Demographics and competitive outcome derive from resource allocation statistics: the governing influence of the distinguishability of individuals

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Abstract

Models used to predict coexistence among species typically start with explicit but *ad hoc* assumptions about the density dependence of demographic rates. In this paper we explore an alternative parsimonious inferential method based on statistical mechanics, maximizing resource allocation entropy, from which an effective density dependence of demographic rates and corresponding coexistence of species naturally emerge. We predict birth and death rates and stable community composition from the same assumption that underlies statistical mechanics: the macrostate (coexisting species and their abundance distribution) in which nature is found is the one associated with the largest number of microstates (the many ways to allocate resources to all individuals). Central to our approach is the idea that the distinguishability of individuals can be viewed on a continuous scale, and the key parameter governing coexistence is the distinguishability of individuals within species relative to that between species.

Keywords species coexistence, resource allocation, density dependence, statistical mechanics, individual distinguishability

1 Introduction

Although the competitive exclusion principle has been extensively studied since first proposed, its connection to actual patterns of biodiversity remains elusive (Hutchinson 1961; Wilson & Lindow 1994; Anderson *et al.* 2002). Consequently the question of how species diversity is maintained under limited resources continues to intrigue ecologists (Wright 2002; Kelly & Bowler 2002; Wilson & Abrams 2005; Calcagno *et al.* 2006; Lobry & Harmand 2006; Tokeshi 2009; Siepielski & McPeek 2010).

In a review of this topic, Chesson (2000) distinguished two mechanisms governing species coexistence: fitness equality (equality in carrying capacity or resource requirement (Tilman 1981; Chave 2004)) and stabilizing mechanisms (higher intraspecific than interspecific negative density dependence (Amarasekare 2003; Lobry & Harmand 2006)). He then partitioned different models using these two factors and concluded that coexistence is only possible when fitness differences are compensated by stabilizing mechanisms. Both fitness equalization and stabilizing mechanisms refer, however, to broad categories of processes contributing to the same model outcome, making this general conclusion difficult to verify or falsify. Furthermore, all of these models assume some type of density dependence of demographic rates, based on which the fitness equality and stabilizing mechanisms of the model are determined.

Both mechanistic and phenomenological models of competitive coexistence often assume density dependence in the form of linear dependence of per capita demographic rates on abundance, e.g. the logistic growth equation and the Lotka-Volterra equations (Volterra 1938; Hassell 1975). Although linearity is convenient, nature is undoubtedly more complex (Abrams & Ginzburg 2000; Chase *et al.* 2002; Melbourne & Chesson 2005), and thus some competition models assume nonlinear equations, either fitted from data (Leirs *et al.* 1997) or derived from more complex mechanisms (Toro *et al.* 1971; Dennis & Desharnais 1995). The more complex the model, however, the more vulnerable it usually is to over parameterization, adding to the difficulty of falsification, and there is no compelling reason to assume any particular functional form for density dependence.

Our goal is a theory that predicts the most phenomena with the fewest unverifiable assumptions. Statistical mechanics provides a widely applicable method for inferring pattern without assuming explicit interactions or other processes. The main idea is that the observed state of a system is the macrostate that is associated with the largest number of microstates, which therefore has the highest probability of being observed. In statistical mechanics the entropy of a macrostate is defined as the natural log of the number of microstates compatible with that macrostate (Boltzmann 1896). Based on the same principle, the inferential method of maximum entropy

(MaxEnt) is developed.

MaxEnt has been used in ecology to predict species spatial distributions from environmental variables (Phillips *et al.* 2006) or species abundance distribution (Pueyo *et al.* 2007) and has nurtured a comprehensive theory (Maximum Entropy Theory of Ecology) that predicts numerous macroecological metrics including the species abundance distribution, the species level spatial abundance distribution and the species area relationship (Harte & Newman 2014). However, there has been little effort to apply MaxEnt to the study of population dynamics and coexistence.

To apply these statistical ideas to competitive coexistence, a way of counting microstates is needed. A natural approach is to equate the number of microstates with the number of ways the available resources can be allocated to the individuals in the system. In a first attempt in this direction (Neill *et al.* 2009), the number of resource allocations for two species is maximized in a constant growth period subject to an energy constraint, from which demographic density dependence is derived. This innovative model leads to the conclusion that coexistence is the ultimate competition outcome under all circumstances, contradicting both theory and observation (Phillips *et al.* 2004; Fargione & Tilman 2005). Their model fails for several reasons. First, unlike most population dynamic models that implicitly include death rate in net growth rate, the MaxEnt part of the model predicted birth rate only, and so populations will grow forever

without further assumptions. To make the system reach an equilibrium, they included death by assuming per capita death probability to be a constant, making the theoretical basis for birth and death in their model inconsistent. Second, this model only includes across-species allocation but not within-species allocation, which as we will show later, can flip the coexistence outcome under certain conditions; third, the model only applies to a chemostat scenario (unlimited resource input with constant energy constraint) and all other possible scenarios are ignored. Another study using similar method to derive abundance distributions by maximizing resource allocation (each resource represented by a functional trait) (Shipley *et al.* 2006) has been criticized for over-constraining with too many functional traits which makes the MaxEnt procedure trivial (Haegeman & Loreau 2009). Their model assumes equal resource requirement for all species and also fails to account for death or within species allocation.

Here we propose and explore a theory that predicts reproduction and survival, i.e. birth and death rates, simultaneously. It is based on maximizing resource allocation entropy, or in other words maximizing the number of ways in which resources can be allocated to individuals and species. The number of within-species allocations is included using an adjustable exponent corresponding to relative within-species individual distinguishability, the effect of which is examined and its implication discussed. The effect of species differences in resource requirement will also

be tested. We start with the simplest case where reproduction and survival are dependent on the same constrained resource. Then we examine more complicated scenarios with different assumptions about the nature of the resource being allocated.

2 Materials and Methods

2.1 Basic concepts

A complete list of symbols used in this paper and their implications is shown in Table 1.

For simplicity, we consider first the case of only two species competing for one resource. Throughout, the term resource is defined generally as "something to be allocated among two species that is beneficial, exclusive and potentially limiting". This definition covers 1) material resources such as food, water, and nitrogen, 2) energy, including solar radiation and heat, and 3) others, such as space and transportation medium. Next we assume populations grow in a discrete manner and define an allocation period as a time interval in which the resource is allocated among all individuals of the two species, a period by which populations shift. We also assume during one allocation period an individual can give birth to at most one offspring. In this particular model, as we explain later, it does not matter whether resource type is flow or stock. For now we consider the resource to be a

constant flow renewed to a constant level R in every allocation period. We

also assume the resource to be a constrained resource, which is defined as a

resource that is fully utilized in each allocation period, or $R_1 + R_2 = R$,

where R_1 and R_2 are the amounts of the resource allocated to species 1 and

2 respectively, in a zero-sum process. Alternatively, an unconstrained

resource is defined as a resource that is not necessarily fully utilized in each

allocation period, or $R_1 + R_2 \leq R$. Scenarios using unconstrained resource

will be discussed later.

$b_{i,t}$ is defined as the discrete birth rate at time t or the number of births at

the t_{th} allocation period for species $i(i = 1, 2)$. $d_{i,t}$ is the corresponding rate

for death. We make no assumptions about the dependence of $b_{i,t}$ and $d_{i,t}$ on

population size; the theory will determine that dependence. By definition:

$$b_{i,t} - d_{i,t} = N_{i,t+1} - N_{i,t} \ (i = 1,2) \tag{1}$$

Note that neither $b_{i,t}$ nor $d_{i,t}$ can be bigger than $N_{i,t}$. Here we introduce a

simple model to predict birth and death rates at the same time: in one

allocation period, each individual of species 1 requires 1 unit of resource to

survive; to reproduce, it has to acquire 1 more unit (2 units in total). Later

we ignore the t component and use N_i, b_i and d_i to represent the abundance,

birth and death rates at any given allocation period for species i. The

consequence for an individual after one allocation is shown in Table 2.

To introduce a difference between the two species, we define θ as the

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relative resource requirement of species 2 so that its resource requirement is that of species 1 times θ (θ to survive while 2θ to reproduce). Since θ is introduced mainly to account for the body size difference between the species, we do not differentiate θ between birth and death assuming survival and reproduction follow the same allometric rules. In this scenario, survival and reproduction are assumed to rely on the same constrained resource. Later the alternative assumption that they rely on two independent resources will be examined and compared.

A microstate is defined as a distinct way of resource allocation among individuals of the two species while a macrostate is the number of births and deaths in populations for each species in one allocation period. The number of microstates corresponding to a macrostate is expressed by the W function. $W(b_1, d_1, b_2, d_2)$ indicates the number of microstates for this macrostate: b_1 births and d_1 deaths for species 1 while b_2 births and d_2 deaths for species 2. In previous work (Neill *et al.* 2009), the number of microstates is just the number of across-species allocations, while here we modify it to be a function of both across-species allocation and within-species allocation as follows:

$$W_{total} = W_{across} W_{within}^{D_r} \tag{2}$$

where W_{across} is the number of across-species allocation while W_{within} is the number of within-species allocation.

D_r is the relative within-species distinguishability, a measure of the extent to which we can treat conspecific individuals as distinguishable as heterospecific individuals in resource allocation. $D_r = 0$ means conspecific individuals are indistinguishable: competition only happens at species level and resources are thoroughly shared within the species, therefore within-species allocation does not matter, as is assumed in Neill *et al.* (2009). At the other extreme, $D_r = 1$ means conspecific individuals are as distinguishable as heterospecific individuals in resource allocation, competition happens at individual level and resources are never shared among any individuals. In that case, within-species allocation should be weighed as much as across-species allocation. $0 < D_r < 1$ describes situations that are in between these two extremes. W_{total} is formulated as Eq. 2 so that when D_r=0, W_{total} is just W_{across}, while when D_r=1, W_{total} is W_{across} times W_{within} since there are W_{within} within-species allocations for each across-species allocation. We note that Eq. 2 is not the only formulation that meets the attributes mentioned above (e.g. D_r^2 instead of D_r on the exponent) but is the simplest to start with. Other functional forms could also be explored.

We can estimate D_r indirectly from other statistical patterns of the species. For example, different assumptions about individual distinguishability lead to different patterns for the species-level spatial distribution derived from the same MaxEnt principle (Young & Willson

1987). Another more direct measure for D_r is relative within-species trait differences compared to across-species trait differences, assuming that the trait used here is relevant to resource acquisition and individuals with similar trait values are more likely to share the resource with each other. Calculation of D_r for a simple two-species case using trait data based on this expression is illustrated in Fig. 1 and Eq. 3-5.

$$D_{within} = \frac{2 \sum_{i=1}^{2} \sum_{j=1}^{N_i} \sum_{k=i+1}^{N_i} |t_{ij} - t_{ik}|}{N_1(N_1 - 1) + N_2(N_2 - 1)} \tag{3}$$

$$D_{across} = \frac{\sum_{j=1}^{N_1} \sum_{k=1}^{N_2} |t_{1j} - t_{2k}|}{N_1 N_2} \tag{4}$$

$$D_r = D_{within}/D_{across} \tag{5}$$

In Eq. 3-5, t_{ij} is the trait value of the j_{th} individual in species i. D_{within} is the mean pairwise trait difference between conspecific individuals while D_{across} is that between heterospecific individuals. Plugging the trait values in Fig. 1 into Eq. 3-5, we get $D_r = 0.9$, indicating that conspecific individuals are 90% as distinguishable as heterospecific individuals. Here we are using the averaged D_r. However, D_r can also be calculated specifically for each species using the mean pairwise trait difference between individuals of that species as D_{within}. Based on this method, multiple traits and potentially genetic data can be used to calculate D_r.

2.2 Calculation

Here the number of allocation microstates is maximized. We first derive W_{across} and W_{within} separately. We use $C(x_1, x_2, ...|X)$ to denote the number of ways to combine X individuals into groups of x_i. Therefore,

$$C(x_1, x_2, ...|X) = \frac{X!}{x_1! x_2! ...} \tag{6}$$

W_{across} is the number of ways the resource can be allocated between the two species. Using the notation defined above,

$$
\begin{aligned}
W_{across}(b_1, d_1, b_2, d_2) &= C(R_1, R_2|R) * C(b_1, d_1, N_1 - b_1 - d_1|N_1) \\
&\quad * C(b_2, d_2, N_2 - b_2 - d_2|N_2)
\end{aligned}
\tag{7}
$$

R_1 and R_2 are resources used by species 1 and 2, respectively. For species 1, each individual that survives obtains one unit of resource while each individual that reproduces obtains two, therefore

$$
\begin{aligned}
R_1 &= \text{number of individuals that survive but do not reproduce} \\
&\quad + 2 * \text{number of individuals that reproduce} \\
&= (N_1 - b_1 - d_1) + 2b_1 = N_1 + b_1 - d_1
\end{aligned}
\tag{8}
$$

For species 2, the resource requirement scales by θ.

$$R_2 = \theta(N_2 - b_2 - d_2) + 2\theta b_2 = \theta(N_2 + b_2 - d_2) \tag{9}$$

W_{within} is the number of ways the resources allocated to each species are allocated among different individuals. If an individual only gets at most one unit of resource, W_{within} is just the number of permutations of the units of resources obtained by each species R_i ($i = 1$ or 2). When an individual gets more than one unit of resource, to calculate W_{within}, each permutation of R_i has to be divided by the number of permutations of the units of resource obtained by that individual, since different orderings within an individual should be counted as one microstate:

$$W_{within}(b_1, d_1, b_2, d_2) = \frac{(N_1 + b_1 - d_1)!}{2^{b_1}} \frac{(\theta(N_2 + b_2 - d_2))!}{(2\theta!)^{b_2}(\theta!)^{N_2 - b_2 - d_2}} \tag{10}$$

Since the resource in this scenario is assumed to be a constrained resource (see definition in the above section), maximization is subject to the constraint

$$R_1 + R_2 = R \tag{11}$$

by which the resource exploitation efficiency $(R_1 + R_2)/R$ is constrained to be 1. Using the method of Lagrange multipliers for constrained maximization, we define an objective function S as

$$S(W_{total}, \lambda) = log(W_{total}) - \lambda(R - R_1 - R_2) \tag{12}$$

where λ is the Lagrange multiplier. S is maximized by solving:

$$\frac{\partial S(W_{total}, \lambda)}{\partial x_i} = 0 \tag{13}$$

Plugging in the expression for W_{total}, with x_i being the births or deaths of species i each time, we get four equations:

$$\frac{\partial S(W_{total}, \lambda)}{\partial b_1} = log\frac{b_1(N_1 + b_1 - d_1)^{1-D_r}}{N_1 - b_1 - d_1} + D_r log2 + \lambda = 0 \tag{14}$$

$$\frac{\partial S(W_{total}, \lambda)}{\partial d_1} = log\frac{d_1}{(N_1 + b_1 - d_1)^{1-D_r}(N_1 - b_1 - d_1)} - \lambda = 0 \tag{15}$$

$$\frac{\partial S(W_{total}, \lambda)}{\partial b_2} = log\frac{b_2(\theta(N_2 + b_2 - d_2)^{\theta(1-D_r)}}{N_2 - b_2 - d_2} + D_r log\frac{(2\theta)!}{\theta!} + \lambda\theta = 0 \tag{16}$$

$$\frac{\partial S(W_{total}, \lambda)}{\partial d_2} = log\frac{d_2}{(\theta(N_2 + b_2 - d_2))^{\theta(1-D_r)}(N_2 - b_2 - d_2)} - log\theta! - \lambda\theta = 0 \tag{17}$$

Combining these equations with the constraint (Eq. 11), b_1, d_1, b_2, d_2 and λ can be solved as functions of current abundances and resource availability (N_1, N_2 and R). Although the equations look intimidating and general forms are not analytically solvable, there is one prominent attribute: when $\theta =$1 and $D_r =$1 (two species have the same resource requirement and conspecific individuals are equally distinguishable as heterospecific individuals), the equations can be reduced to a simple form as the following:

$$\frac{b_1}{b_2} = \frac{d_1}{d_2} = \frac{N_1}{N_2} \tag{18}$$

This suggests that when $\theta = 1$ and $D_r = 1$, demographic rates are linearly dependent on current abundance/density and the per capita growth rates are the same for the two species. This is not hard to understand since in this case, all individuals are equivalent and thus have equal chance to get resource. Therefore, birth and death rates are proportional to the number of individuals in each species. In this case, the competition outcome will be a neutral equilibrium where the two species could end up with any abundance ratio since their per capita growth rates are the same.

To get more general patterns for different θ and D_r, in the next section, the equations are solved numerically and the effect of each parameter examined. Numerical equation solving is done in R 3.1.0 using function *nleqslv* under the package with the same name.

3   Results

3.1   Density dependence of net growth rate

Here we compare how per capita net growth rate $(b_1 - d_1)/N_1$ responds to per capita resource availability $R/(N_1 + N_2)$ and abundance proportion $N_1/(N_1 + N_2)$ among different parameter settings for D_r and θ. We only examine the pattern for species 1 since the two species are symmetrical

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₂₅₅ depending on different values of θ (species 1 at $\theta = 2$ is equivalent to species

₂₅₆ 2 at $\theta = 0.5$).

₂₅₇   The prediction from the two-species competitive Lotka-Volterra equations

₂₅₈ is also plotted in each graph as a comparisons. One classic expression of the

₂₅₉ discrete two-species competitive Lotka-Volterra equations (May *et al.* 1974;

₂₆₀ Hassell & Comins 1976) is as follows:

$$N_{1,t+1} = N_{1,t}exp(1 - \frac{\alpha_{11}N_{1,t} + \alpha_{12}N_{2,t}}{K_1}) \tag{19}$$

₂₆₁   For species 2 the subscripts are switched. r_i is the intrinsic per capita

₂₆₂ growth rate for species i. Since in our model we restricted each individual to

₂₆₃ only one birth in one allocation period, to make the models comparable we

₂₆₄ set $r_i=1$ in the Lotka-Volterra equations for both species. K_i is the carrying

₂₆₅ capacity for species i in the absence of the other species, corresponding to R

₂₆₆ (for species 1) and R/θ (for species 2) in our model. α_{ij} is the effect of

₂₆₇ species j on species i. Since we only consider exploitative competition in

₂₆₈ this model, this is just the relative resource requirement of species j

₂₆₉ compared to species i, therefore $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = \theta$ and $\alpha_{21} = 1/\theta$. With

₂₇₀ all these assumptions the discrete two-species competitive Lotka-Volterra

₂₇₁ equations can be re-expressed using parameters of our model as:

$$\frac{N_{1,t+1} - N_{1,t}}{N_{1,t}} = exp(r_1(1 - \frac{\alpha_{11}N_{1,t} + \alpha_{12}N_{2,t}}{K_1})) - 1$$
$$= exp(1 - \frac{N_{1,t} + \theta N_{2,t}}{R}) - 1 \tag{20}$$

$$\frac{N_{2,t+1} - N_{2,t}}{N_{2,t}} = exp(r_2(1 - \frac{\alpha_{22}N_{2,t} + \alpha_{21}N_{1,t}}{K_2})) - 1$$
$$= exp(1 - \frac{\theta N_{2,t} + N_{1,t}}{R}) - 1 \tag{21}$$

Notice that $(N_{1,t+1} - N_{1,t})/N_{1,t}$ is the per capita net growth rate corresponding to $(b_1 - d_1)/N_1$ at the t_{th} allocation period in our model. Unless specified otherwise, all calculations are done with the following parameter setting: N_1= 150, N_2= 100, R=250.

From Fig. 2a we can see that, for our model, per capita net growth rate increases linearly with increased per capita resource availability. While for the Lotka-Volterra equations, per capita net growth rate increases with resource availability in a concave curve, first faster then slower than our model. When $\theta = 1$, while the two models give similar predictions at intermediate resource level, at both low and high resource level our model predicts higher per capita net growth rate than the Lotka-Volterra equations, indicating lower resource exploitation efficiency for the latter. When θ=2, the Lotka-Volterra equations predicts the per capita net growth rate to be much lower compared to when θ=1, especially at low resource availability, while we predict a slight decrease at high resource availability. For both situations $\theta = 1$ and 2, D_r does not influence the pattern. In all,

we predict higher resource exploitation efficiency and a more steady

response of the per capita net growth rate to varied resource availability

and relative resource requirement, regardless of the value of D_r.

The pattern of the response of per capita net growth rate to the

abundance proportion $N_1/(N_1 + N_2)$, however, is much more complicated

(Fig. 2b). First we can see that for both $\theta = 1$ and $\theta = 2$, the prediction of

our model is significantly different from that of the Lotka-Volterra

equations. When $\theta = 1$, the per capita net growth rate predicted by the

Lotka-Volterra equations does not change with changing abundance ratio

between the two species. In our model, however, only when $D_r = 1$ does the

same pattern emerge. When $D_r < 1$, at comparatively low abundance, our

model predicts a higher per capita net growth rate than the Lotka-Volterra

equations. It decreases with increased abundance proportion, indicating an

effective compensating stabilizing mechanism (Chesson 2000) that helps

reduce the abundance difference. As the abundance proportion increases to

a certain level, the per capita net growth rate of our model drops below

that of the Lotka-Volterra equations. With abundance proportion

increasing it even starts to increase with increasing abundance proportion.

When the abundance proportion approaches 1, our prediction approaches

that of the Lotka-Volterra equations.

For $\theta = 2$, the Lotka-Volterra equations predict a linearly increasing per

capita net growth rate with increased abundance proportion, which is

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significantly different from our prediction in all cases. For cases where $D_r < 1$, similar to when $\theta = 1$, the per capita net growth rate predicted by our model first decreases then increases with rising abundance proportion. For $D_r = 1$, our model predicts per capita net growth rate to increase monotonically with abundance proportion, but with a slower slope than that of the Lotka-Volterra equations. For all D_r, the model output starts higher than that of the Lotka-Volterra equations, drops below, and finally approaches the latter as the abundance proportion approaches 1.

In summary, our model shows more stabilizing mechanisms than the Lotka-Volterra equations: at low abundance proportion, per capita net growth rate is higher, expediting growth of the rarer species. With abundance increasing, this compensation weakens and per capita net growth rate drops below the prediction of the Lotka-Volterras equations beyond a certain level of abundance proportion. One notable result is that the larger D_r is, the closer our model gets to the Lotka-Volterra equations, indicating an effective stabilizing mechanism of increasing strength and thus higher chance of coexistence when conspecific individuals are less distinguishable compared to heterospecific individuals.

3.2 Two-species population dynamics and competition outcome

In this section, the two-species population dynamics through time is simulated to show the long term competition outcome predicted by our

331 model under different conditions (Fig. 3). The same parameter setting for

332 initial abundance and resource amount is used ($N_{1,t=0}$= 150, $N_{2,t=0}$= 100,

333 R=250), with N_1 and N_2 updated at each allocation period using Eq. 1

334 repeatedly. To examine whether initial conditions affect the outcome, a

335 simulation is also done with a more extreme initial abundance difference

336 ($N_{1,t=0} = 245$, $N_{2,t=0} = 5$). While the time to equilibrium changes, the

337 general pattern and final equilibrium is the same as with the base case

338 initial conditions.

339   When θ =1 and $D_r < 1$, the final competition outcome is equal

340 abundance coexistence. However, as D_r increases, the time for the two

341 populations to converge increases, until when D_r =1 they become parallel:

342 the two species stay in their initial state and never converge, consistent with

343 neutral equilibrium.

344   When θ =1.5 and $D_r < 1$, the final competition outcome is still

345 coexistence but with unequal abundances. As D_r increases, there are two

346 variations to the dynamics: first, the time to converge gets longer; second,

347 the difference between the equilibrium abundances of the two species gets

348 larger with larger D_r, until at D_r =1 species 1 totally excludes species 2.

349   Since for D_r =1, $\theta = 1$ and $\theta = 1.5$ have primarily distinct competition

350 outcomes (neutral equilibrium vs exclusion), the dynamics when $\theta = 1.01$ is

351 simulated to test if a slight difference in resource requirement could also

352 cause exclusion. From Fig.3 we can see that, although it takes a very long

time (in our case time $\approx$ 5000 steps) for one species to be completely excluded, the final outcome for $\theta = 1.01$ is definitely exclusion. This corresponds to the classic expression of the competitive exclusion principle: a slight difference in fitness between species competing for one resource will lead to the exclusion of the inferior one (when $D_r = 1$).

In summary, population dynamics shows a pattern consistent with the result of demographic density dependence: the higher D_r is, the less stabilizing mechanism, represented by slower species converge in abundances (when $D_r = 1$, they do not converge) and a more extreme abundance ratio at equilibrium. Meanwhile, θ also influences the final outcome: $\theta = 1$ leads to equal abundance equilibrium for all $D_r < 1$ and neutral equilibrium when $D_r = 1$, while a deviation from 1 (however little) leads to unequal abundance at equilibrium for $D_r < 1$ and exclusion $D_r = 1$.

3.3 Other resource use scenarios

To examine the effect of our assumptions about resource use, the same analysis is done for several different scenarios where 1) reproduction and survival can rely on two independent resources and 2) an unconstrained resource is used (the resource might not be fully utilized, or $R_1 + R_2 \leq R$ instead of $R_1 + R_2 = R$). The definition of each scenario and the corresponding patterns are summarized in Table 3. Details on derivations for each of the scenarios are included in the Appendix. For all of these

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scenarios, the general effects of D_r and θ are the same as in the first scenario explored in the previous Section. Meanwhile there are also interesting patterns emerging. First, with higher D_r, scenarios where resource use is not constrained get closer to the constrained scenarios, indicating higher resource exploitation efficiency at higher D_r. Second, when $\theta > 1$, scenarios where reproduction and survival rely on two different resources lead to a reversed abundance advantage between the two species, especially when D_r is closer to 1. Instead of species 1 having higher abundance than species 2, in these scenarios species 2 outnumbers species 1 despite its higher resource requirement. When $D_r = 1$, species 2 excludes species 1.

4   Discussion

Our theory provides a new approach to understanding the origin and form of demographic density dependence, leading to various competition outcomes under different conditions. It provides a parsimonious explanation of why competitive exclusion is not always observed in nature. Results from comparing the Lotka-Volterra equations with our predictions indicate that while they overlap in certain conditions, our theory generally predicts more stabilizing mechanism and thus higher chance of coexistence.

In addition to the Lotka-Volterra equations, there are clearly other connections between this and previous theories. For example, factors

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representing Chesson's fitness equality and stabilizing mechanism can be found in this theory: $\theta = 1$ suggests fitness equality and the lower D_r is, the greater the strength of the effective stabilizing mechanism. The tradeoff between fitness difference and stabilizing mechanism is also apparent: $D_r = 1$ (no stabilizing mechanism) only leads to exclusion when θ does not equal 1 (fitness difference); on the other hand, the more different θ is from 1, the more different equilibrium abundances are, which means a large enough θ could practically lead to exclusion of one species even when $D_r = 0$. Model settings at the two extremes of a coexistence-exclusion spectrum are 1) $D_r = 0$ and $\theta = 1$, which leads to equal abundance coexistence, and 2) $D_r = 1$ and $\theta \neq 1$, which leads to exclusion of one species. Any setting between these two extremes will generate a pattern in between: coexistence with differential abundance (when both D_r and θ are different from 1).

So far we have shown that the two parameters: relative resource requirement θ and relative within species distinguishability D_r are key elements that determine outcomes. While the concept of θ is straightforward and can be related to body size, the question of what species attribute is related to relative distinguishability D_r and how to measure it is less obvious. Results from the various scenarios suggest that D_r not only affects competitive outcome, it also determines the total resource exploitation efficiency ($(R_1 + R_2)/R$); without a hard constraint on resource exploitation efficiency, the higher D_r, the higher total resource exploitation efficiency is.

The distinguishability of conspecific individuals is not a new concept in ecology and has been discussed in the context of species level spatial abundance distributions (Young & Willson 1987), where different levels of distinguishability lead to different distribution patterns. So far, however, distinguishability has only been treated as a binary value (distinguishable vs indistinguishable). Neither the continuous definition nor any method to measure this important attribute has been proposed. To test our theory and better incorporate this attribute in the general theoretical ecology, both an indirect measure for D_r based on other statistical patterns and a direct measure based on traits proposed earlier in this paper should be explored, from which many potentially interesting implications could emerge.

For example, our proposed direct measure for D_r (Fig. 1) suggests that when D_{within} is comparatively fixed, the more the two species overlap on the trait axis, the lower the D_{across} and the higher the D_r, indicating a connection between relative distinguishability and niche overlap. However, we should emphasize that D_r does not affect which resource is allocated or how resource requirements differ between species (which is represented by θ). Instead, it only affects how different allocations among individuals within the same species should be weighted. This also suggests that theories predicting coexistence based on niche difference (Silvertown 2004; Fargione & Tilman 2005) might have reached the right answer for the wrong reason: instead of a disparity in the resource types that species rely on, difference in

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functional traits might be contributing to coexistence solely by changing relative distinguishability of conspecific individuals. With $D_r < 1$, it is likely that two species will coexist even if they both totally rely on the same resource. On the other hand, when D_{across} is comparatively fixed, the more variation in trait values within the same species, the higher are D_{within} and D_r, indicating a connection between within-species variation and inter-specific competition outcome. Since within-species variation is also related to evolution potential (Lewontin 1974), the implication of our study (especially when genetic data is used to calculate D_r) on the interplay between evolutionary mechanisms and species competition is worth future exploration.

In this paper, as a first simplification, D_r is assumed to be the same for different species, as θ is assumed to be a single value across all individuals of the same species. The alternatives, i.e. D_r differs among species and/or θ has a range instead of being a single value, can be easily explored with the introduction of more parameters, which is beyond the scope of this paper but will be explored in future work.

In our model, it does not matter if the resource is a constant stock like space or a flow like solar energy. First of all, almost all resources can be construed as either flow or stock resources depending on the time frame. A flow resource in the short term might be treated as a stock in the long run, as for example with a recycled resource such as nitrogen. Clearly a constant

flow resource like sunlight is the same at each interval (ignoring clouds and solar variability). For a stock resource that can be recycled within an allocation cycle, and for which individuals cannot preempt the resource, then from one time to another it is the R= $R_{remaining} + R_{occupied}$ that is allocated and this amount is also a constant from interval to interval time (as long as the stock size does not change). Because the resource dependence of net growth rate is monotonic (increasing) for all scenarios, when the flow or stock size fluctuates through time, it should not change the final competitive outcome but will probably change the time to equilibrium.

In other scenarios of this model we found that species with higher resource requirement (usually the bigger one) does not necessarily end up with lower abundance: under certain circumstances (when reproduction and survival rely on different resources), species with higher resource requirement could even exclude the other. This result is consistent with the frequently observed violations (White *et al.* 2007; Blackburn & Gaston 1994; Marquet *et al.* 1995) of the hypothesized size-abundance relationship (Damuth 1993).

There are many potential future extensions to this model. First, more species can readily be included. So far the model only predicts a two-species system and including more species might significantly change the model behavior. Second, other types of interaction can be incorporated. Like the general form of the Lotka-Volterra equations, this model can be generalized

to predict many types of interspecific interactions. For example, instead of allocating resource among two species, individuals of one species could be allocated among another to predict predator-prey interactions. Third, based on the first extension, once more species are included we can examine implications for community level metrics such as the species abundance distribution (SAD). Using the same assumption of fitness equality as in neutral theory (Hubbell 2001), for example, we can set $\theta = 1$ and examine how the SAD shape changes with D_r. Finally, by examining the roles of relative within-species distinguishability in both processes, the relationship between evolution and competition can be addressed with this new theory.

In conclusion, instead of assuming demographic density dependence as most models predicting competition do, we started with only a simple rule of maximizing resource allocation entropy (number of microstates) and obtained results that resonate with previous established theories yet cover more general situations. Relative within species distinguishability is an important parameter that significantly affects competitive outcome and resource exploitation efficiency. It is deserving of further investigation. Our work reveals a promising approach to utilizing fundamental principles of statistics to explain competitive coexistence, density dependence and, potentially, abundance distributions, size-abundance relationships, trophic interaction network structure and dynamics, and other ecological patterns.

5   Acknowledgement

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Figure 1: Calculation of D_r using a trait relevant to resource acquisition. This is illustrated with a simple two-species case where there are three individuals for the first species and two for the second. Trait values for all individuals are plotted on the trait axis with a distinct point type for each species. t_{ij} represents the trait value of the j_{th} individual in species i. Within- and across- species pairwise distances are represented by line segments of different types. D_r is the relative individual distinguishability calculated from pairwise trait distances using Eq. 3-5. In this graph, $t_{11} = 5$, $t_{12} = 30$, $t_{13} = 60$, $t_{21} = 50$, $t_{22} = 90$, plugging in Eq. 3-5, we get $D_{within} = 2 * (25 + 30 + 55 + 40)/(6 + 2) = 37.5$, $D_{across} = (45 + 85 + 20 + 60 + 10 + 30)/6 = 41.67$, $D_r = 37.5/41.67 = 0.9$.

Figure 2: Per capita net growth rate in response to per capita resource availability (a) and abundance proportion (b). N_1 and N_2 are the abundances for species 1 and species 2, respectively, R is the total amount of resource available, θ is the relative resource requirement, D_r is the individual distinguishability. Responses of per capita net growth rate $(N_{1,t+1} - N_{1,t})/N_{1,t}$ to the per capita resource availability $R/(N_1 + N_2)$ and the abundance ratio of species 1, $N_1/(N_1 + N_2)$, are compared for different D_r values and the Lotka-Volterra equations.

Figure 3: Population dynamics through time. N_1 and N_2 are the abundances for species 1 and species 2, respectively. At time t=0, $N_1 = 150$, $N_2 = 100$. θ is the relative resource requirement, D_r is the individual distinguishability. Predictions for dynamic variation in abundances for both species are compared for different D_r values.

Table 1: Symbols used

Symbols	Interpretations
R	The total amount of resources allocated in one allocation period. R_i indicates the amount allocated to species i.
N_i, $N_{i,t}$	Abundance of species i (i=1,2) at any given or the t_{th} allocation period.
W_{across}, W_{within}	Number of ways to allocate resources across two species or within one species.
W_{total}	Total number of ways to allocate resources, combining across and within species allocation (microstates).
b_i, d_i	Birth or death rate for species i at any allocation period (macrostates).
t_{ij}	The trait value of the j_{th} individual of species i.
D_{across}, D_{within}	Mean pairwise difference of a trait relevant to resource acquisition across or within species.
D_r	Individual level distinguishability within species relative to across species. Can be measured with D_{within}/D_{across}.
θ	Relative resource requirement for species 2 compared to species 1.
$C(x_1, x_2, ..., |X)$	Number of ways to combine X individuals into groups of x_i. $C(x_1, x_2, ..., |X) = X!/(x_1!x_2!...)$
S, λ	S is the objective function for constrained maximization: $S = log(W_{total}) - \lambda(R - R_1 - R_2)$, where λ is the Lagrange multiplier.

Table 2: Resource allocation consequence for an individual

Units of resource allocated to the individual	Consequence
0	Death
1	Survive (but not reproduce)
2	Survive and reproduce

Table 3: Resource use scenarios and their implications for demographics and competition outcome

| Scenario	Description	Competition outcome			
		$D_r < 1$		$D_r = 1$	
		$\theta = 1$	$\theta > 1$	$\theta = 1$	$\theta > 1$
S1	Reproduction and survival rely on the same constrained resource	Coexistence with equal abundance, $R_1 + R_2 = R$	Coexistence with $N_1 > N_2$	Neutral equilibrium, $R_1 + R_2 = R$	Species 1 excludes species 2
S2	Same with S1 with unconstrained resource	Coexistence with equal abundance, $R_1 + R_2 < R$	Same as S1	Same as S1	Same as S1
S3	Reproduction and survival rely on two resources that are both constrained	Same as S1	Same as S1 at low D_r, $N_2 > N_1$ at high D_r	Same as S1	Species 2 excludes species 1
S4	Resource constrained for survival, unconstrained for reproduction	Same as S2	Same as S3	Same as S1	Same as S3
S5	Opposite case of S4	Same as S2	Same as S3	Same as S1	Same as S3
S6	Same with S3 with unconstrained resource	Same as S2	Same as S3	Same as S1	Same as S3
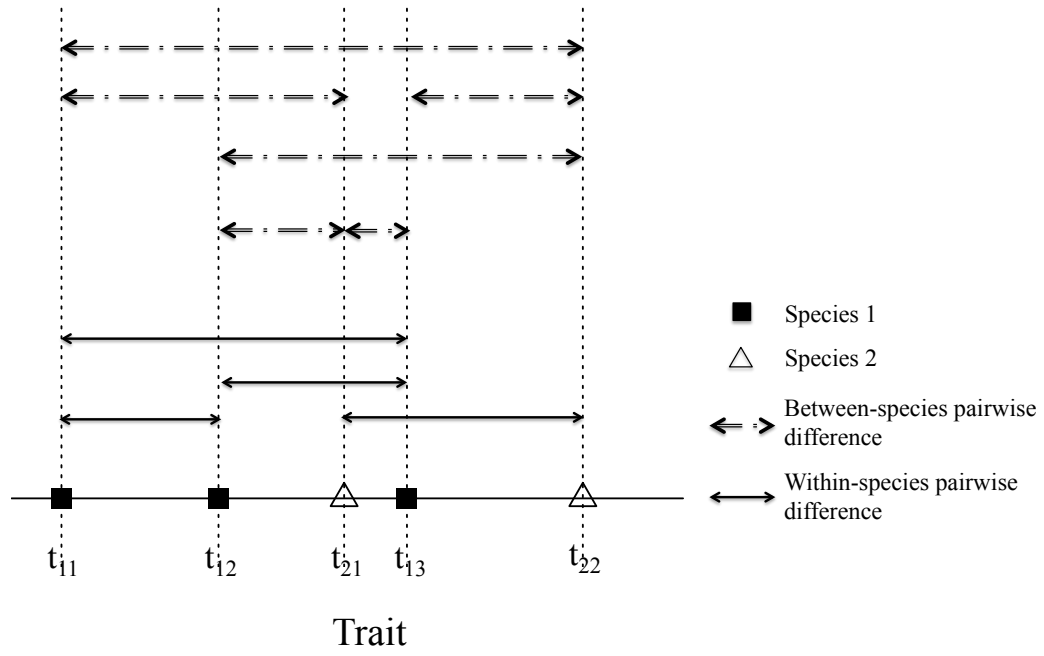
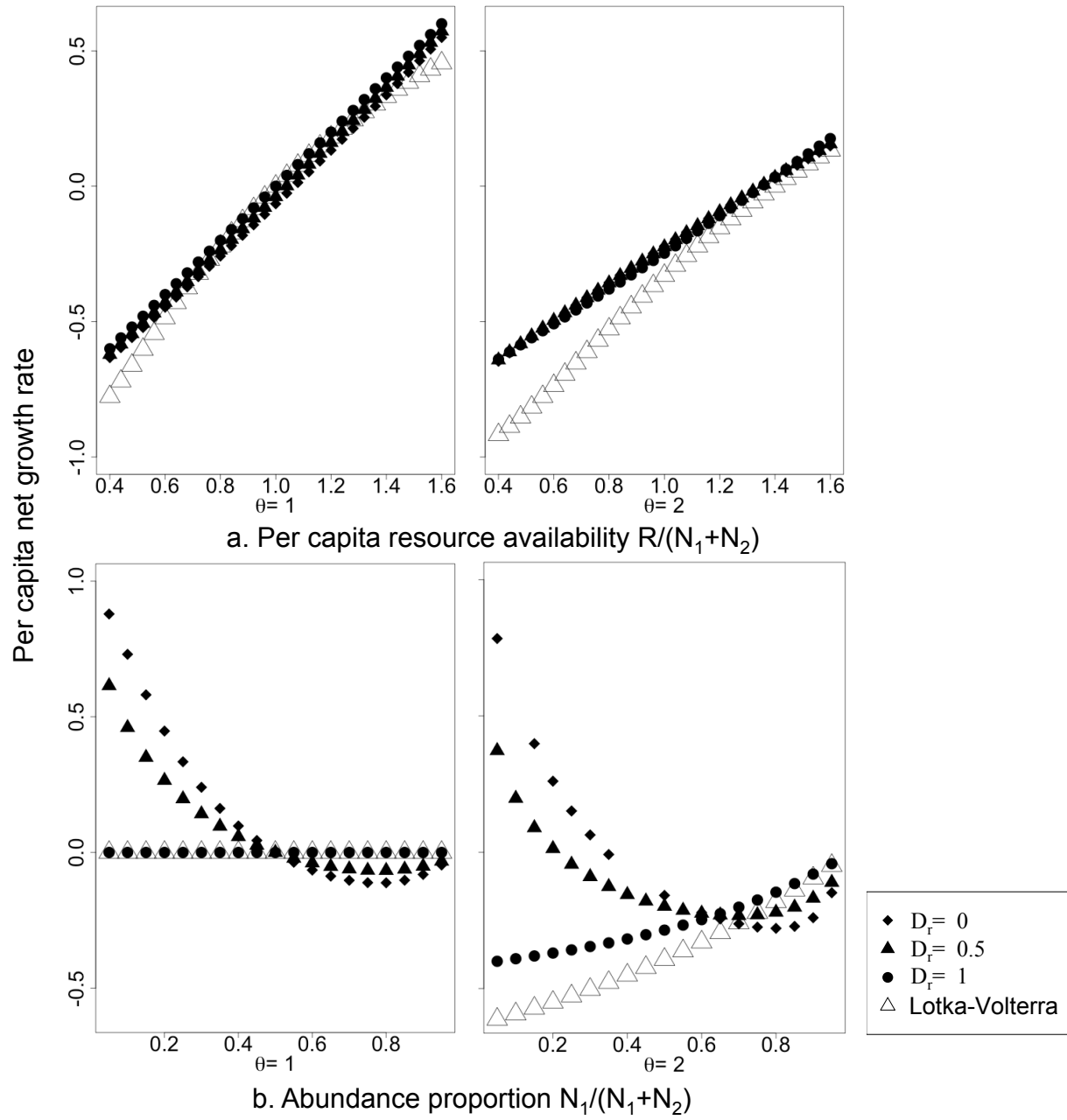Figure 1: Calculation of D_r using a trait relevant to resource acquisition.

Figure 2: Per capita net growth rate in response to per capita resource availability (a) and abundance proportion (b).
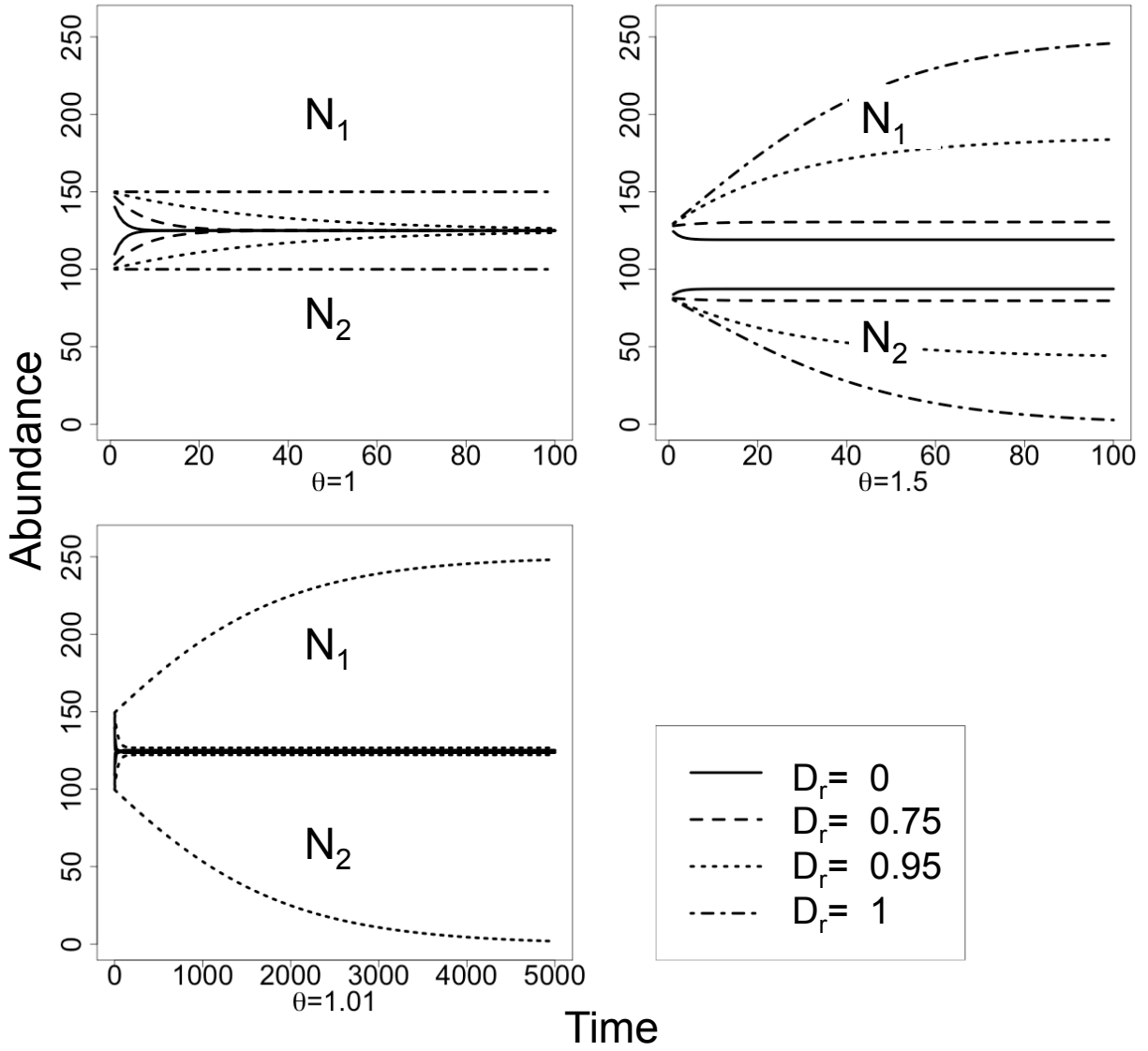
Figure 3: Population dynamics through time.

Appendix: Maximization procedure and differential equations for all scenarios

Additional resource types

When reproduction and survival rely on two different resources

Resources relevant to reproduction or survival only but not both are defined as partial resources, as opposed to essential resources that are relevant to both reproduction and survival. Based on the definitions of the scenarios (Table 3 in main text), resources in scenarios S1 and S2 are essential resources while those in scenarios S3, S4, S5 and S6 are partial resources. W functions (number of microstates) for essential resources have been included in main text (Eq. 4-7). For a partial resource,

$$W_{across}(n_1, n_2) = C(R_1, R_2, R - R_1 - R_2|R) * C(n_1, N_1 - n_1|N_1) \qquad (22)$$
$$* C(n_2, N_2 - n_2|N_2)$$

$$W_{within}(n_1, n_2) = \frac{n_1!(\theta n_2)!}{\theta^{n_2}} \qquad (23)$$

n_i is the number of individuals that get resource in one allocation period for species i (i=1,2). It can be birth rate (b_i) or survival rate (s_i), depending on whether the resource being considered is relevant to reproduction or survival. In the latter case, death rate $d_i = N_i - s_i$. Resources allocated to each species are simply

$$R_1 = n_1 \tag{24}$$

$$R_2 = \theta n_2 \tag{25}$$

When resource is not constrained to be fully utilized

Unconstrained resources are defined as resources that are not necessarily fully utilized in every allocation $(R_1 + R_2 \leq R)$, as opposed to constrained resources which satisfy $R_1 + R_2 = R$ in each allocation period. Based on the definitions of the scenarios (Table 3 in main text), resources in scenarios S1 and S3, survival resource in S4 and reproduction resource in S5 are constrained resources while resources in scenarios S2 and S6, reproduction resource in S4 and survival resource S5 are unconstrained resources. Maximization for constrained resources have been included in main text (Eq. 8-10). For unconstrained resources, total number of allocations W_{total} is maximized without constraint. When resource is essential (see definition in the above section),

$$\frac{\partial(log(W_{total}))}{\partial b_i} = \frac{\partial(log(W_{total}))}{\partial d_i} = 0 \tag{26}$$

When resource is partial (see definition in the above section),

$$\frac{\partial(log(W_{total}))}{\partial n_i} = 0 \tag{27}$$

n_i can be birth rate b_i or survival rate s_i ($i = 1,2$), depending on whether the resource is reproduction or survival relevant.

Differential equations for all scenarios

In all derivations Stirling's approximation is used:

$$log(n!) \approx nlog(n) - n \text{ (when n is large)} \tag{28}$$

To facilitate calculation, instead of $log(W)$ we take the derivative of $-log(W)$ which should not affect the result.

essential and constrained (S1)

For constrained resources that are relevant to both reproduction and survival (scenario S1), see Eq 11-14 in main text.

essential and unconstrained (S2)

For unconstrained resources that are relevant to both reproduction and survival (scenario S2), there are four equations (two for each species):

$$\frac{\partial(-log(W_{total}))}{\partial b_1}$$

$$= log\frac{b_1(N_1 + b_1 - d_1)^{1-D_r}}{(N_1 - b_1 - d_1)(R - (N_1 + b_1 - d_1) - \theta(N_2 + b_2 - d_2))} + D_r log2$$

$$= 0$$

(29)

$$\frac{\partial(-log(W_{total}))}{\partial d_1} = log\frac{d_1(R - (N_1 + b_1 - d_1) - \theta(N_2 + b_2 - d_2))}{(N_1 + b_1 - d_1)^{1-D_r}(N_1 - b_1 - d_1)} = 0 \quad (30)$$

$$\frac{\partial(-log(W_{total}))}{\partial b_2}$$

$$= log\frac{b_2(\theta(N_2 + b_2 - d_2))^{\theta(1-D_r)}}{(N_2 - b_2 - d_2)(R - (N_1 + b_1 - d_1) - \theta(N_2 + b_2 - d_2))^\theta} + D_r log\frac{(2\theta)!}{\theta!}$$

$$= 0$$

(31)

$$\frac{\partial(-log(W_{total}))}{\partial d_2} = log\frac{d_2(R - (N_1 + b_1 - d_1) - \theta(N_2 + b_2 - d_2))^\theta}{(\theta(N_2 + b_2 - d_2))^{\theta(1-D_r)}(N_2 - b_2 - d_2)} - log\theta!$$

$$= 0$$

(32)

partial and unconstrained (S4, S5, S6)

For resources that are relevant to reproduction or survival only and unconstrained (reproduction resource in S4, survival resource in S5, both resources in S6), there are two equations (one for each species):

$$\frac{\partial(-log(W_{total}(n_1, n_2)))}{\partial n_1} = log\frac{n_1^{2-D_r}}{(N_1 - n_1)(R - n_1 - \theta n_2)} = 0 \qquad (33)$$

$$\frac{\partial(-log(W_{total}(n_1, n_2)))}{\partial n_2} = log\frac{(\theta n_2)^{\theta(1-D_r)}n_2}{(N_2 - n_2)(R - n_1 - \theta n_2)^{\theta}} - D_r log(\theta!) = 0 \quad (34)$$

n_i can be birth rate b_i or survival rate s_i depending on the scenario ($i =$ 1,2).

partial and constrained (S3, S4, S5)

For resources that are relevant to reproduction only and constrained (survival resource in S4, reproduction resource in S5, both resources in S3), there are also two equations:

$$\frac{\partial S(W_{total}(n_1, n_2), \lambda)}{\partial n_1} = log\frac{n_1^{2-D_r}}{N_1 - n_1} + \lambda = 0 \qquad (35)$$

$$\frac{\partial S(W_{total}(n_1, n_2), \lambda)}{\partial n_2} = log\frac{(\theta n_2)^{\theta(1-D_r)}n_2}{N_2 - n_2} + \lambda\theta - D_r log(\theta!) = 0 \qquad (36)$$

Again n_i can be birth rate b_i or survival rate s_i depending on the scenario (i = 1,2).