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

Yu J. Zhang [a,*], John Harte [b]

[a] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA
[b] Energy and Resource Group, University of California, Berkeley, CA, USA

HIGHLIGHTS

- Species dynamics derive from maximizing the Boltzmann entropy of resource allocation.
- Competition outcome depends on the relative individual distinguishability D_r.
- A smaller D_r leads to a stronger stabilizing mechanism in support of coexistence.
- Species abundance distribution and the energetic equivalence rule naturally emerge.

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.

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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 and 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 and Bowler, 2002; Wilson and Abrams, 2005; Calcagno et al., 2006; Lobry and Harmand, 2006; Tokeshi, 2009; Siepielski and McPeek, 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 and 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).

Although these simple function forms are convenient and neat, nature is undoubtedly more complex (Abrams and Ginzburg, 2000;

* Correspondence to: 305 Hilgard Hall, University of California, CA94704, USA.
  E-mail addresses: yzh828@berkeley.edu (Y.J. Zhang), jharte@berkeley.edu (J. Harte).

Chase et al., 2002; Melbourne and Chesson, 2005). And while some competition models have assumed more complex equations, either fitted from data (Leirs et al., 1997) or derived from more nonlinear mechanisms (Toro et al., 1971; Dennis and Desharnais, 1995), the more complex the model, the more vulnerable it usually is to over parameterization, adding to the difficulty of falsification. More importantly, since most studies only look at a handful of species, the form of the population growth function varies from study to study. How this variation is generated would be better understood if a theory involving only general principles, potentially applicable to all species, existed.

Our goal is such a theory, one that predicts the most phenomena with the fewest unverifiable assumptions. Statistical mechanics provides a widely applicable method, maximum entropy (MaxEnt), for inferring the most likely form of the pattern of interest given limited information available. MaxEnt based on Shannon entropy (Jaynes, 1982) has been used in ecology to predict species spatial distributions from environmental variables (Phillips et al., 2006) or from the species abundance distribution (Shipley et al., 2006) and has nurtured a comprehensive theory that predicts numerous macroecological metrics including the species abundance distribution, the species level spatial abundance distribution and the species area relationship (Harte, 2011; Harte and Newman, 2014; see also Dewar and 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 ($\approx 1.38 \times 10^{-23}$ m^2 kg s^{-2} 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 and 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:

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