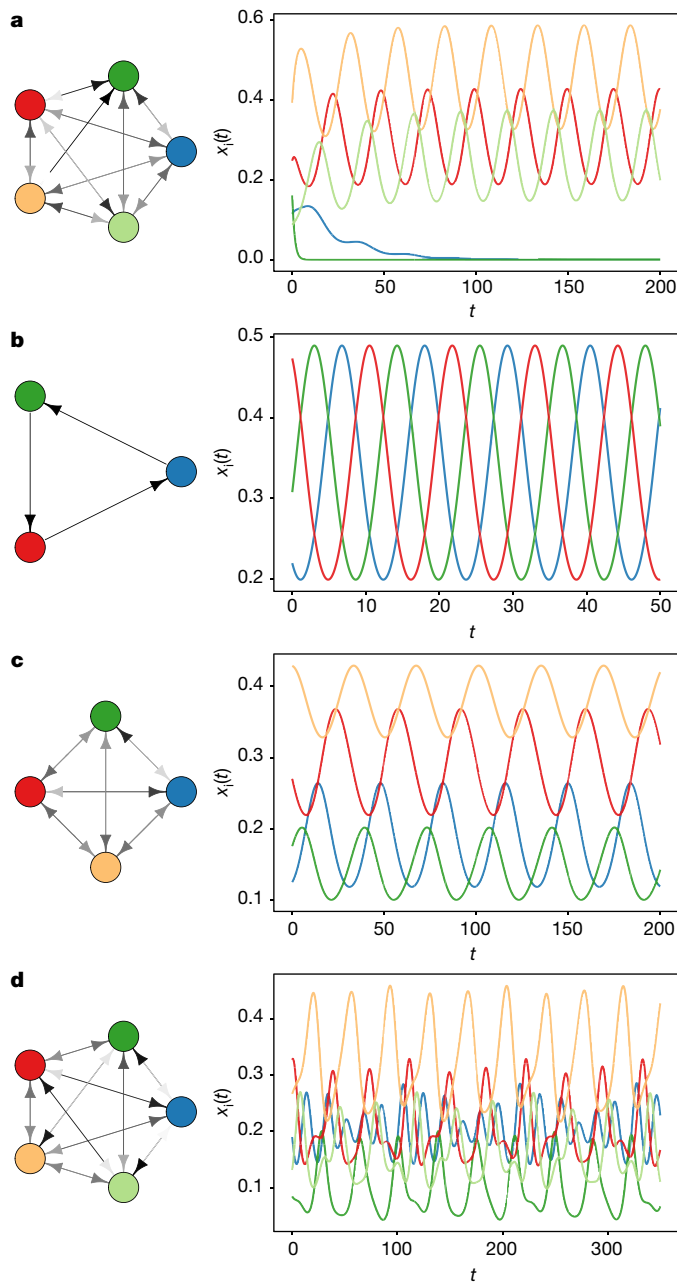


Figure 1 | Sampling two seedlings leads to neutral cycles. Dynamics of a forest where two randomly sampled seedlings compete to fill the gap in the canopy opened by the death of a tree. We represent the competitive relationships between the species as a graph in which each coloured node corresponds to a species, and nodes i and j are connected by arrows representing the probability that i wins against j (H_{ij} , darker arrowheads correspond to higher probability), and that j wins against i (H_{ji}), respectively. For all pairs, $H_{ij} + H_{ji} = 1$. For each system, we show a time series obtained by integrating the dynamics of equation (1). The y-axis represents $x_i(t)$, the relative abundance of species i at time t . **a**, When starting with n species, $n - k$ species go extinct, and k coexist. Given a matrix H , the identity of the species coexisting or going extinct is the same irrespective of initial conditions. The k species that coexist cycle neutrally around a single equilibrium point. **b**, The same result is found when dominance is complete, such as in the rock–paper–scissors game¹⁹. **c**, For any possible species-abundance distribution x^* , we can build a matrix H such that the species coexist and x^* is an equilibrium of equation (1) (Supplementary Information S1). This is true even when x^* contains an even number of species—though this case is not robust to small changes in parameters (Supplementary Fig. 4). **d**, The same holds for any number of species in the system.

in which an even number of species coexist is degenerate: the system has infinitely many neutrally stable equilibria, and a slight change of H would result in the extinction of at least one species (Supplementary Information and Supplementary Fig. 4).

In summary, the model in equation (1) can lead to arbitrarily many species coexisting even when competitive abilities are drawn at random; moreover, it can generate any possible species-abundance distribution. Although the neutral cycling around the equilibrium is problematic (such cycles are not observed in nature, and would lead to monodominance in a noisy, stochastic world; see Supplementary Information section S4), the main issue with this model is that it is highly unrobust: any deviation from perfectly identical death rates and fecundities for all species destabilizes dynamics, leading to monodominance (Supplementary Information section S2 and Supplementary Fig. 4).

Following recent mathematical results²⁷, we explore a possible solution to this problem. So far, we have taken exactly two seedlings, competing with each other to fill the gap in the canopy. In nature, we would observe a much richer seedbank, potentially leading to competition among many seedlings. We therefore study a model in which we take three seedlings at random, compete the first with the second, and the winner with the third. The deterministic approximation of this model reads as follows (see Methods):

$$\frac{dx_i(t)}{dt} = x_i(t) \sum_{j,k} (2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj})x_j(t)x_k(t) - x_i(t) \quad (3)$$

where $H_{ij}H_{ik}$ is the probability that i beats both j and k , $H_{ij}H_{jk}$ is the probability that j beats k , but ultimately is beaten by i , and $H_{ik}H_{kj}$ is the probability that first k beats j , and then i beats k . Surprisingly, this small modification leads to a major change in the dynamics: though the equilibrium point is unchanged, it is now globally stable (Fig. 2 and Supplementary Information section S1). Increasing the number of seedlings that compete to fill each gap simply accelerates the dynamics, speeding up convergence to the equilibrium (Supplementary Fig. 3).

Whereas the model in which we sample two seedlings yields the replicator equation for a two-player, symmetric matrix game, equation (3) is equivalent to the replicator equation for a three-player game (Supplementary Information section S1):

$$\frac{dx_i(t)}{dt} = x_i(t) \sum_{j,k} P_{ijk}x_j(t)x_k(t) \quad (4)$$

where P is a 3-index tensor encoding the payoff of player 1 playing strategy i when player 2 plays j and player 3 plays k . The payoffs can be calculated from the matrix H : $P_{ijk} = 2H_{ij}H_{ik} - H_{ji}H_{jk} - H_{ki}H_{kj}$ (where the first term includes the probability of i winning against both j and k , and the remaining two terms are the probabilities that either j or k dominate).

This latter formulation makes it clear that the stabilizing effect is due to higher-order interactions^{5,12}. Suppose the matrix H is constructed as in a rock–paper–scissors game; then the presence of the rock–plant can reverse the outcome of the competition between the paper–plant and the scissors–plant. In our model, higher-order interactions do not alter equilibrium values, but have a dramatic stabilizing effect, leading to globally stable fixed points instead of neutral cycles. Including fourth- or higher-order terms simply accelerates the convergence to equilibrium (see Supplementary Fig. 3). As such, as long as there is a chance of competing more than two seedlings at a time, the dynamics will converge. Most importantly, results are qualitatively robust to the perturbations of the death rates and fecundities of the competitors (Supplementary Information and Supplementary Fig. 4).

One formidable challenge of estimating higher-order interactions empirically is that for n species we have $\binom{n}{2} = n(n-1)/2$ pairs of interactions, but the number of triplets is much higher $\left(\binom{n}{3} = n(n-1)(n-2)/6\right)$ —requiring many experiments. Instead of

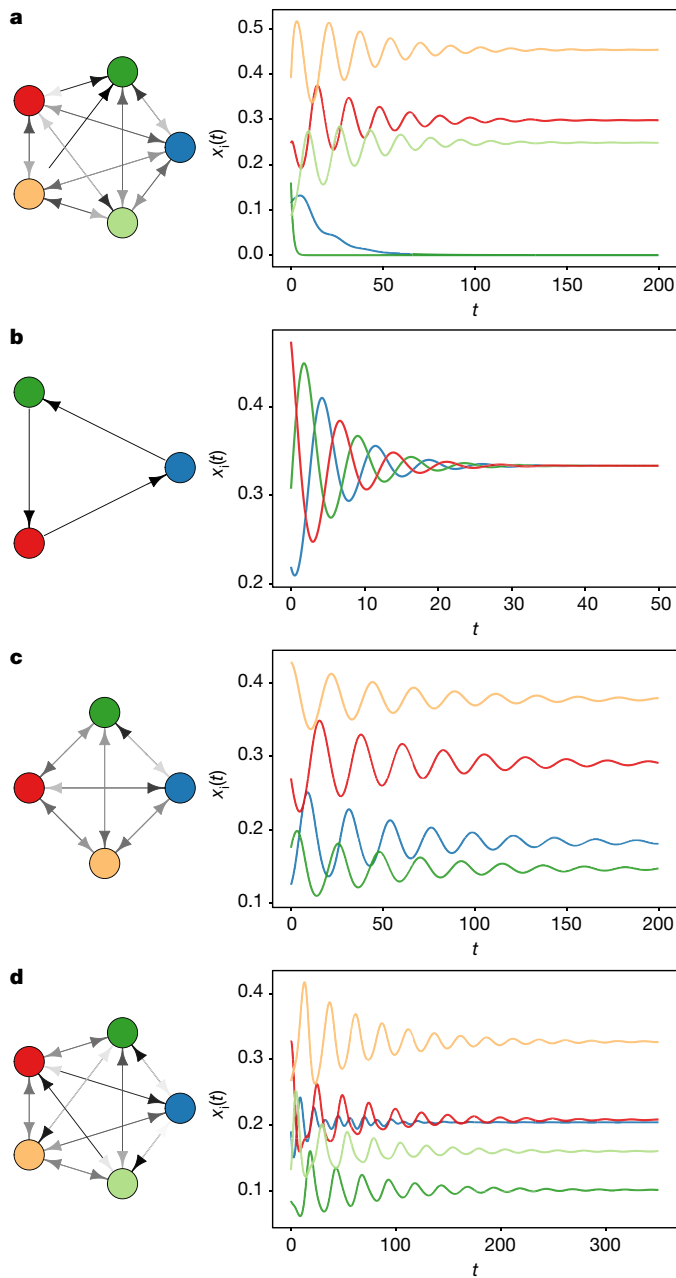


Figure 2 | Sampling three seedlings produces stability. When we sample three seedlings at a time instead of two, and we compete the first with the second and the winner with the third, the equilibrium point is unchanged, but is now globally attractive. The four cases correspond to those in Fig. 1.

introducing new coefficients, here we have chosen the most ‘natural’ and conservative parameterization: higher-order interactions are fully determined by pairwise interactions, as shown by the fact that we can write all models in terms of the pairwise relationships encoded in H . This makes the models empirically testable by, for example, competing bacteria in laboratory conditions¹⁷.

We have shown the equivalence of models in which competition happens in a sequence of bouts (equation (3)), using models in which interactions are simultaneous and involve more than two species at a time (equation (4)). Because of a separation of timescales (the filling of a gap is fast, compared to the lifespan of trees), the two types of models have the same deterministic form, blurring the traditionally held distinction between so-called interaction chains and ‘proper’ higher-order interactions^{5,28}. Our results may have important implications for a variety of ecological systems; for example, in

models in which reproduction is not instantaneously coupled with consumption, an animal could consume a resource, but be consumed before reproduction—yielding the same mechanism that stabilizes our competitive communities when we sample three seedlings at a time. Similarly, the stabilizing role of higher-order interactions in random replicator equations has been recently proposed²⁹, and our analytical results shed light on these findings.

Moving from deterministic to stochastic models, we find that the presence of higher-order interactions, which make equilibrium points attractive, dramatically increases³⁰ time to extinction in isolated systems, allowing for the prolonged coexistence of species (Supplementary Information section S4). When we open the system to the introduction of new species (Supplementary Information section S5), we recover many of the main results of neutral theory, but remove the artefactual relationship between a species age and its abundance—one of the main drawbacks of neutral models¹¹.

Our results strengthen the theory of coexistence in zero-sum competitive networks in several ways. First, we have widespread coexistence without having to invoke either of two extreme cases: perfect ecological equivalence (the neutral model) or complete dominance (coexistence through intransitive competition). In nature, the outcome of competition could be mediated by a number of factors (for example, soil chemistry, presence of consumers), so that competitive dominance could range from neutral to complete. Second, many species coexist even when we draw parameters at random, meaning that the results are highly robust. Third, in this formulation, the notion of intransitivity, which is central to coexistence in competitive networks in which dominance is complete¹⁹, is no longer necessary for coexistence (Supplementary Information section S3). Fourth, the artefact of neutral cycling is due to the choice of only two competitors per bout—a choice dictated by mathematical convenience rather than by empirical evidence. Including more biological realism in the form of multiple competing species removes the artefact, leading to dynamics that are stable against perturbations of species abundances and robust against changing model parameters.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions S.A. conceived the study, and drafted the manuscript and the code. J.G. performed the analysis of the models. All authors edited the manuscript and code.

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METHODS

To exemplify the role of higher-order interactions in shaping ecological dynamics, we consider a model of a forest in which whenever a tree dies, a certain number of seedlings compete to fill the gap in the canopy (Supplementary Fig. 1). We start by writing the microscopic rate $W_{ij}^{(m)}$ at which species j loses an individual ($\eta_j \rightarrow \eta_j - 1$), while species i gains an individual ($\eta_i \rightarrow \eta_i + 1$). The index m specifies that we consider the case in which m seedlings at a time compete to fill in the gap. When there are many individuals we can track proportions ($x_i(t) = \eta_i(t)/\sum_j \eta_j(t)$), and setting $m = 2$, we can write this rate as:

$$W_{ij}^{(2)} = d_j x_j \frac{f_i x_i}{\sum_l f_l x_l} \sum_k 2H_{ik} \frac{f_k x_k}{\sum_l f_l x_l} \quad (5)$$

in which f_i and d_i are the fecundity and death rate of trees belonging to species i . Using the notation $F(x) = \sum_l f_l x_l$, the term $f_i x_i / F(x)$ is the proportion of seeds in the seedbank belonging to species i . Finally, the matrix H encodes the probability of winning for every pair of species, so that H_{ik} is the probability of seedling of species i beating those of species k , and the factor 2 arises from the fact that we could sample i first and k second, or vice versa. Then, the term $W_{ij}^{(2)}$ can be interpreted as the rate at which (a) a tree of species j dies, and (b) two seedlings of species i and k are sampled, with i filling the gap. Because the identity of k does not matter, we sum over all possible choices.

When the number of trees is sufficiently large, we can neglect stochasticity and write:

$$\frac{dx_i}{dt} = \sum_j (W_{ij}^{(2)} - W_{ji}^{(2)}) = x_i \left(\frac{D(x)}{F(x)^2} \sum_k f_i H_{ik} f_k x_k - d_i \right) \quad (6)$$

where we have introduced $D(x) = \sum_i d_i x_i$. In Supplementary Information section S4 we present stochastic simulations that show strong agreement with the predictions of this deterministic approximation. We can derive equations like equation (6) for any choice of m . We write:

$$W_{ij}^{(m)} = d_j x_j q_i^{(m)} \quad (7)$$

where $q_i^{(m)}$ is the probability that a seedling of species i wins when competing against $m - 1$ other seedlings. We build $q_i^{(m)}$ recursively:

$$\begin{aligned} q_i^{(1)} &= \frac{f_i x_i}{F(x)} \\ &\dots \\ q_i^{(m)} &= \frac{f_i x_i}{F(x)} \sum_k H_{ik} q_k^{(m-1)} + q_i^{(m-1)} \sum_k H_{ik} \frac{f_k x_k}{F(x)} \end{aligned} \quad (8)$$

which has a simple interpretation: $\frac{f_i x_i}{F(x)} \sum_k H_{ik} q_k^{(m-1)}$ is the probability that i wins against the winner of the competition involving the first $m - 1$ seedlings, while $q_i^{(m-1)} \sum_k H_{ik} \frac{f_k x_k}{F(x)}$ is the probability that i is the winner of the competition among the first $m - 1$ seedlings, and beats the last seedling. Consistently with the fact that these are probabilities, $\sum_i q_i^{(m)} = 1$ for any m . In this way, we can (for example) recover the rate $W_{ij}^{(2)}$ we have introduced above:

$$\begin{aligned} W_{ij}^{(2)} &= d_j x_j q_i^{(2)} = d_j x_j \left(\frac{f_i x_i}{F(x)} \sum_k H_{ik} q_k^{(1)} + q_i^{(1)} \sum_k H_{ik} \frac{f_k x_k}{F(x)} \right) \\ &= d_j x_j \frac{f_i x_i}{F(x)} \sum_k 2H_{ik} \frac{f_k x_k}{F(x)}. \end{aligned} \quad (9)$$

In general, the dynamics when considering m seedlings become:

$$\frac{dx_i}{dt} = \sum_j (W_{ij}^{(m)} - W_{ji}^{(m)}) = D(x) q_i^{(m)} - d_i x_i \quad (10)$$

Using this formulation, we write the system of equations describing the model in which three seedlings are sampled. We calculate $q_i^{(3)}$:

$$\begin{aligned} q_i^{(3)} &= \frac{f_i x_i}{F(x)} \sum_k H_{ik} q_k^{(2)} + q_i^{(2)} \sum_k H_{ik} \frac{f_k x_k}{F(x)} \\ &= \frac{f_i x_i}{F(x)} \sum_{j,k} 2H_{ij} \frac{f_j x_j}{F(x)} H_{jk} \frac{f_k x_k}{F(x)} + \frac{f_i x_i}{F(x)} \sum_{j,k} 2H_{ij} \frac{f_j x_j}{F(x)} H_{ik} \frac{f_k x_k}{F(x)} \\ &= \frac{f_i x_i}{F(x)} \sum_{j,k} \left((2H_{ij} H_{jk} + 2H_{ij} H_{ik}) \frac{f_j x_j}{F(x)} \frac{f_k x_k}{F(x)} \right) \\ &= \frac{f_i x_i}{F(x)} \sum_{j,k} \left((H_{ij} H_{jk} + H_{ik} H_{kj} + 2H_{ij} H_{ik}) \frac{f_j x_j}{F(x)} \frac{f_k x_k}{F(x)} \right) \end{aligned}$$

yielding the system of equations:

$$\begin{aligned} \frac{dx_i}{dt} &= \sum_j (W_{ij}^{(3)} - W_{ji}^{(3)}) \\ &= x_i \left(\frac{D(x)}{F(x)^3} f_i \sum_{j,k} (2H_{ij} H_{ik} + H_{ij} H_{jk} + H_{ik} H_{kj}) f_j x_j f_k x_k - d_i \right) \end{aligned} \quad (11)$$

Having derived this general case, we dedicate Supplementary Information section S1 to the study of the simplified model we have introduced in the main text, in which $f_i = d_i = 1$ for all i . It is easy to derive a number of results for this simplified formulation, including the existence and uniqueness of the coexistence equilibrium, the stability properties of such equilibrium when sampling two or more than two seedlings, the expected number of coexisting species when H is random, and the construction of an algorithm that takes as input a desired species-abundance distribution x^* , and produces infinitely many H such that x^* is an equilibrium of the system.

In Supplementary Information section S2, we return to the more general case introduced above to test the robustness of our findings when we relax the strong constraint of identical physiological rates for all species. Supplementary Information section S3 is dedicated to the discussion of intransitivity. Finally, Supplementary Information sections S4 and S5 extend these models to situations in which the number of individuals is finite, and therefore demographic stochasticity becomes important. We first consider the case of an isolated ecological community (Supplementary Information section S4), and then open the community to the introduction of new species by immigration or speciation (Supplementary Information section S5), allowing for a direct contrast with neutral models.