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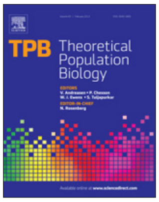

Unlimited niche packing in a Lotka–Volterra competition game

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ABSTRACT

A central question in the study of ecology and evolution is: "Why are there so many species?" It has been shown that certain forms of the Lotka–Volterra (L–V) competition equations lead to an unlimited number of species. Furthermore, these authors note how any change in the nature of competition (the competition kernel) leads to a finite or small number of coexisting species. Here we build upon these works by further investigating the L–V model of unlimited niche packing as a reference model and evolutionary game for understanding the environmental factors restricting biodiversity. We also examine the combined eco-evolutionary dynamics leading up to the species diversity and traits of the ESS community in both unlimited and finite niche-packing versions of the model. As an L–V game with symmetric competition, we let the strategies of individuals determine the strength of the competitive interaction (like competes most with like) and also the carrying capacity of the population. We use a mixture of analytic proofs (for one and two species systems) and numerical simulations. For the model of unlimited niche packing, we show that a finite number of species will evolve to specific convergent stable minima of the adaptive landscape (also known as species archetypes). Starting with a single species, faunal buildup can proceed either through species doubling as each diversity-specific set of minima are reached, or through the addition of species one-by-one by randomly assigning a speciation event to one of the species. Either way it is possible for an unlimited number or species to evolve and coexist. We examine two simple and biologically likely ways for breaking the unlimited niche-packing: (1) some minimum level of competition among species, and (2) constrain the fundamental niche of the trait space to a finite interval. When examined under both ecological and evolutionary dynamics, both modifications result in convergent stable ESSs with a finite number of species. When the number of species is held below the number of species in an ESS coalition, we see a diverse array of convergent stable niche archetypes that consist of some species at maxima and some at minima of the adaptive landscape. Our results support those of others and suggest that instead of focusing on why there are so many species we might just as usefully ask, why are there so few species?

Introduction

Hutchinson (1959) in his "Homage to Santa Rosalia" asks "Why are there so many species?" This succinctly summed up and anticipated the enduring and important question of what promotes and maintains biodiversity. The development of the Lotka–Volterra (L–V) competition equations (Volterra 1926; Volterra 1928; Lotka 1927) and Gause's (1931, 2003) empirical application of this model led to Gause's Principle or the Competitive Exclusion Principle. For similar species to coexist they must occupy separate niches. With explicit resource dynamics in models of competition, this general result requires that the number of coexisting species cannot exceed the number of distinct resources (including both opportunities and hazards) (Tilman 1982). In typical consumer-resource models the niche axis offers discrete resources such as A or B with nothing in between.

What happens when the niche axis is continuous? Does this provide an infinite number of resources and hence the potential for unlimited niche packing? MacArthur (1958) found five species of warblers dividing up the foliage height and breadth of conifers — five species and five foliage habitats. Yet, in reality the number

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of habitats recognized by MacArthur was a continuum. The presence of the five bird species in somewhat discrete and predictable locations within the tree defined the five habitats. Fewer or more species would have led to different conclusions. A finite number of distinct species coexisting on continuous niche axes have led to an interest in limiting similarity and Hutchinson's ratios (MacArthur and Levins, 1967). Key questions that are central to the study of ecology but for which we still do not have clear answers are: How similar can two species be to each other and still coexist? Do traits such as the ratio of body sizes, beak sizes, or other functional traits associated with close competitors provide useful insights into community organization and species coexistence?

Just as the Lotka–Volterra competition equations provided useful insights into the coexistence or exclusion of species from a community, they have provided an equally valuable tool for modeling and understanding eco-evolutionary dynamics (Morris and Lundberg, 2011) where the number of species and their traits are allowed to evolve in response to ecological interactions. Roughgarden (1979) used Gaussian functions for the resource axis (distribution of carrying capacities) and for the competition coefficients (like competes most with like) to show how unlimited niche packing can occur along any discrete interval of the resource axis. In essence, the community of competitors becomes a continuum of species whose share in the community also follows a Gaussian curve (Roughgarden, 1979; Barabás et al., 2012).

A number of empirical objections can be raised regarding this model of unlimited niche packing: sexual reproduction, minimum viable population sizes, boundaries to the length of resource axes, deviations from the idealized Gaussian distributions just to name a few (Gyllenberg and Meszéna, 2005; Barabás et al., 2012). Indeed, modifications of the L–V model as an evolutionary game have provided insights into niche coevolution, speciation, and community structure where the number of species at the eco-evolutionary equilibrium involve a fixed number of species with discrete traits (Brown and Vincent, 1987, 1992; Metz et al., 1996; Cohen et al., 1999; Ripa et al., 2009). Here we build upon and extend these prior works. We add to prior work of the L–V model with unlimited niche packing by examining the ecological and evolutionary dynamics that can lead to faunal buildup. This model provides an idealized model that, while unlikely in nature, can be used as a starting point for understanding how biodiversity in nature evolves and coexists. With a world full of resource continuum, we can rephrase Hutchinson's (1959) observation of "why are there so many species?" to "why are there so few species?". Unlimited niche packing is possible in theory, and yet not seen in nature. Asking why not might provide new insights into questions of biodiversity. The L–V competition evolutionary game with unlimited niche packing provides an excellent reference model for understanding limiting similarity, Hutchinson's ratios, and community organization. It also complements other game theory models of species coexistence based on predator–prey models (Ripa et al., 2009) such as the cyclic dynamics seen in versions of rock–paper–scissor games (Szolnoki et al., 2014).

Our goal is to explore Roughgarden's model of unlimited niche packing in greater detail that explicitly considers evolutionary dynamics, and the properties of various convergent stable points of the adaptive landscape when species numbers fall below that of the ESS. We will do this as an evolutionary game while preserving the resource and competition curves proposed by Roughgarden (1979) and studied extensively by others (Bulmer, 1974; Sasaki and Ellner, 1995; Sasaki, 1997; Szabó and Meszéna, 2006; Parvinen and Meszéna, 2009; Barabás et al., 2013; D'Andrea et al., 2013). The model produces unlimited niche packing and a continuum of species with specific characteristics and population sizes (Meszéna et al., 2006; Barabás and Meszéna, 2009). What emerges is a model of faunal buildup (taken as far as 1024 coexisting species) through continual adaptive speciation as the number of species grows towards unlimited niche packing . In this model, we show that any finite number of species will evolve to a convergent stable, non-ESS, "niche archetype". While mostly demonstrated by simulations we obtain analytic solutions for the two species case which allows us to draw explicit conclusions regarding the effects of niche breadth and competition parameters on character divergence and population sizes. In going towards an unlimited number of species, we show that the ultimate contiguous distribution of "species" is a game-theoretic, Nash solution. We show that the convergent stable community of 1024 species essentially fits this distribution. We then follow the lead of those (Gyllenberg and Meszéna, 2005; Barabás et al., 2012) who showed that the competition functions that permit unlimited niche packing are not robust. Any modification to the functional form leads to a collapse of the continuum of coexisting species to finite numbers. Here, we add eco-evolutionary dynamics to two modifications of the competition function to study the diversity of species at the ESS, and faunal buildup to the ESS starting with a one or a reduced number of species. Finally, we add eco-evolutionary dynamics to a modified competition function proposed by Leimar et al. (2013) characterized by the possibility of unlimited niche packing within the context of convergent stable maxima rather than minima. Ultimately, the factors that cause the continuum of species to cease may be the model's greatest value for understanding what actually happens in the nitty-gritty of real biological communities in nature.

An eco-evolutionary Lotka–Volterra model

Following Roughgarden (1979) and Brown and Vincent (1987), we develop an evolutionary game based on the Lotka–Volterra competition model. To do this we imagine a continuous valued trait, u, that can potentially take on any value from negative infinity to positive infinity. Carrying capacity, K, is influenced by the individual's own strategy, v. We let the vector $\mathbf{u} = (u_1, \ldots, u_n)$ denote the different strategies currently found among individuals within the ecological community. For this paper, we will assume that the different u_i's represent distinct strategies associated with different species. Furthermore, we assume that species breed true. The total number of species currently within the community is n. The vector $\mathbf{x} = (x_1, \ldots, x_n)$ represents the current population sizes of each of the species such that x_i is the population size of species u_i. With these assumptions, we can now write the expected per capita growth rate (i.e. fitness) of a focal individual using strategy, v, as a Lotka–Volterra competition game:

$$G(v, \mathbf{u}, \mathbf{x}) = \frac{r}{K(v)}\left[K(v) - \sum_{j=1}^{n} a\left(v, u_j\right) x_j\right]. \tag{1}$$

We assume that competition is most intense between individuals using the same strategy and that competition between two species declines as the difference in their strategy values increases. Like competes most with like. Hence, we let the competition coefficient, $a\left(v, u_j\right)$, be a Gaussian relationship based on the difference between the focal individual's strategy and that of the competitor. The function reaches a maximum of 1 when $v = u_i$ and declines as the strategies of the competitors diverge (Fig. 1A). This yields the following:

$$a(v, u_i) = \exp\left[-\frac{(v - u_i)^2}{2\sigma_a^2}\right]. \tag{2}$$

For the carrying capacity we assume a Gaussian relationship between the individual's strategy, v, and K. The relationship is centered on $v = 0$ such that $K(v)$ reaches a maximum of K_m when