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

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Abstract

Model predictions for species competition outcomes highly depend on the assumed form of the population growth function. In this paper we apply an alternative inferential method based on statistical mechanics, maximizing Boltzmann entropy, to predict resource-constrained population dynamics and coexistence. Within this framework, population dynamics and competition outcome can be determined without assuming any particular form of the population growth function. The dynamics of each species is determined by two parameters: the mean resource requirement θ (related to the mean metabolic rate) and individual distinguishability D_r (related to intra- compared to interspecific functional variation). Our theory clarifies the condition for the energetic equivalence rule (EER) to hold, and provide a statistical explanation for the importance of species functional variation in determining population dynamics and coexistence patterns.

Keywords species coexistence, population dynamics, resource allocation, Boltzmann entropy, 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 (Volterra 1938; 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 & McPeck 2010).

In a review of this topic, Chesson (2000) identified two properties of mechanisms of population dynamics that shape the species coexistence outcomes: equalizing, which leads to diminishing average fitness difference between species (Tilman 1981; Chave 2004); and stabilizing, which leads to higher intraspecific than interspecific density dependence (Amarasekare 2003; Lobry & Harmand 2006). He then partitioned different models using these two properties and concluded that coexistence is only possible when fitness differences (the opposite of equalizing mechanisms) are compensated by stabilizing mechanisms. The equalizing and stabilizing behaviors of a model, however, are largely determined by the form of the population growth function the model assumes, which is usually chosen phenomenologically, applying functions most familiar to ecologists, e.g. linear, exponential and logistic (Volterra 1938; Hassell 1975).

38 Although these simple function forms are convenient and neat, nature is
39 undoubtedly more complex (Abrams & Ginzburg 2000; Chase *et al.* 2002;
40 Melbourne & Chesson 2005). And while some competition models have
41 assumed more complex equations, either fitted from data (Leirs *et al.* 1997)
42 or derived from more nonlinear mechanisms (Toro *et al.* 1971; Dennis &
43 Desharnais 1995), the more complex the model, the more vulnerable it
44 usually is to over parameterization, adding to the difficulty of falsification.
45 More importantly, since most studies only look at a handful of species, the
46 form of the population growth function varies from study to study. How
47 this variation is generated would be better understood if a theory involving
48 only general principles, potentially applicable to all species, existed.

49 Our goal is such a theory, one that predicts the most phenomena with the
50 fewest unverifiable assumptions. Statistical mechanics provides a widely
51 applicable method, maximum entropy (MaxEnt), for inferring the most
52 likely form of the pattern of interest given limited information available.
53 MaxEnt based on Shannon entropy (Jaynes 1982) has been used in ecology
54 to predict species spatial distributions from environmental variables
55 (Phillips *et al.* 2006) or from the species abundance distribution (Shipley
56 *et al.* 2006) and has nurtured a comprehensive theory that predicts
57 numerous macroecological metrics including the species abundance
58 distribution, the species level spatial abundance distribution and the species
59 area relationship (Harte 2011; Harte & Newman 2014; see also Dewar &

Porté 2008).

So far there has been little effort to apply MaxEnt to the study of population dynamics and species interaction. It is not obvious how to do so basing such an application on Shannon entropy. But it is much more straightforward starting with the definition of Boltzmann entropy (Boltzmann 1896), which is applicable to any discrete process, such as resource allocation that can be easily associated with demographic processes. The Boltzmann entropy of a macrostate is defined to be the natural log of the number of microstates compatible with the macrostate:

$$S = k_b \log(W) \tag{1}$$

Where S is the thermodynamic entropy of a macrostate, k_b is the Boltzmann constant ($\approx 1.38 \times 10^{-23} \text{m}^2 \text{kg s}^{-2} \text{K}^{-1}$), and W is the number of microstates associated with the macrostate. The second law of thermodynamics states that the entropy of an isolated system cannot decrease and the most likely state of a system is the one associated with the highest entropy. Consistent with Eq. 1, according to which maximizing the Boltzmann entropy gives the macrostate that is associated with the largest number of microstates, the state with the highest entropy has the highest probability to be observed.

To apply this idea to a resource allocation scenario, 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 each constant growth period subject to an energy
constraint, from which the form of population growth function is derived.
This innovative model, however, 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, the MaxEnt part of the model
predicted birth rate only, while death was introduced by imposing a
constant per capita death rate, making the theoretical basis for birth and
death inconsistent. Second, this model only includes between-species
allocation but not within-species allocation, which as we will show later,
can flip the coexistence outcome under certain conditions; third, the model
allocates two resources (a constrained “energy” and an unconstrained
“resource”) at the same time, adding to the number of parameters and *ad*
hoc assumptions, while the more fundamental scenario of allocating one
resource was unexamined. Another study uses a similar method to derive
abundance distributions by maximizing the number of ways to allocate total
biomass to each species subject to constraints on traits (Shipley 2010a).
Unlike Neill *et al.* (2009), this model does not separately specify the birth
and death processes and also does not account for within-species allocation.

Here we propose and explore a theory that simultaneously predicts the birth and death rates of two species competing for one constrained resource. It is based on maximizing the Boltzmann entropy of resource allocation, or as will be elaborated on later, the number of ways in which resources can be allocated to individuals and species. Within-species allocation is included using an adjustable exponent corresponding to the within-species individual distinguishability relative to the between-species individual distinguishability. Under this framework, the population growth function, the steady state abundance distribution, the metabolic rate-abundance relationship and the form of the population dynamics can be analytically or numerically determined. Implications of the results and future extensions of this simplest scenario are discussed.

2 Materials and Methods

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

2.1 Scenario setting

Throughout, the term “community” is interpreted as a group of species that significantly depend on and actively compete for the same resource that is essential for their survival and reproduction; the term “resource” is defined

generally as something beneficial, exclusive and potentially limiting that is to be allocated among individuals within and between species. 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. While this framework can be extended to more complicated scenarios (see Discussion), we focus here on the case of a two-species community competing for one resource. 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; it is also the shortest interval during which population shifts are assumed to occur. A resource unit is defined as the minimum “batch” of resource that can be allocated independently in an allocation period. We also assume during one allocation period an individual can give birth to at most one offspring. We assume the total amount of resource R that is allocated in each allocation period to be the same, corresponding to both the case that the resource is constantly replenished (e.g. solar radiation, food source) and the case that the resource is a constant stock recycled within the community (e.g. space). Finally we are assuming that in each allocation period, the resource is completely exploited with no resource left, 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.

$B_{i,t}$ is defined as the discrete species level 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. Capital letters are used here to indicate that these are measures over the whole species instead of per capita. We make no assumptions about the dependence of $B_{i,t}$ and $D_{i,t}$ on abundance; the theory will determine that dependence. By definition:

$$N_{i,t+1} = N_{i,t} + B_{i,t} - D_{i,t} \quad (i = 1, 2) \quad (2)$$

Next we introduce a simple model to predict birth and death rates at the same time: in any allocation period, each individual of species i requires θ_i resource units to survive; to reproduce, a surviving individual has to acquire an extra amount of θ_i , in total $2\theta_i$ resource units. The values of θ_i are determined by the relative magnitude between the amount of resource required for an individual to survive and the size of a resource unit. Since our theory does not incorporate individual growth (individuals become adults instantly after they are born), the extra resource requirement for reproduction is assumed to be the same as that for survival so that the actual resource used is always proportional to the updated abundance of the species (see Eq. 3). The ratio θ_1/θ_2 quantifies how resource demanding species 1 is compared to species 2. The consequence for an individual after one allocation is shown in Table 2.

Based on the above, we can easily calculate $R_{i,t}$ which is the number of resource units used by species i at allocation period t .

$$\begin{aligned}
R_{i,t} &= \theta_i \times \text{number of individuals that survive but do not reproduce} \\
&\quad + 2\theta_i \times \text{number of individuals that reproduce} \\
&= \theta_i(N_{i,t} - B_{i,t} - D_{i,t}) + 2\theta_i B_{i,t} \quad (3) \\
&= \theta_i(N_{i,t} + B_{i,t} - D_{i,t}) \\
&= \theta_i N_{i,t+1}
\end{aligned}$$

Later we suppress t in the annotation and use R_i , N_i , B_i and D_i to represent the resource consumption, abundance, birth and death rates at any given allocation period for species i .

2.2 Allocation macrostate and microstate

A macrostate in a given allocation period (with N_1 and N_2 given as initial abundances) is defined as any particular combination of the species level birth and death rates for each species, represented by Ω_{B_1,D_1,B_2,D_2} . In contrast, a microstate is a unique way to allocate each distinct resource unit to individuals of the two species. Multiple microstates could be associated with the same macrostate.

To better illustrate these concepts, we use a simple example where there are $R = 4$ resource units and two species each with 3 individuals at the start of an allocation period ($N_1 = N_2 = 3$) as is shown in Fig. 1. We assume $\theta_1 = \theta_2 = 1$ so that individuals of both species could at most get 2 resource

units in one allocation period. One specific example for a macrostate under this scenario is $\Omega_{B_1=1,D_1=1,B_2=0,D_2=2}$, indicating there is one birth and one death for species 1 while no birth and two deaths for species 2. From Eq. 3 we can get $R_1 = 3$ and $R_2 = 1$. To see what a microstate of this macrostate looks like, in the following the resource allocation process is broken down to separate steps. We assume that the different patterns within each allocation step should be equally weighted, corresponding to a maximally uninformative prior distribution (Shipley 2010b).

1. Demographic grouping: Individuals of the same species are divided into three different demographic groups: individuals that reproduce, survive or die. In this example (Fig. 1a) there are $\frac{3!}{1!1!1!} = 6$ different ways of grouping for species 1 and $\frac{3!}{0!1!2!} = 3$ different ways of grouping for species 2, combining into $6 \times 3 = 18$ ways of demographic grouping for the two species.

2. Between-species allocation: Resource is divided into two batches, each for one of the species. From Fig. 1b we can see that for the macrostate $\Omega_{B_1=1,D_1=1,B_2=0,D_2=2}$ there are $\frac{4!}{3!1!} = 4$ ways to allocate between the two species.

After these two steps, we have a range of combinations between demographic grouping and between-species allocation. If we ignore the difference between the various ways to allocate resource units within each species (among the individuals that reproduce or survive), as is implicitly assumed in Neill *et al.* (2009), each of the $18 \times 4 = 72$ combinations is a

microstate, which can be defined as a unique way to allocate resources between species to individual-specified demographic groups (Fig. 1c).

On the other hand, we might not want to ignore the possible difference among various allocation patterns at the individuals-within-species level, which can be specified in a third step where resource is further allocated within each species:

3. Within-species allocation: Resource is allocated within each species among individuals that reproduce or survive (Fig. 1d). For species 1 in the above example, for each combination between step 1 and 2, there are $\frac{3!}{2!1!} = 3$ to allocate the $R_1 = 3$ resource units between $B_1 = 1$ individual that reproduces (and thus gets 2 resource units) and $N_1 - B_1 - D_1 = 1$ individual that survives (and thus gets 1 resource unit). Similarly for species 2, there are $\frac{1!}{1!} = 1$ ways of within-species allocation. If we take each of these outcomes where the within-species allocation pattern is specified as a microstate, a microstate can be defined as a specific way to allocate resource units to the individual level.

2.3 Relative individual distinguishability

In the section above we introduced two alternative ways to define the microstate (depending on whether within-species allocation is ignored).

Here we introduce a critical parameter that makes it possible for our model to switch between the two definitions, and more importantly, to explore the

220 space in between the two underlying assumptions. This parameter is named
 221 relative individual distinguishability, represented by D_r , which is defined to
 222 be an attribute that quantifies the mean relative distinguishability between
 223 two individuals of the same species (conspecific) compared to two
 224 individuals of different species (heterospecific). The rationale behind this
 225 definition is that, if conspecific individuals are as different from each other
 226 as heterospecific individuals, in which case $D_r = 1$, the difference between
 227 two microstates generated by relocating resource units between two
 228 conspecific individuals should be equally weighted as that generated by
 229 relocating resource units between two heterospecific individuals. Therefore
 230 in calculating the number of microstates, the number of within-species
 231 allocations should be equally weighted as the number of between-species
 232 allocations . In contrast, if conspecific individuals are totally
 233 indistinguishable from each other, in which case $D_r = 0$, no difference is
 234 generated by relocating resource units within the species, therefore
 235 within-species allocation should be ignored and only the number of
 236 between-species allocation will be counted as microstates. A case in
 237 between is represented by $0 < D_r < 1$. The simplest mathematical
 238 representation of the above is:

$$W_{total}(\Omega) = W_{grouping}(\Omega) \times W_{between}(\Omega) \prod_i^2 W_{within,i}(\Omega)^{D_r} \quad (4)$$

239 Where the total number of microstates for a given macrostate Ω

(annotated with W_{total}) is the number of ways to group conspecific individuals into demographic groups ($W_{grouping}$) times the number of ways to allocate resource between the species ($W_{between}$) times the weighted number of ways to allocate resource units among the individuals of the same species, the exponent being the relative individual distinguishability of that species ($W_{within,i}^{D_r}$).

Although D_r defined in the above is primarily a statistical attribute, to attach some empirical sense to it, we further interpret D_r as the ecological distinguishability (the converse of substitutability) of conspecific compared to heterospecific individuals. To elaborate on that, the lower the D_r , the more indistinguishable and thus substitutable conspecific individuals are, therefore the smaller the difference among situations where resource units are relocated within the species. While there are many potential measures for ecological substitutability, here we propose one possible approach assuming that the ecological substitutability of individuals is represented by their relative similarity in one or more functional traits. Empirically, which trait(s) to use for D_r measurement depends on the resource as well as the species. To give a specific example, when the resource to be allocated is space and species are plants, the relevant trait might be body size, since it certainly makes a difference for a bigger plant to occupy the space unit compared to when it is occupied by a smaller plant (through influence on the microclimate and biotic interactions). Calculation of D_r for a simple

two-species case using trait data is illustrated in Fig. 2, where we have used:

$$D_{within} = \frac{2 \sum_{i=1}^2 \sum_{j=1}^{N_i} \sum_{k=i+1}^{N_i} |t_{ij} - t_{ik}|}{N_1(N_1 - 1) + N_2(N_2 - 1)} \quad (5)$$

$$D_{across} = \frac{\sum_{j=1}^{N_1} \sum_{k=1}^{N_2} |t_{1j} - t_{2k}|}{N_1 N_2} \quad (6)$$

$$D_r = D_{within} / D_{across} \quad (7)$$

In Eqs. 5-7, 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. Substituting the trait values in Fig. 2 into Eqs. 5-7, we get $D_r = 0.9$, indicating that conspecific individuals are 90% as distinguishable as heterospecific individuals. While D_{within}/D_{across} could potentially be bigger than 1 (when the trait distribution is over-dispersed) and so is D_r , in this paper we only discuss the situations where D_r falls within the range $[0,1]$, or within-species variation cannot be bigger than between-species variation. Based on this method, multiple traits and potentially genetic data can be used to calculate D_r .

For simplicity we have assumed that the two species have equal D_r . This can be easily relaxed, with D_{within} calculated separately for each species, and the exponent of W_{within} in Eq. 4 being the species specific D_r . Also notice that the measure proposed in the above is only a preliminary attempt based on the assumption that trait difference can be proxy for ecological substitutability (and further for statistical distinguishability).

Also if we had used different units for the traits, or a log scale rather than the scale in Fig. 2, Eq. 7 would be different. Further implications and alternative assumptions will be addressed later in the discussion section.

2.4 Calculation

Next we calculate the maximal total number of allocation microstates $W_{total}(\Omega)$ over all possible Ω , with which the most likely macrostate $\hat{\Omega}$ is associated. To do this we first need to express $W_{total}(\Omega)$ as a function of the macrostate variables (B_1, D_1, B_2, D_2) . Then we will separately derive each term on the right side of Eq. 4. Throughout, $C(x_1, x_2, \dots | X)$ denotes the number of ways to combine X individuals into groups of x_i :

$$C(x_1, x_2, \dots | X) = \frac{X!}{x_1! x_2! \dots} \quad (8)$$

$W_{grouping}$ is the number of ways to group conspecific individuals into demographic groups, i.e. reproducing, surviving and dead individuals.

Using the notation defined above,

$$\begin{aligned} W_{grouping}(\Omega_{B_1, D_1, B_2, D_2}) &= C(B_1, D_1, N_1 - B_1 - D_1 | N_1) \\ &\quad \times C(B_2, D_2, N_2 - B_2 - D_2 | N_2) \\ &= \prod_{i=1}^2 \frac{N_i!}{B_i! D_i! (N_i - B_i - D_i)!} \end{aligned} \quad (9)$$

292 $W_{between}$ is the number of ways to divide resource into two batches
 293 (R_1, R_2) , each for one of the species. Combining Eq. 3 and Eq. 8, we have

$$\begin{aligned}
 W_{between}(\Omega_{B_1, D_1, B_2, D_2}) &= C(R_1, R_2 | R) \\
 &= C(\theta_1(N_1 + B_1 - D_1), \theta_2(N_2 + B_2 - D_2) | R) \\
 &= \frac{R!}{[\theta_1(N_1 + B_1 - D_1)]! [\theta_2(N_2 + B_2 - D_2)]!}
 \end{aligned} \tag{10}$$

294 $W_{within,i}$ is the number of ways the resources allocated to each species are
 295 allocated among the reproducing or surviving individuals. For species i ,
 296 each reproducing individual gets $2\theta_i$ resource units and each surviving
 297 individual gets θ_i :

$$\begin{aligned}
 W_{within,i}(\Omega_{B_i, D_i, B_i, D_i}) &= C(\underbrace{\theta_i, \theta_i, \theta_i, \dots}_{N_i - B_i - D_i}, \underbrace{2\theta_i, 2\theta_i, 2\theta_i, \dots}_{B_i} | R_i) \\
 &= \frac{R_i!}{(\theta_i!)^{N_i - B_i - D_i} [(2\theta_i)!]^{B_i}} = \frac{[\theta_i(N_i + B_i - D_i)]!}{(\theta_i!)^{N_i - B_i - D_i} [(2\theta_i)!]^{B_i}}
 \end{aligned} \tag{11}$$

298 Substituting Eqs. 9-11 into Eq. 4, we can get $W_{total}(\Omega_{B_1, D_1, B_2, D_2})$ as a
 299 function of B_1, D_1, B_2 and D_2

$$\begin{aligned}
 W_{total}(\Omega_{B_1, D_1, B_2, D_2}) &= R \prod_{i=1}^2 \left\{ \frac{N_i!}{B_i! D_i! (N_i - B_i - D_i)! [\theta_i(N_i - B_i - D_i)]!} \right. \\
 &\quad \left. \times \left\{ \frac{[\theta_i(N_i + B_i - D_i)]!}{(\theta_i!)^{N_i - B_i - D_i} [(2\theta_i)!]^{B_i}} \right\}^{D_i} \right\}
 \end{aligned} \tag{12}$$

300 Since the resource in this scenario is assumed to be constrained (see
 301 illustration in Section 2.1), maximization is subject to the constraint

$$R = R_1 + R_2 = \sum_{i=1}^2 \theta_i (N_i + B_i - D_i) \quad (13)$$

302 Applying the method of Lagrange multipliers for constrained
 303 maximization(Bellman 1956), we define an objective function S as

$$S(\Omega_{B_1,D_1,B_2,D_2}) = \log(W_{total}(\Omega_{B_1,D_1,B_2,D_2}) - \lambda[R - \sum_{i=1}^2 \theta_i (N_i + B_i - D_i)] \quad (14)$$

304 where λ is the Lagrange multiplier. The constrained maximal $W_{total}(\Omega)$
 305 can be obtained by substituting Eq. 12 into Eq. 14 and maximizing by
 306 setting to zero the derivatives of $S(\Omega_{B_1,D_1,B_2,D_2})$ over each macrostate
 307 variable (B_1, D_1, B_2, D_2) :

$$\frac{\partial S(\Omega_{B_1,D_1,B_2,D_2})}{\partial B_i} = \log \frac{B_i [\theta_i (N_i + B_i - D_i)]^{\theta_i (1-D_r)}}{N_i - B_i - D_i} + D_r \log \frac{(2\theta_i)!}{\theta_i!} + \lambda \theta_i = 0 \quad (15)$$

$$\frac{\partial S(\Omega_{B_1,D_1,B_2,D_2})}{\partial D_i} = \log \frac{D_i}{[\theta_i (N_i + B_i - D_i)]^{\theta_i (1-D_r)} (N_i - B_i - D_i)} - D_r \log \theta_i! - \lambda \theta_i = 0 \quad (16)$$

308 In deriving Eqs. 15 - 16, Stirling's approximation to a factorial is applied
 309 assuming the highest digits are bigger than 10 ($< 1\%$ correction), as is also
 310 assumed in Neill *et al.* (2009). These equations combined with the
 311 constraint (Eq. 13) compose the determining equations of this macrostate.
 312 From them the macrostate variables associated with the most likely

macrostate (B_1, D_1, B_2, D_2) can be solved as functions of the initial conditions $(N_1, N_2, R, \theta_1, \theta_2$ and $D_r)$.

Combining Eqs. 3 and 13, we can derive that $\theta_1 N_{1,t} + \theta_2 N_{2,t} = R$ for all $t > 0$. With $g_{i,t}$ defined as the per capita population growth rate of species i at time t , we can further derive that $\theta_1 g_{1,t} + \theta_2 g_{2,t} = 0$ for all $t > 0$ (because $R = \theta_1 N_{1,t} + \theta_2 N_{2,t} = \theta_1 N_{1,t}(1 + g_{1,t}) + \theta_2 N_{2,t}(1 + g_{2,t}) = \theta_1 N_{1,t+1} + \theta_2 N_{2,t+1}$). These two equations will be referred to as the zero-sum condition in later discussions.

3 Results

In this section we will show the result of solving the determining equations (Eqs. 13, 15 and 16) under various conditions. Specifically, we will derive the population growth function and steady state abundances analytically, and track the population dynamics numerically.

3.1 Special case: When $D_r = 1$

Because solving the equations for the most general case (arbitrary θ_i and D_r) is comparatively difficult, we will start with the simplest case where $D_r = 1$ and thus the term $[\theta_i(N_i + B_i - D_i)]^{\theta_i(1-D_r)} = 1$ and can be dropped from the equations. Under this condition, Eqs. 15-16 reduce to:

$$\frac{B_i}{N_i - B_i - D_i} = \frac{\theta_i! e^{-\lambda \theta_i}}{(2\theta_i)!} \quad (17)$$

$$\frac{D_i}{N_i - B_i - D_i} = \theta_i! e^{\lambda \theta_i} \quad (18)$$

331 From which we can solve B_i and D_i :

$$B_i = \frac{N_i}{\frac{(2\theta_i)!}{C^{2\theta_i}} + \frac{(2\theta_i)!}{\theta_i! C^{\theta_i}} + 1} \quad (19)$$

$$D_i = \frac{N_i}{\frac{C^{2\theta_i}}{(2\theta_i)!} + \frac{C^{\theta_i}}{\theta_i!} + 1} \quad (20)$$

332 where $C = e^{-\lambda}$, a constant determined by the resource constraint:

$$R = \sum_{i=1}^2 (N_i + B_i - D_i) = \sum_{i=1}^2 N_i \theta_i \frac{2C^{2\theta_i} + \frac{(2\theta_i)!}{\theta_i!} C^{\theta_i}}{C^{2\theta_i} + \frac{(2\theta_i)!}{\theta_i!} C^{\theta_i} + (2\theta_i)!} \quad (21)$$

333 The per capita net population growth rate g_i is given by:

$$g_i = \frac{B_i - D_i}{N_i} = \frac{C^{2\theta_i} - (2\theta_i)!}{C^{2\theta_i} + \frac{(2\theta_i)!}{\theta_i!} C^{\theta_i} + (2\theta_i)!} \quad (22)$$

334 From Eq. 22 we can see that when $D_r = 1$, $\theta_1 = \theta_2$ always leads to
 335 $g_1 = g_2$. Previously we have shown that g_1 and g_2 have to follow the
 336 relationship $\theta_1 g_1 + \theta_2 g_2 = 0$ due to the zero-sum condition imposed by the
 337 resource constraint. Therefore $g_1 = g_2$ always means $g_1 = g_2 = 0$ since both
 338 θ_1 and θ_2 are positive. This means that when $D_r = 1$ and $\theta_1 = \theta_2$, the
 339 system has neutral equilibrium states along the resource constraint line, or

the community can end up with any N_1 and N_2 that satisfy

$$\theta_1 N_1 + \theta_2 N_2 = R.$$

Given $D_r = 1$, when $\theta_1 \neq \theta_2$, however, the species with smaller θ will always exclude the other. To see this, first $\theta_1 \neq \theta_2$ suggests that $g_1 \neq g_2$. Because $\theta_1 g_1 + \theta_2 g_2 = 0$, g_1 and g_2 cannot be both positive or negative, and therefore $g_1 \neq g_2$ means that g_1 and g_2 are of opposite signs. Eq. 22 suggests that all else equal, the bigger the θ_i , the smaller the g_i . Therefore the g_i corresponding to the lower θ_i is always positive while the other is always negative. This will eventually lead to the species with lower θ_i excluding the other. These inferences will be confirmed below from numerical solutions tracking the population dynamics of the two species.

3.2 Population growth rate variation in relation to abundances of both species

When $D_r \neq 1$, B_i and D_i cannot be solved analytically and therefore we take a different approach to determine the g_i by defining a new variable r_i :

$$r_i = \frac{B_i}{D_i} \tag{23}$$

Combining r_i with Eqs. 15-16 we can solve analytically for the relationship between g_i or N_i and r_i (a detailed derivation is in the Appendix)

$$g_i = \frac{r_i - 1}{2^{D_r \theta_i} r_i^{\frac{1}{2}} + r_i + 1} \quad (24)$$

$$N_i = \frac{2}{e} (C' \theta_i r_i^{\frac{1}{2\theta_i}})^{\frac{1}{D_r - 1}} \frac{2^{D_r \theta_i} r_i^{\frac{1}{2}} + r_i + 1}{2^{D_r \theta_i} r_i^{\frac{1}{2}} + 2r_i} \quad (25)$$

Here C' is another constant that equals $2e^{\lambda-1}$; given r_1 and r_2 , it is determined from

$$\begin{aligned} R &= R_1 + R_2 = \sum_{i=1}^2 \theta_i (N_i + B_i - D_i) \\ &= \sum_{i=1}^2 \theta_i N_i (1 + g_i) = \sum_{i=1}^2 \theta_i \frac{2}{e} (C' \theta_i r_i^{\frac{1}{2\theta_i}})^{\frac{1}{D_r - 1}} \end{aligned} \quad (26)$$

For any given N_1 and N_2 (and R), g_1 and g_2 can be solved by first combining Eqs. 25 (for both species) and 26 to solve for r_1 and r_2 (and C'), then substituting into Eq. 24. Notice that N_1 and N_2 have to satisfy the zero-sum condition ($\theta_1 N_1 + \theta_2 N_2 = R$), therefore an increase in N_1 is always associated with a decrease in N_2 and vice versa. The relationship between g_i and N_i resulting from this procedure is shown in Fig. 3.

From Fig. 3 we can see that, in all cases, the per capita population growth rate of the species is positive when its abundance is below the steady state level (when $g_1 = g_2 = 0$) and negative when it is above the steady state level, suggesting the steady state in this case ($D_r < 1$) is stable as long as both species start with positive abundances ($0 < N_i < R/\theta_i$).

Specifically, the curves for g_1 and g_2 are symmetrical and the steady state abundances for both species are the same when $\theta_1 = \theta_2$, which makes intuitive sense because of the symmetry of the model. However when $\theta_2 > \theta_1$, the curves are asymmetrical and the community converges to a steady state where $N_1 > N_2$, a result that can be analytically proved in the next section. Moreover, the smaller the D_r , the faster the system converges to the steady state, indicated by the bigger absolute values of g_1 and g_2 at any given N_1 and N_2 different from the steady state.

3.3 Analytical solution to steady state abundances

When both species are at steady state, $B_1 = D_1$, $B_2 = D_2$ and $r_1 = r_2 = 1$. Substituting this into Eq. 24 and again applying Stirling's approximation, we have

$$\hat{N}_i = \frac{2}{e} (C' \theta_i)^{\frac{1}{D_r - 1}} \quad (27)$$

$\hat{N}_i$ is the steady state abundance for species i ; C' is the same constant as in Eqs. 24- 25. Since $D_r < 1$, $\hat{N}_i$ is a negative function of θ_i . Therefore species with higher resource requirement ends up with lower abundance at steady state. Taking the ratio of steady state abundances between the two species we have:

$$\frac{\hat{N}_1}{\hat{N}_2} = \left(\frac{\theta_1}{\theta_2}\right)^{\frac{1}{D_r-1}} \quad (28)$$

In other words, when $\frac{\theta_1}{\theta_2}$ is constant, the bigger the D_r , the more different the steady state abundances are. When $D_r = 1$ and $\theta_1 \neq \theta_2$, the steady state is complete exclusion of one species ($\hat{N}_1/\hat{N}_2 = 0$ or ∞) as was discussed in Section 3.1. On the other hand, holding D_r constant, the abundance distribution at steady state is solely determined by the relative resource requirement θ_1/θ_2 . Specifically when $D_r = 0$, Eq. 27 indicates that $N_i \propto \theta_i^{-1}$, the implication of which will be discussed later in the next section.

3.4 Two-species population dynamics

In this section, the two-species population dynamics under the zero-sum resource constraint is examined by numerically solving the determining equations and updating species abundances through time:

$$N_{i,t+1} = N_{i,t}(1 + g_{i,t}) \quad (29)$$

Results are shown in Fig. 4. We can see from each graph that given θ_i , the higher the D_r , the more different the steady state abundances between the species, as is suggested by the analytical solution in Section 3.3. When $D_r = 1$, our result is consistent with the inference in Section 3.1: when

resource requirements are equal between the species (Fig. 4a), $D_r = 1$ is corresponding to a neutral equilibrium; when resource requirements are not equal (Fig. 4b and c), $D_r = 1$ results in the species with higher θ_i to exclude the other. What's more, from the dynamics we can see that the closer the resource requirements between the species (Fig. 4c compared to Fig. 4b), the longer it takes for exclusion to happen. In spite of that, exclusion is definite eventually as long as $D_r = 1$ and $\theta_1 \neq \theta_2$.

Compared across graphs, for the same $D_r < 1$, the more different the resource requirements (θ_1 and θ_2), the more different the steady state abundances between the two species, as is also suggested by the analytical solution to the steady state. Specifically when $\theta_1 = \theta_2$, except for the case where $D_r = 1$ which leads to a neutral equilibrium, the two species always end up with the same abundance at steady state. Another implication of the analytical solution is that, when D_r is held constant, the steady state is solely determined by the ratio θ_1/θ_2 , which is also demonstrated in Fig. 4. In addition, the graph shows that with this ratio held constant, while steady state abundances are the same, it takes longer time for steady state to be reached when θ_1 and θ_2 are both smaller.

4 Discussion

In this paper a new theory is established to understand factors affecting the form of the population growth function that leads to various competition outcomes. It reveals the conditions for competitive exclusion or coexistence to happen. Most prominently, we have shown that relative individual distinguishability is a key parameter governing coexistence; a smaller value indicates a higher chance of coexistence. Based on the current results, some important inferences and insights for future studies are discussed in the below.

4.1 Species resource requirement and energy equivalence rule (EER)

While the absolute values of the species resource requirements θ_1 and θ_2 do not affect the steady state abundances which only depend on the relative resource requirement θ_1/θ_2 , they do affect the time to reach steady state. As discussed when introducing the parameters, the absolute values of θ_1 and θ_2 are determined by the ratio of the amount an individual needs to survive to the size of a resource unit. Our result shows that all else equal, the bigger the resource unit and therefore the smaller the absolute values of θ_1 and θ_2 , the longer it takes for steady state to be reached.

In the current framework we have assumed θ_i to be independent of D_r ,

and that θ_i is the same for all individuals of species i . The alternatives, i.e. D_r is correlated with θ_i and θ_i varies within the species, are worth future examination. Intuitively, the species resource requirement θ can be related to metabolic rate, based on which the implication of our results for the metabolic energy distribution can be examined. Specifically, when $D_r = 0$, $N_i \propto \theta_i^{-1}$, and if we take θ_i as the metabolic rate of species i , Eq. 27 is consistent with the energetic equivalence rule (EER, Nee *et al.* 1991), which states that the total metabolic rate is the same across all species in the community. Within the theoretical framework introduced here, the energetic equivalence rule should hold only when conspecific individuals can be treated as identical compared to heterospecific individuals ($D_r = 0$); deviations from $D_r = 0$ could explain the widely observed violations of the energetic equivalence rule (White *et al.* 2007; Blackburn & Gaston 1994; Marquet *et al.* 1995).

Notice that we have assumed D_r to be the same for both species but the alternative, i.e. D_r is different between the species, could also be easily explored under this framework, in which case both the relative and the absolute values of θ_1 and θ_2 could potentially affect the steady state. Fig. 2 presents one way to measure D_r under both assumptions. Choosing between them, however, requires better understanding of what D_r really means ecologically.

4.2 Relative individual distinguishability: Challenges and promises

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; Harte 2011), where different levels of distinguishability lead to different distribution patterns. In the context of species coexistence, the effect of social factors, i.e. interactions among conspecific individuals, have been discussed in contrast to niche difference among the species (Chesson 1991; McPeck 2012). 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.

In this paper we only gave one example of an interpretation (Fig. 2) of this very important attribute D_r , but we do not want to limit its interpretation. Figure 2 assumes that higher relative individual distinguishability (lower ecological substitutability) can be associated with higher intraspecific compared to interspecific variation in functional traits (and vice versa). The latter is also known as functional overdispersion (Swenson & Enquist 2009), the importance of which is an active topic in plant functional ecology (Albert *et al.* 2010; Auger & Shipley 2013). If the relevant functional trait is related to the type of food source, a high D_r could also indicate more generalists in the community. Based on these

interpretations, a series of macroecological inferences follow from our result,
which can be used to generate hypotheses for empirical studies:

Hypothesis 1 The species abundance distributions are more skewed in
communities where functional overdispersion is prevalent (higher D_r).

Hypothesis 2 Steady state can be reached faster, and thus the system is
more resilient, when the community has more specialists (lower D_r).

Combined with the assumption that the species resource requirement θ_i
is positively correlated to its metabolic rate and therefore to body size,
there are two additional inferences:

Hypothesis 3 The body size distribution is more skewed (or difference
in body size results in larger difference in abundance) in a community with
more generalists/functional overdispersion (higher D_r).

Hypothesis 4 The system is more resilient for a community where
individuals of species are generally bigger (bigger absolute values of θ_i)

Notice that in the last hypothesis, it is assumed that the length of
allocation period is independent of body size. Violation of this assumption
(e.g. a positive relationship between body size and population growth
period) might confound the result.

Many other hypotheses can be similarly made from the trait-focused
point of view illustrated in the above. Alternatively, the ecological
substitutability of conspecific individuals can be obtained from measures of

the population structure, based on the assumption that individuals from the same “subgroup” (e.g. a local population in a metapopulation structure, a certain age group) are more substitutable for each other compared to those outside the subgroup. Under this interpretation, D_r can be measured by the level of intraspecific subgrouping: the more distinct subgroups there are within the species, the less substitutable two random conspecific individuals and thus the higher the D_r . Finally, since within-species variation is also related to evolutionary potential (Lewontin 1974), the interplay between evolutionary mechanisms and species competition could also be studied with this framework.

4.3 Comparison with previous theories

Instead of including specific equalizing or stabilizing mechanisms, our theory predicts species interactions from two species attributes, θ and D_r , which are the biological constraints for the stochastic process of the theory and assumed to be fixed for the time being considered. Although this does not affect the formula or predictions, we believe that the mechanism-based explanation of this theory lies in the interpretation of these attributes, which we have made some first attempts in the above two sections. In particular, closer values of θ between species has an effect similar to that obtained from an equalizing mechanism in models describing species interaction (by imposing a similar maximal abundance R/θ_i between the

species), while a smaller D_r has an effect similar to that obtained by including a stabilizing mechanism (by causing faster convergence to the steady state). Although the actual values of these attributes are probably the outcome of a series of evolutionary and biophysical mechanisms and have to be empirically determined (guidelines have been given in previous sections), our theory has revealed that species coexistence is the general outcome for most cases ($D_r < 1$), providing a new approach to the long standing conundrum of why species coexistence is possible.

Unlike many models involving spatial or temporal fluctuations (Chesson 2000; Barabás *et al.* 2012), the theory focuses on a zero-sum scenario under fixed resource supply. Under this framework, each species has to have a positive abundance to start with ($N_{i,0} > 0$). However, if we assume a non-zero invasion rate for both species, based on the criterion derived from Kang & Chesson (2010), our model predicts permanent coexistence when $D_r < 1$.

Our theory is more like a null hypothesis (or null theory), with no explicit biological mechanisms incorporated in the resource allocation process. In other words, when our predictions resemble real patterns, it suggests that a stochastic process similar to the one described by this theory is capable of describing the resource allocation process and the associated population dynamics. Similarly, deviations from our predictions suggest the need to incorporate explicit biological mechanisms in describing

these dynamics. This, however, does not mean that there is no biology/ecology in this theory. The biology/ecology of this theory lies implicitly in the species attributes: θ (related body size) and D_r (related to functional variation), the determinant parameters for the stochastic process discussed here. The evolutionary and biophysical mechanisms and constraints influencing these attributes are not the focus of this theory.

Although the key process of the theory is based on a statistical principle (maximum entropy), our result has highlighted the effect of a biological constraint that has previously been neglected: the relative individual distinguishability D_r , which we have suggested could be related to functional variation of the species. In this interpretation, species coexistence might be more governed by internal biological constraints than previously thought. Combining our theory with the theories focusing more on external, abiotic factors (Levin 1970; Armstrong & McGehee 1980; Chesson 2000; Barabás *et al.* 2012), we might ultimately be able to resolve the species coexistence problem combining mechanisms from a spectrum of spatial, ecological and temporal scales.

4.4 Future extensions

There are many potential future extensions to this model. To summarize in a most general way, first, more species (> 2) can readily be included, the implication for community structure and species abundance distribution be

570 examined. Second, more than one resource could be incorporated, which
571 might significantly change the model behavior. Third, other types of
572 interaction can be incorporated. For example, instead of allocating resource
573 among two species, individuals of one species could be allocated among
574 another to predict predator-prey interactions. Combining all three
575 directions, the theory can be used to predict the network structure of food
576 web. Finally, by examining the roles of relative individual distinguishability
577 in both processes, insight into the relationship between evolution and
578 competition might be possible with this theory.

579 The mathematical forms of population growth functions and species
580 interactions vary from species to species in a poorly understood manner,
581 making it hard to make general predictions for species coexistence. In this
582 paper, we started with only a simple rule of maximizing the Boltzmann
583 entropy (number of microstates) for a resource allocation process and
584 predicted a variety of population dynamics and steady state patterns, from
585 which general inferences about conditions leading to species coexistence can
586 be made. Relative individual distinguishability has been highlighted as an
587 important attribute governing species interactions. Our work reveals a
588 promising approach to utilizing fundamental principles of statistics to
589 explain the structure and dynamics of important patterns in ecology.

5 Acknowledgement

This research was funded by the U. S. National Science Foundation and by the Gordon and Betty Moore Foundation. We are grateful to Justin Kitzes, Ben Blonder, Andy Rominger and Erica Newman for useful discussions and to the Rocky Mountain Biological Laboratory where the work was completed.

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Figure 1: Resource allocation process. With total resource $R = 4$, equal abundances $N_1 = N_2 = 3$ and equal resource requirements $\theta_1 = \theta_2 = 1$, the many ways (microstates) to realize the macrostate $\Omega(B_1 = 1, D_1 = 1, B_2 = 0, D_2 = 2)$ (resulting in $R_1 = 3, R_2 = 1$) is shown in the figure. Resource units and individuals are numerically and alphabetically labeled, respectively, to be differentiated from each other. The three steps of resource allocation are separately shown in a) demographic grouping, divide each species into groups of reproducing, surviving and dead individuals; b) between-species allocation (divide resources into two batches, each for one of the species); c) shows that combining a) and b) gives specific allocation patterns to the demographic group level; d) within-species allocation at the individual level. In this case there are 3 unique ways - each represented by a specific arrow type (solid, dashed or dotted) - to allocate the resource units to the surviving or reproducing individuals chosen in the first two steps within each species.

Figure 2: 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. 5-7. In this graph, $t_{11} = 5, t_{12} = 30, t_{13} = 60, t_{21} = 50, t_{22} = 90$, substituting in Eq. 5-7, we get $D_{within,1} = 2 * (25 + 30 + 55)/6 = 36.67, D_{within,2} = 2 * 40/2 = 40$ $D_{across} = (45 + 85 + 20 + 60 + 10 + 30)/6 = 41.67, D_{r,1} = 36.67/41.67 = 0.88, D_{r,2} = 40/41.67 = 0.96$

Figure 3: Predicted relationship between per capita population growth rate g_i and N_1, N_2 . For all calculations, the resource requirement of species 1 and the total resource are fixed ($\theta_1 = 1, R = 200$). Different colors are used for different species (black for species 1, light gray for species 2). Different combinations for resource requirement of species 2 (θ_2) and the relative individual distinguishability (D_r) are represented by curves of different types.

Figure 4: Population dynamics through time predicted by maximizing resource allocation entropy between two species. N_1 and N_2 are the abundances for species 1 and species 2, respectively. At time $t=0$, $N_1 = 300, N_2 = 50$. D_r is the relative individual distinguishability. Predictions for dynamic variation in abundances for both species are compared for different relative values between θ_1 and θ_2 across the graphs (a, b and c), and within each graph, among different combinations of the absolute values of θ_1 and θ_2 and D_r (represented by different line types).

Table 1: Symbols used

Symbols ($i = 1, 2$)	Interpretations
R, R_i	The total amount of resources allocated in one allocation period or the amount allocated to species i .
$N_i, N_{i,t}, \hat{N}_i$	The abundance of species i ($i=1,2$) at any given time, at the t_{th} allocation period, or at steady state.
B_i, D_i	Species level birth and death rates, i.e. the total number of births and deaths for species i in one allocation period.
Ω_{B_i, D_i}	A macrostate of resource allocation, indicating that in the given allocation period, species i has B_i births and D_i deaths
$W_{grouping}$	Number of ways to group individuals into demographic groups, i.e. individuals that reproduce, survive, or die (Fig. 1a).
$W_{between}$	Number of ways to allocate resources between the two species (Fig. 1b).
$W_{within,i}$	Number of ways to allocate resources within species i (Fig. 1c).
W_{total}	Total number of ways to allocate resources, combining demographic grouping, between-species allocation and within-species allocation (see Eq.4).
g_i	Per capita net population growth rate at any allocation period.
t_{ij}	The trait value of the j_{th} individual of species i .
$D_{between}, D_{within}$	Mean pairwise difference of a trait relevant to resource acquisition between or within species (see Eq. 5 and 6).
D_r	Individual level distinguishability within species relative to across species.
θ_i	Relative resource requirement for species i .
S, λ	The objective function for constrained maximization and the Lagrange multiplier (see Eq. 14).

Table 2: Resource allocation consequence for an individual of species i

Units of resource allocated to the individual	Consequence
0	Death
θ_i	Survive (but not reproduce)
$2\theta_i$	Survive and reproduce

Figure 1: Resource allocation process.

771

772 Figure 2: Calculation of D_r using a trait relevant to resource acquisition.

Figure 3: Predicted relationship between per capita population growth rate and abundance.

Figure 4: Predicted population dynamics through time.

A Appendix: Derivation for the relationship between g_i , N_i and r_i (Eqs. 24 -25)

Substituting Eq. 23 into Eqs. 15 - 16 then taking Eq. 15 - Eq. 16, we have

$$2\theta_i(1 - D_r)\log[\theta_i(N_i + B_i - D_i)] + \log(r_i) + D_r\log 2\theta_i! + 2\lambda\theta_i = 0 \quad (\text{A.1})$$

From which we can solve for $N_i + B_i - D_i$, which is also $N_i(1 + g_i)$ based on the definition of g_i (Eq. 22):

$$N_i(1 + g_i) = N_i + B_i - D_i = \frac{2}{e}(C'\theta_i r_i^{\frac{1}{2\theta_i}})^{\frac{1}{D_{r,i}-1}} \quad (\text{A.2})$$

Where $C' = 2e^{\lambda-1}$. Combining Eqs. 22 and 23 we have

$$B_i = \frac{N_i g_i r_i}{r_i - 1} \quad (\text{A.3})$$

$$D_i = \frac{N_i g_i}{r_i - 1} \quad (\text{A.4})$$

Substituting A.3 and A.4 back into Eq. 15:

$$2\theta_i(1 - D_r)\log[\theta_i N_i(1 + g_i)] + \log \frac{\frac{N_i g_i r_i}{r_i - 1}}{N_i(1 + g_i) - N_i g_i \frac{2r_i}{r_i - 1}} + D_r \log \frac{(2\theta_i)!}{\theta_i!} + \lambda\theta_i = 0 \quad (\text{A.5})$$

Combining A.2 and A.5 we can solve for N_i and g_i separately as functions of r_i , θ_i , D_r and C' , as is shown in Eqs. 24 - 25.