Evolutionary Ecology Research, 2009, **11**: 265–294

Predicting relative abundance using evolutionary game theory

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ABSTRACT

Questions: Can game theoretic models of competition-driven co-evolution help us to understand patterns of species abundance within a community? Can we use these models to predict the presence and abundance of species in a 'real' biological community where species are represented by their ecologically important strategies?

Mathematical methods: We use an evolutionary game approach to model the assembly of biological communities. We examine several modifications of the Lotka-Volterra competition model using Vincent and Brown's approach with Darwinian dynamics.

Key assumptions: We define an ecological community as a group of species that obey the same rules of ecological engagement and that compete in a local area for the same or similar resources. We also assume that strategies can influence the outcome of the 'ecological engagement' in the manner of an evolutionary game and that species are defined by their population's mean strategy. New strategies are allowed to arise via evolutionary dynamics.

Predictions: Unimodal carrying capacity functions produce relative abundance distributions with many common species and few rare species. Polymodal carrying capacity functions produce relative abundance distributions with few common species and many rare species. Polymodal carrying capacity functions that contain one high peak lead to strong dominance for one species. Increasing the competitive asymmetries leads to changes in rank order of species. In addition, we use our modelling approach to predict community structure of *Geospiza* finches on Isla Wolf of the Galapagos Islands. We predict the evolutionary co-existence of only two beak strategies and that the relative abundance of the larger-beaked strategy should be about 30% that of the smaller-beaked strategy.

Keywords: community assembly, competition co-evolution, Darwin's finches, evolutionary games, *Geospiza*, relative abundance.

INTRODUCTION

Biological communities are made up of populations of locally interacting species. It has been well over half a century since ecologists first noted that the relative abundances of species within communities show recurring patterns [i.e. few species are very abundant,

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some are common, but most are rare (Fisher *et al.*, 1943)]. It is possible to see this pattern in public databases such as the USGS Patuxent Wildlife Research Center breeding bird surveys. Figure 1 illustrates typical plots obtained from this data set[1]. Although relative abundance plots are often shown with abundance on a log scale, we use a linear scale here. The vertical axis is the frequency of a given species and the horizontal axis identifies the species in terms of rank (in descending frequency). In Fig. 1(i) the Wilson Snipe (rank 1) is the most abundant at slightly over 50% of all individuals and the Red-necked Phalarope (rank 10) is the least abundant at less than 1%. The convex curve obtained by 'connecting the dots' is very typical, but can vary somewhat as in Fig. 1(ii), where three pairs of species occur at the same relative abundance. Note, however, that the overall pattern is concave, rather than convex.

The quest to understand why these relative abundance patterns occur is now experiencing an exciting period of debate. As old ideas of statistical curve-fitting and niche pre-emption [where the abundance of a species is equivalent to the portion of niche space pre-empted (e.g. May, 1975; Sugihara, 1980)] are reconciled with new models that include stochastic dispersal [where random assemblies of individuals can fill space in a community (e.g. Hubbell, 2001; Tilman, 2004; Diez and Pulliam, 2007)], a debate about the importance of 'neutral theory' assumptions versus 'morphology–niche' assumptions has emerged. Hubbell (2001) initially introduced the 'unified neutral theory', which dictates that species are competitively identical and that their presence and abundance in a community is a zero-sum game where individuals are drawn at random to fill a set number of community slots that become available as individuals die. In contrast, 'morphology–niche' ideas of community assembly aim to explain abundance patterns in terms of differing morphological traits inherent to each species and their effect on resource acquisition and species interactions (e.g. Kunin and Gaston, 1997; Gurd, 2007). One might argue that the heat between these two ideas stems from the contrast between the egalitarian notion that patterns in community assembly result from neutrally substitutable individuals versus the rather more discriminatory central tenet of biology: that adaptive traits resulting from Darwinian evolution are important. For example, individual morphological traits have been shown to affect evolutionary fitness via environmental conditions, including other individuals with the same or different traits (e.g. O'Neil, 1999; Benkman, 2003; Schluter, 2003; Grant and Grant, 2008). In addition, morphological traits and niche overlap have been shown to constrain patterns of abundance (e.g. Murray *et al.*, 2002; Meehan *et al.*, 2004; Mason *et al.*, 2008). So, does the assembly of a community have a Darwinian core?

We present here a modelling approach that creates models of community assembly from an evolutionary point of view. This approach is extremely useful because not only can it predict species richness and abundance, but also (1) uses the rules of natural selection, (2) incorporates the morphological traits of individuals, (3) has variable parameters to allow for a variety of relative abundance distributions, and (4) can be applied to the empirical study of communities. Our modelling approach is based on the *G*-function method of Vincent and Brown (2005).

The *G*-function approach is based on the following assumptions. First, like Hubbell's (2001) neutral theory, we define an ecological community as a 'group of trophically similar, sympatric species that actually or potentially compete in a local area for the same or

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[1] Data come from USGS Patuxent Wildlife Research Center, 2003. North American Breeding Bird Survey internet data set, 9 December 2003 (http://www.mp2-pwrc.usgs.gov/bbs/retrieval/). It has been shown (Link and Sauer, 1998) that these data can be used to calculate within-route relative abundances without bias.

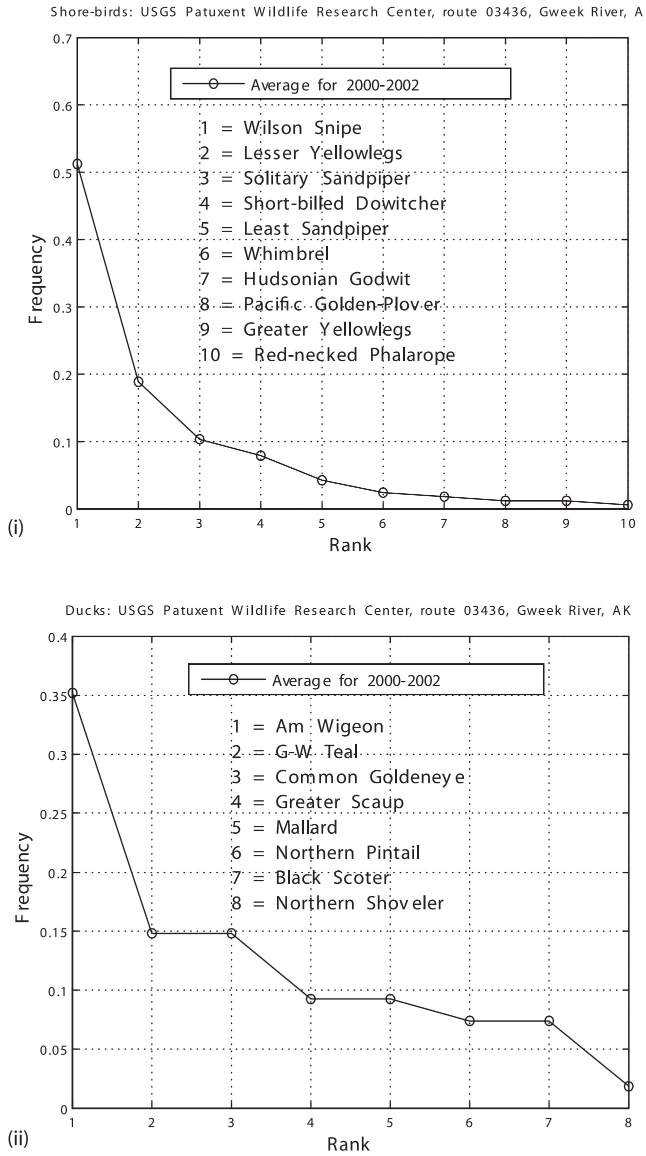

Fig. 1. (i) Relative abundance of shorebirds. (ii) Relative abundance of ducks.

similar resources' (Hubbell, 2001, p. 5). Second, like Hubbell, the probability of giving birth among these species is identical and they must likewise 'obey exactly the same rules of ecological engagement' (ibid., pp. 6–7). We call species with these characteristics evolutionarily identical individuals (Vincent and Brown, 2005) because they share the same *G*-function and thus play by the same rules. This restrictive view of a 'community' can be best applied to species radiations, like those of silverswords, fruitflies or finches on particular Hawaiian or Galapagos islands, because species within these communities likely share the same *G*-function. If we were to model the 'bird community of Great Britain', many species would likely have different *G*-functions (e.g. raptors vs. dabbling ducks). Multiple *G*-functions may be used to model more inclusive communities, but we do not use them in this paper.

Unlike Hubbell's model, however, individual traits (strategies) can influence population interactions in the manner of an evolutionary game. Furthermore, our model has no explicit spatial scale. In the *G*-function model we present below, all results are 'trait-centric' and 'species' are defined by the mean strategy within a population of individuals. New strategies can arise via evolutionary dynamics (as we model here) or by invasion (not modelled here, but discussed). We model the evolution of scalar strategies that are one-dimensional in magnitude. Although it is possible to incorporate multi-dimensional vector traits into a single *G*-function model, we do not show that here. The results of our modelling are given in terms of the relative abundance and rank order of species within an evolutionarily stable coalition of strategies (that is, an evolutionarily stable community).

We have chosen to model our relative abundance curves using the Lotka-Volterra competition equations. These equations have the advantage of specifying competition among strategies (species) in general terms (ultimately, the negative effect on carrying capacity), encompassing any number of means by which competition may occur. These equations also have been studied extensively in an evolutionary setting (Case, 1982; Rummel and Roughgarden, 1983; Vincent *et al.*, 1993). Since these equations are a useful paradigm for evolutionary processes, we have examined and will re-examine them here as a possible model for the study of relative abundance (Vincent and Vincent, 2007).

In this basic model, the strategies are scalars (that is, a one-dimensional strategy describing something like beak depth in finches) and the fitness function for any species may be obtained from the *G*-function

$$G(v, \mathbf{u}, \mathbf{x}) = r - \frac{r}{K(v)} \sum_{j=1}^{n_s} \alpha(v, u_j) x_j \,, \tag{1}$$

where v is a virtual variable that represents the focal individual of any type i using strategy u_i (Vincent and Brown, 2005). The variable n_s is the total number of different species currently in the community, r is the intrinsic growth rate common to all types, $K(v)$ is the carrying capacity of the environment for a population of individuals with strategy v, and $\alpha(v, u_j)$ is the competitive effect of type j using strategy u_j on the fitness of individuals using the focal strategy v. We express K and α in terms of v and use the functions described in Roughgarden (1983). In this notation, they become

$$K(v) = K_m \exp\left[-\frac{v^2}{2\sigma_k^2}\right] \tag{2}$$

and

$$\alpha(v, u_j) = \exp\left[-\frac{(v - u_j)^2}{2\sigma_\alpha^2}\right]. \tag{3}$$

The K function reflects the maximal population size (carrying capacity) of the environment with respect to a particular strategy *without other strategies present*. In this case, the function is a unimodal peak that we can broaden or narrow as a function of σ_k. For large values of σ_k, it approximates a straight line over a range of v values. For each point along the strategy axis, the α function gives the effect on a particular strategy's population size due to the competitive interactions of all other possible strategies. In this case, competitive effects are greater among more similar strategies. The resulting function is also a unimodal peak that we can broaden (lessen competitive effect) or narrow (increase competitive effect) as a function of σ_α.

The carrying capacity K in the Lotka-Volterra model can be expressed in various functional forms. The simplest functional form, $K(v) = K_m$ where K_m is a constant, when used in conjunction with (3) results in an evolutionarily stable community [ESS coalition (*sensu* Vincent and Brown, 2005)] with an infinite number of strategies, all at the same equilibrium population density of $x_i^* = K_m$. This is not a very interesting or realistic biological community. Similarly, our model with $K(v)$ as written in (2) is of little consequence for the study of relative abundance because it is unable to produce stable equilibrium populations composed of more than one species (Vincent *et al.*, 1993). However, Vincent and Vincent (2007) showed that this model could be used to predict relative abundance distributions by modifying it in numerous ways to produce ESS coalitions greater than one. We found that some modifications (those with polymodal K-curves) mimicked natural abundance curves, while others did not (those with unimodal K-curves). In this paper, we will briefly review and then expand on these results to understand why certain species are abundant and others are rare. We will then conduct several modelling scenarios to understand how abundance distributions change with an addition or deletion of a species. Finally, we will apply this model to data collected on *Geospiza* finches (Schluter and Grant, 1984) from Isla Wolf in the Galapagos archipelago.

Numerical simulations

Simulation results based on the above model (or modifications below) are obtained by integrating the following set of differential equations:

$$\dot{x}_i = x_i\, G(v, \mathbf{u}, \mathbf{x})|_{v=u_i}$$

$$\dot{u}_i = \sigma_i^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x}, R)|_{v=u_i}}{\partial v}\bigg|_{v=u_i}$$

with $G(v, \mathbf{u}, \mathbf{x})$ given by (1). The first equation describes the population dynamics in terms of the G-function. The second equation describes strategy dynamics in terms of the G-function (Vincent and Brown, 2005). Strategy dynamics are the means by which natural selection drives evolution in this model. The term σ_i^2 is related to the variance in the distribution of strategies around a mean strategy u_i of species i and scales the rate of evolutionary change. This variance allows the model to 'climb hills' of greater fitness as the fitness landscape changes with time. In the simulations we present below, we set $\sigma_i^2 = 0.5$. This is not an unrealistic number for variance in beak widths within a population of Darwin's finches (Grant and Grant, 2008, Fig. 9.3). We set $r = 0.25$. Positive population growth rates for Darwin's finch *Geospiza fortis* have been shown to approach $r = 1$ only under the best environmental conditions (Hairston *et al.*, 2005) and, as such, $r = 0.25$ may be considered a modest intrinsic growth rate for our model.

Adaptive landscape

For a given **u** (vector of mean strategies of all species) and **x** (vector of population sizes of all species), an adaptive landscape is a plot of the per capita growth rate, $G(v, \mathbf{u}, \mathbf{x})$, as a function of a focal individual's strategy, v. It is similar to Wright's fitness landscape (Wright, 1931, 1969). However, unlike Wright's rigid fitness landscape, the adaptive landscape is pliable. It readily changes shape with changes in population densities and strategies within and among the various species. This means that, while strategy dynamics constantly move species towards higher points in the landscape, the landscape can shift, causing valleys and peaks to appear and disappear in the landscape as the system moves towards equilibrium (Vincent and Brown, 2005, pp. 113–116). One feature of the adaptive landscape is that for a coalition of species [such as the shore birds of Fig. 1(i)] to be at an ESS, the strategy used by each species must lie on a global maximum point of the adaptive landscape [ESS maximum principle (Vincent and Brown, 2005)].

As illustrated in Vincent and Vincent (2007), plots of the components that make up the G-function are given by $\sum_{j=1}^{n_s} \alpha(v, u_j)\, x_j^*$ (denoted as S-curve) and $K(v)$ (denoted as K-curve) and give us insight into the processes that generate each model's adaptive landscape. For example, the left-hand panel of Fig. 2(i) is a plot of the adaptive landscape for two species at ecological equilibrium (but not at an ESS). The right-hand panel of Fig. 2(i) is a plot of the S-curve and the K-curve. It follows from (1) that equilibrium ($G = 0$) is obtained only when the two curves cross or are tangent. The two curves intersect at values of v corresponding to the strategies we have chosen. Since the K-curve is greater than the S-curve between the two intersections, we see from the adaptive landscape that any strategy between the two values used in the simulation will result in a higher fitness. It is because of this that the chosen strategies are not evolutionarily stable. If we allow each of the strategies to evolve, they will both 'climb' the adaptive landscape until they arrive at the peak ESS solution $u = 0$ as shown in Fig. 2(ii). Similarly, if we allow the system to be invaded by other strategies, the system will ultimately arrive at the ESS solution by trial and error, but evolutionary dynamics allow for this end much more surely and directly.

The K-curve is the carrying capacity population size with respect to strategy. The K-curve is limited by the environmental conditions that affect the performance of a species with a particular strategy (e.g. maximal extraction of resources with respect to strategy), given no competitive interactions with other species. The S-curve gives the effect of competition with all strategies present, weighted by their numbers, for a particular strategy (e.g. resource utilization with respect to strategy, given all individuals presently in the community). If we think of these two curves in terms of resources available in the environment, then in those regions where the K-curve is above the S-curve, the resources are under-utilized, allowing another 'more efficient' species with a higher fitness to invade. In this example, there exists an evolutionarily stable community of one species (an ESS coalition of one) with

$$u_1 = 0, \quad x_1^* = 100.$$

The left-hand panel of Fig. 2(ii) illustrates that this solution satisfies the ESS maximum principle. Because the S-curve is always higher than the K-curve except at the point of tangency, the strategy at that tangent is the most efficient species and the resource is totally utilized, resulting in a single-species biomass greater than the sum of the biomasses obtained in the two-species ecological equilibrium case of Fig. 2(i). Because the resource is

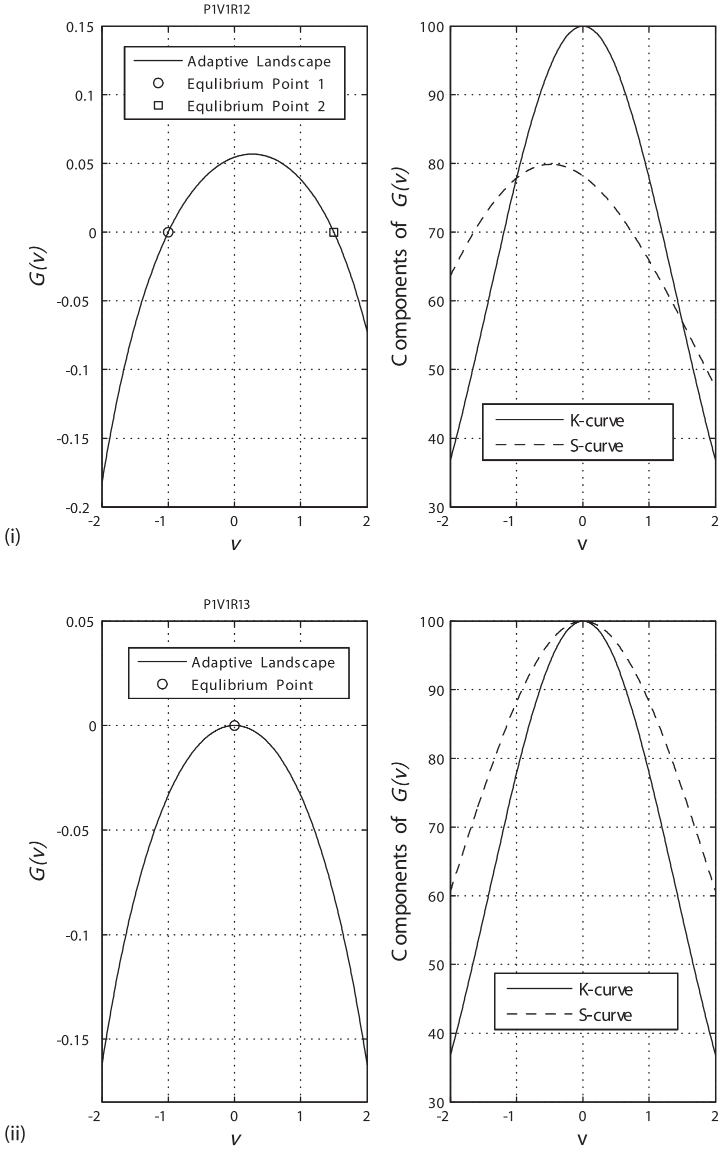

Fig. 2. (i) Co-existence of two species that are at an ecologically stable equilibrium, but are not evolutionarily stable. (ii) The standard model has only an ESS coalition of one.

totally utilized by the ESS solution, there is no chance of having evolutionarily stable solutions greater than one with this model except for the singular case that occurs when the *K*-curve and *S*-curve coincide (in this case, an infinite number of species can co-exist). As will be shown below, by varying σ_K and using a slight modification of (3), coalitions of more than one can be obtained for the ESS.

MODELS OF RELATIVE ABUNDANCE

Frequency-dependent selection is when the payoff to an individual depends on all strategies used within the community. It enters our Lotka-Volterra competition model through the competition coefficients $\alpha(v, u_j)$. As noted by Brown and Vincent (1987), when $\alpha(v, u_j)$ is symmetric as given by (3), frequency dependence (but not density dependence) is lost as a factor in determining an ESS and solutions greater than one cannot occur[2]. However, by modifying the functional form of $\alpha(v, u_j)$, it is possible to obtain multiple evolutionarily stable solutions. This is a necessary first step if we are going to use this model to study relative abundance (Vincent and Vincent, 2007). For example, with K still given by (2), adding a fixed competitive cost to α such as

$$\alpha(v, u_j) = \alpha_{\text{comp}} + \exp\left[-\frac{(v-u_j)^2}{2\sigma_a^2}\right] \tag{4}$$

allows for an ESS coalition of strategies greater than one. Inclusion of α_{comp} ensures that there will be some minimum competitive effect with the introduction of any species even when this species is using a strategy greatly different from the focal strategy v. The competitive effect can no longer be made vanishingly small. This situation could arise when the introduction of a new species always takes up space even though it may not compete strongly for a limiting resource.

Competition can also be made asymmetric by adding another term, β, to the competition term as given by

$$a(v, u_j) = \alpha_{\text{comp}} + \exp\left[-\frac{(v+\beta-u_j)^2}{2\sigma_a^2}\right]. \tag{5}$$

This allows one species to have more or less of an effect on a second species than the second species has on the first. The value of β shifts the value of v required for maximum competitive effect (Brown and Vincent, 1987).

The fixed competitive cost (with and without asymmetry) provides small differences between the S-curve and K-curve that allow co-existence among species. However, with K given by (2), communities composed of ESS coalitions greater than one do not mimic relative abundance curves found in most field data. For example, using

$$K_m = 100,\ r = 0.25,\ \sigma_\alpha = 2,\ \alpha_{\text{comp}} = 0.5,\ \beta = 2$$

and running the simulation with four different values for σ_K, the relative abundance curves of Fig. 3 are obtained.

In this case, the relative abundance curves obtained are bowed outward (instead of inward), resulting in communities that are more even than usual, possessing many abundant species and few rare species. In essence, with a unimodal K-curve, the environment has a single optimal strategy solution but other species can co-exist around the peak of this curve because of frequency-dependent interactions.

The unimodal K-curve has limited usefulness for understanding relative abundance because ESS coalitions greater than one can only be found by increasing the value of σ_K, producing a flatter and flatter K-curve (indicating an environment that can be exploited

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[2] In the scalar strategy case, it is possible to have two solutions if the strategy set is bounded.

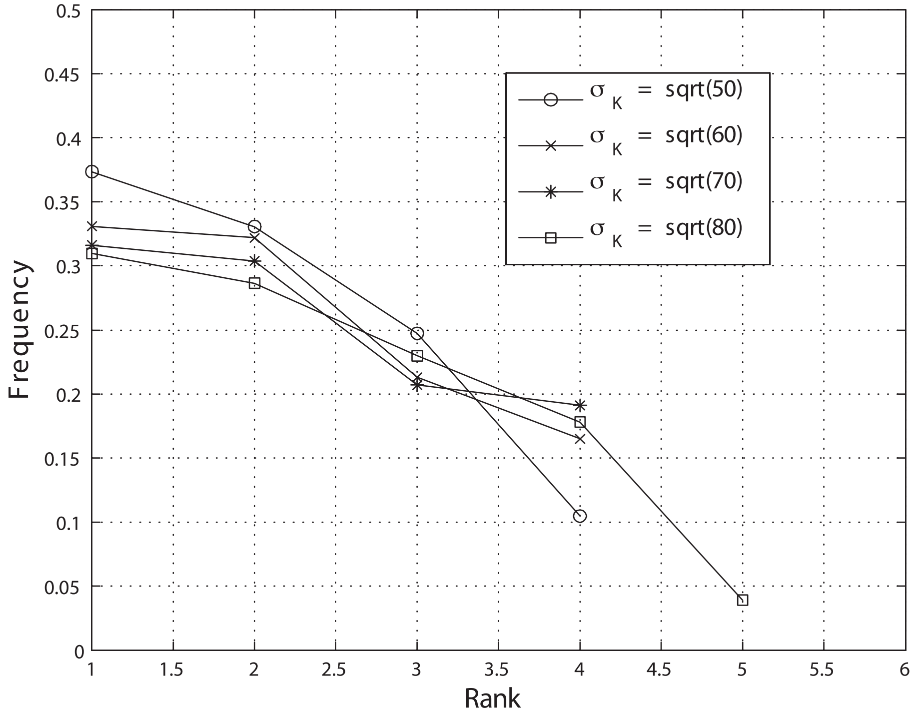

Fig. 3. Relative abundance distributions obtained with a unimodal *K*-curve.

almost equally well by any strategy). Increasing the number of species in the ESS coalition in this manner results in relative abundance curves that tend towards a uniform distribution not typically found in natural systems. Moreover, there are practical difficulties in finding an ESS coalition in this model because the evolutionary process that drives the system towards an equilibrium solution must seek out smaller and smaller differences between $K(v)$ and $\sum_{j=1}^{n_s} \alpha(v, u_j)x_j$ (see, for example, Vincent and Vincent, 2007, Figure 11).

The simulation results of Fig. 3 suggest that we must look to other factors to produce relative abundance curves that mimic field data. It is for this reason that we introduce polymodal K functions. The rational for doing this is based on the observation that real systems generally have many limiting factors (multiple resources, predation, toxicity, etc.) (Molles, 1999, p. 238). In addition, a particular type of limiting factor (e.g. seeds for Darwin's finches or crossbills) may occur as distinct types (e.g. species of plants with differing seed shape and hardness) that can be best exploited by particular magnitudes only along a strategy spectrum [e.g. bill depth in Darwin's finches or crossbills (Schluter and Grant, 1984; Benkman, 2003)]. A polymodal $K(v)$ function captures this complexity. The value of K may increase, fall, increase again, etc., with v throughout the range of values available for the adaptive parameter. For example, a species using strategy u_1 will have a carrying capacity given by $K\ (u_1)$. Two species using strategies u_1 and u_2 will generally have two different carrying capacities, etc. The equilibrium populations for the species depend on, but generally are not equal to, their carrying capacities because of frequency dependence. Polymodal K-curves (with log beak depth as strategy) have been found for Galapagos finches (Schluter and Grant, 1984), indicating that polymodal curves may not be unusual. In addition, based on the results obtained below, polymodal K-curves may be common because it is possible to obtain ESS coalitions with relative abundance distributions that mimic field data using these curves. It turns out that with a polymodal K-curve, the fixed competitive cost α_{comp} is no longer needed to obtain co-existence and it is set equal to zero in the simulations below.

Polymodal carrying capacity curves

By introducing polymodality to the $K(v)$ function (with valleys of low carrying capacity between peaks of high carrying capacity), evolution no longer needs to seek out small differences between the K-curve and the S-curve to produce an ESS coalition of two or more species. Instead, each species can evolve to a location near an obvious peak in resource availability. For example,

$$K(v) = K_{m_1} \exp\left[-\frac{v^2}{2\sigma_k^2}\right] + K_{m_2} \exp\left[-\frac{(v-5)^2}{2\sigma_k^2}\right] + K_{m_3} \exp\left[-\frac{(v+5)^2}{2\sigma_k^2}\right]$$

introduces three peaks in the K function, one at zero and two at ±5 with the maximal heights of the peaks in the K-curve given by the vector $\mathbf{K}_m = [K_{m_1}\ K_{m_2}\ K_{m_3}]$. The introduction of multiple peaks puts frequency dependence back into the model even with $\beta = 0$ and $\alpha_{\text{comp}} = 0$. Using the same competition coefficient as given by (5), with the parameter values

$$\mathbf{K}_m = [100 \quad 70 \quad 60],$$

$$\beta = 0,\ \alpha_{\text{comp}} = 0,\ \sigma_k = \sqrt{2},\ R = 0.25,\ \sigma_\alpha = 2,$$

an ESS coalition of three is obtained,

$$\mathbf{u} = [-5.1412 \quad -0.0090 \quad 5.1207]$$

$$\mathbf{x}^* = [56.2802 \quad 95.6842 \quad 66.3202],$$

as illustrated in Fig. 4.

In this example, the rank order of species at the ESS is the same as the ordering of the peak heights. The highest peak has the greatest relative abundance, the second and third highest peaks have the second and third levels of relative abundance. This seems intuitively obvious because the peak heights reflect the carrying capacity of the environment with respect to strategy. This can be expected with little inter-specific competition, especially if it is symmetric. However, this result is not true in general. With this six-peak example

$$K(v) = K_{m_1} \exp\left[-\frac{v^2}{2\sigma_k^2}\right] + K_{m_2} \exp\left[-\frac{(v-2)^2}{2\sigma_k^2}\right] + K_{m_3} \exp\left[-\frac{(v+2)^2}{2\sigma_k^2}\right]$$
$$+ K_{m_4} \exp\left[-\frac{(v-4)^2}{2\sigma_k^2}\right] + K_{m_5} \exp\left[-\frac{(v+5)^2}{2\sigma_k^2}\right] + K_{m_6} \exp\left[-\frac{(v-6)^2}{2\sigma_k^2}\right]$$

with parameter values

$$\mathbf{K}_m = [94 \quad 92 \quad 91 \quad 85 \quad 105 \quad 80]$$

$$\beta = 0.1,\ \alpha_{\text{comp}} = 0.5,\ \sigma_k = \sqrt{0.5},\ R = 0.25,\ \sigma_\alpha = 2$$

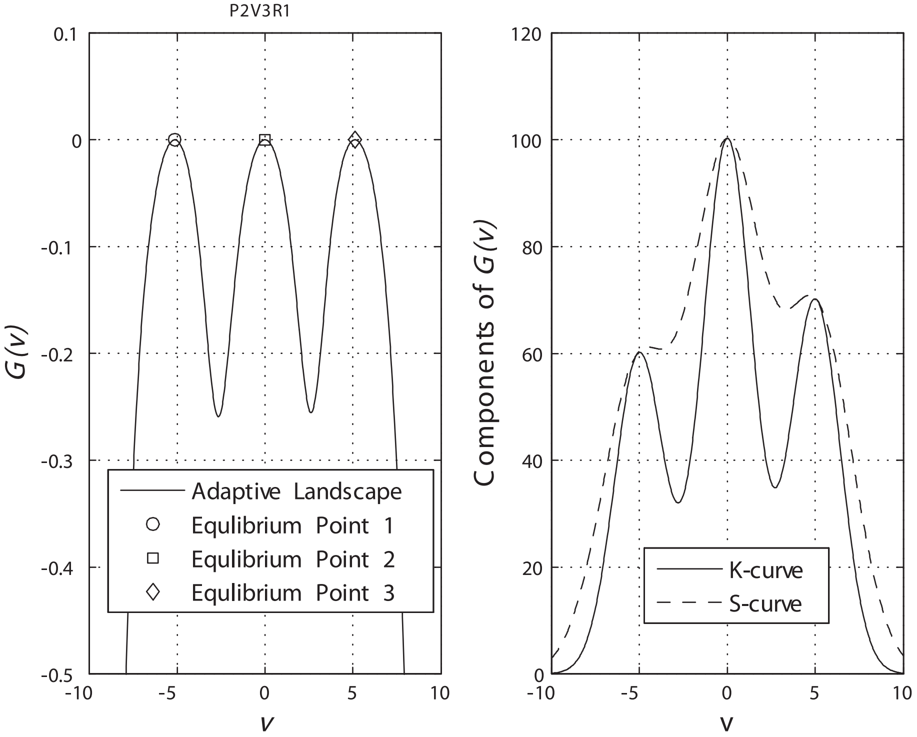

Fig. 4. An ESS coalition of three using $\alpha_{\text{comp}} = 0$, symmetric α, and a polymodal non-symmetric K.

we obtain an ESS solution for **u** in this case as an ESS coalition of six located near each of the strategy peaks with equilibrium population values $\mathbf{x}^*$ given by

$$\mathbf{u} = [-5.0064 \quad -1.9535 \quad -0.0155 \quad 2.0221 \quad 4.0149 \quad 5.9907]$$

$$\mathbf{x}^* = [45.1413 \quad 3.8864 \quad 24.4104 \quad 16.5199 \quad 6.6415 \quad 18.0914]$$

In this case, the highest peak corresponds to $K_{m_5} = 105$ (at $v = -5$), the second highest corresponds to $K_{m_1} = 94$ (at $v = 0$), and so on. However, we see from Fig. 5(i) that the ordering of the relative abundance ranks need not follow this same pattern. For example, the strategy $v = 5.9907$ has the third highest relative abundance yet it is located close to the lowest peak. The reason relative abundance does not necessarily follow the peak heights is because of the frequency dependence created by stronger inter-specific competition. The size of the relative maxima of the K-function alone does not necessarily determine the relative size of the equilibrium populations at the ESS. Figure 5(ii) illustrates that the relative abundance distribution obtained in this case does mimic field data.

To understand what our polymodal K-curve model tells us about abundance and rarity, and the implications brought about by invasion or extinction of species within a community, we conduct a series of modelling scenarios. In the following sections, we will use the Shannon diversity index to compare the different communities that we model. This index is given by

$$H_s = -\sum_{i=1}^{n_s} p_i \ln p_i .$$

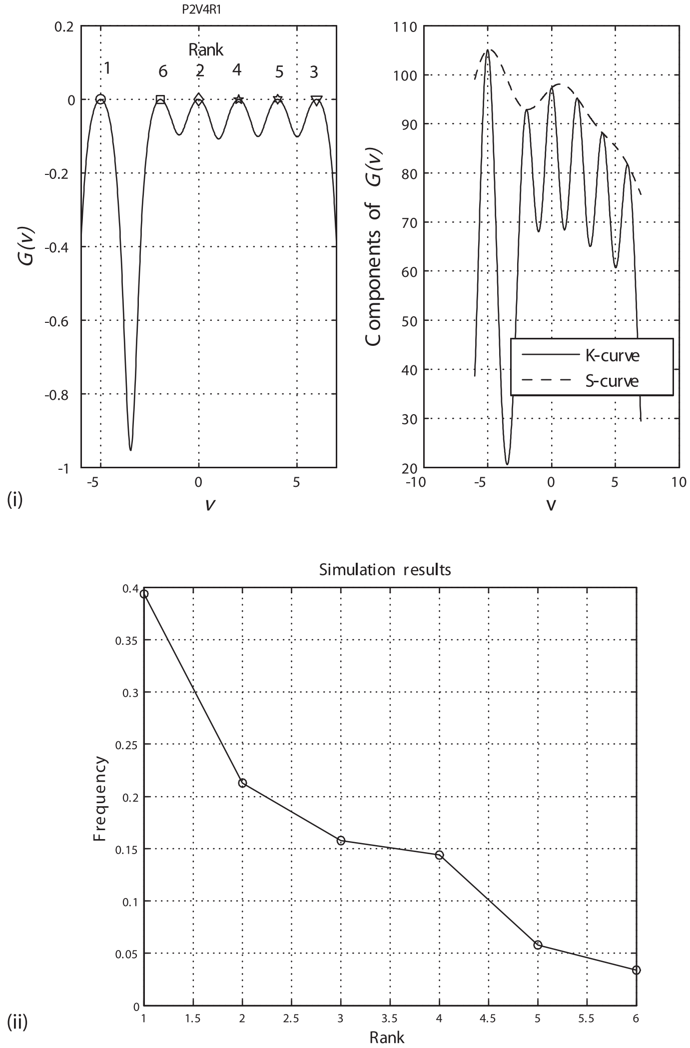

Fig. 5. (i) Non-symmetric polymodal *K*-curve. (ii) Simulation of relative abundance for six species.

The Shannon index takes into account both evenness in relative abundance and number of species within a community. Either increasing the number of species or increasing species evenness increases the value of H_s. Because our main interest is in relative abundance (species evenness), we use the normalized Shannon diversity index given by

$$E = \frac{H_s}{\ln n_s}.$$

If all species are of equal abundance, then the numerator and denominator are equal and this corresponds to the maximum value for the index (Magurran, 1988). For a given number of species, the richest communities are the most even (i.e. where $E \to 1$). Communities where population sizes are uneven have species that are 'dominant' and species that are 'rare', resulting in a smaller value for E.

SCENARIOS FOR COMMUNITY ASSEMBLY

Uniform *K* distribution

As we have found, relative abundance ranking does not necessarily follow from the peak heights of the *K*-curve. To explore the effect of frequency dependence on abundance and rarity, we will now consider a *K*-curve that has uniformly spaced peaks with uniform heights. Keeping the heights uniform provides competition in a 'fair' environment that does not favour one 'peak' strategy over another in terms of potential carrying capacity without competition. For our model, to keep all the peaks at the same height, the distribution functions at each end must have slightly higher $\mathbf{K}_m$ values. This is because end peaks have neighbouring peaks on one side only. For all others, the neighbouring peaks add a small contribution giving peak values greater than their $\mathbf{K}_m$. Simulation results using the parameters

$$\mathbf{K}_m = [81.5 \quad 80 \quad 80 \quad 80 \quad 80 \quad 80 \quad 80 \quad 81.5] \tag{6}$$

$$\beta = 0,\ \alpha_{\text{comp}} = 0,\ \sigma_k = 0.7071,\ R = 0.25,\ \sigma_\alpha = 2.1 \tag{7}$$

are illustrated in Fig. 6(i). Due to the symmetry of the distribution, Fig. 6(ii) has a step-wise relative abundance curve similar to the graph of duck data in Fig. 1(ii). $E = 0.84$ for this community.

The highest ranked species have strategies located near the peaks at both ends of the *K*-curve. In this 'fair' environment, species at the tails of a strategy distribution have the greatest population sizes because there are no competing populations on one side of the strategy space relative to their own strategy. We also see that the lowest ranked species are adjacent to the highest ranked species. This makes sense because they not only compete on both sides of the strategy spectrum, they compete strongly with the highest ranked species. Recall that for this model the strength of competition decreases as species diverge along the strategy distribution (3), and remember that for the *S*-curve competition scales with the number of individuals playing the competing strategy. The next highest ranks are then adjacent to the lowest ranked species moving inward because there is less competition from one side of the strategy space (where the lowest ranked species are), and so forth to the middle. Thus the rank order of a species in an environment with uniform peaks in carrying capacity can be determined by its strategy relative to others in the community. As a general rule, the extreme ends of the strategy space will be most dominant and species will alternate from rarest to second dominant to second rarest to third dominant, etc., along the strategy space as one moves to the middle from both sides.

Asymmetric competition–unfair strategy advantage

Symmetry in the α function in the above example resulted in a stair-like abundance distribution. While some data have this characteristic, it can be eliminated by introducing asymmetry into the model. One way to do this is to set $\beta > 0$. From (5), we see this implies that an individual with a large strategy value has a larger negative effect on a focal individual with a small strategy value than the smaller has on the larger. Such might be the case where larger competitors have a greater competitive effect on smaller individuals than vice versa.

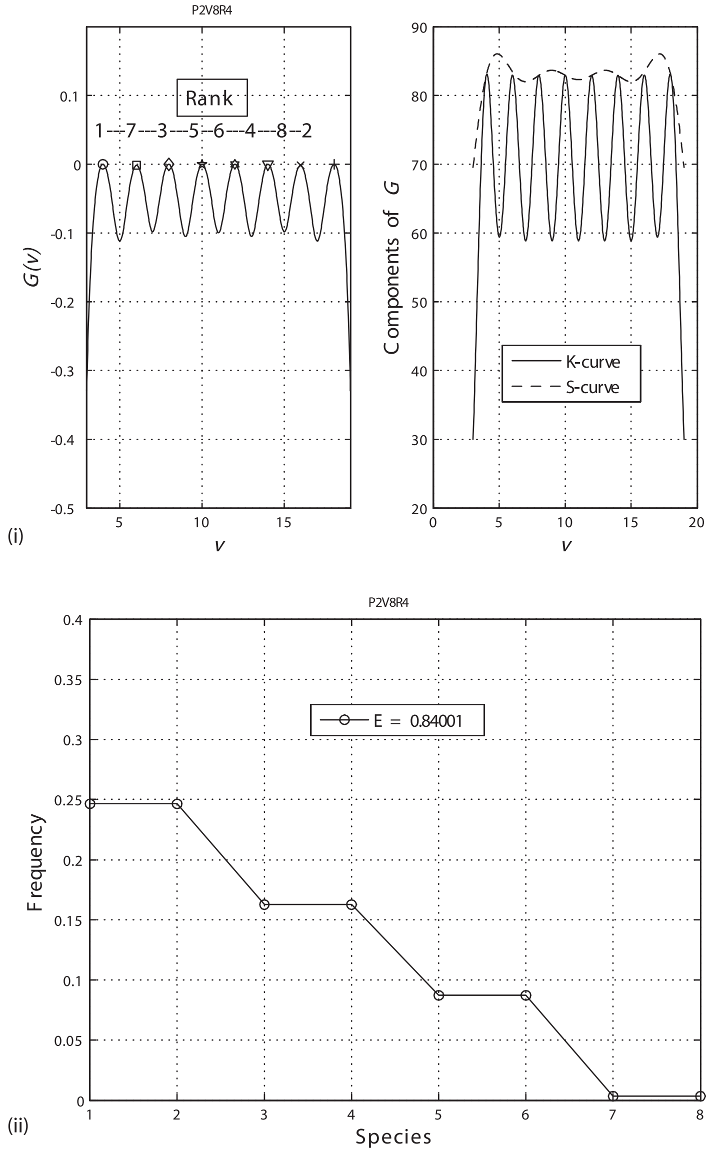

Fig. 6. (i) An ESS coalition of eight strategies. (ii) A step-wise distribution is obtained in this case.

Choosing the same parameters given by (6) and (7), except for setting $\beta = 0.5$, results in a dramatically different relative abundance curve (see Fig. 7). No longer are there pairs of species with equal relative abundance, and one species is lost from the evolutionarily stable coalition. $E = 0.87$ for this community, indicating that with the loss of one species, the remaining species have slightly more even population numbers than the previous example with symmetric competition. There may be fewer species than peaks in the *K*-curve because of inter-specific competition, and the height and proximity of the peaks to each other.

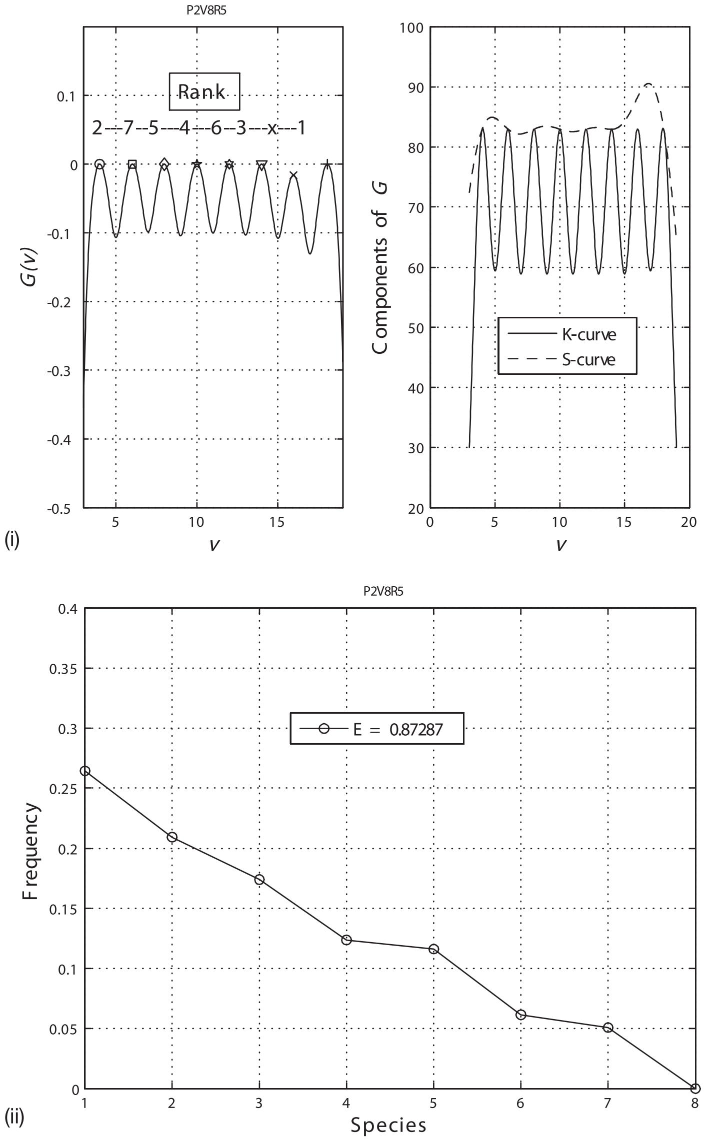

Fig. 7. (i) Adding asymmetry results in an ESS coalition of seven strategies. (ii) With asymmetry, the step-wise distribution is lost.

The rank order still follows the general rule of thumb of alternating dominant–rare strategies moving from the outside to the middle of the strategy spectrum. The largest strategy value is the most dominant because it has a greater negative effect on smaller strategies than vice versa. Keeping the asymmetry at $\beta = 0.5$, but reducing the effect of competition, $\sigma_\alpha < 2.1$, it is possible to regain the lost species. In fact as $\sigma_\alpha \to \sigma_k$, all species will have approximately the same population size regardless of asymmetric effects ($E = 1$). For example, setting $\sigma_\alpha = 1.75$, with all other parameters given by (6) and (7), all eight species are again present with a relative abundance curve similar to that in Fig. 7(ii) except the least abundant species is at a frequency of approximately 2% instead of zero. Also, the Shannon index of evenness increases to $E = 0.9254$.

We note that a mirror image of Fig. 7(i) is obtained (with the same value of E) if the sign of β is changed from plus to minus. That is, strategies with a smaller magnitude have a greater competitive effect on bigger strategies than the bigger strategies have on the smaller ones. The relative abundance curve also has a mirror image; compare Tables 1 and 2.

Table 1. Results for Fig. 7 with $\beta = 0.5$, with all other parameters given by (6) and (7)

Rank	2	7	5	4	6	3	8	1
x^*	62.93	15.29	34.91	37.20	18.52	52.31	0.00	79.50
u	4.00	6.01	7.99	10.01	12.00	14.00	15.97	18.06

Note: The rank 8 population went extinct because its peak in the G-function at $u = 15.97$ is less than zero.

Table 2. Mirror image of Fig. 7 (not illustrated) with $\beta = -0.5$, with all other parameters given by (6) and (7)

Rank	1	8	3	6	4	5	7	2
x^*	79.50	0.00	52.31	18.52	37.20	34.91	15.29	62.93
u	3.94	6.03	8.00	10.00	11.99	14.01	15.99	18.00

Note: The rank 8 population went extinct because its peak in the G-function at $u = 6.03$ is less than zero.

These results show that asymmetries in competitive effect due to strategy value can influence which end of the strategy spectrum is likely to have the highest ranked species, but it does not change the alternating dominant–rare rule of thumb for ranking of strategies.

Asymmetric competition–unfair environment

In the previous example, species at one end of the strategy distribution had an 'unfair' advantage in competition with those at the other end (magnitude of strategy matters). Another approach to creating asymmetric competition is to create an 'unfair' environment that allows some species to have greater carrying capacities than others (magnitude in population density matters). In this second case, we can make adjustments to the peaks of the K-curve such that one peak reflects more abundant resources available at a particular point along the strategy distribution than anywhere else:

$$\mathbf{K}_m = [160 \quad 40 \quad 40 \quad 40 \quad 40 \quad 40 \quad 40 \quad 40] \tag{8}$$

$$\beta = 0,\ \alpha_{\text{comp}} = 0,\ \sigma_k = 0.7071,\ R = 0.25,\ \sigma_\alpha = 1.75. \tag{9}$$

The addition of a dominant peak in the K-curve produces results that look more like the graph of shorebird relative abundance [compare Fig. 1(i) with Fig. 8(ii)]. In this case, adding and changing β (unfair strategy advantage) has little effect on which species will be dominant, but it does influence the rank order of other (much rarer) species. Tables 3–5 summarize these results.

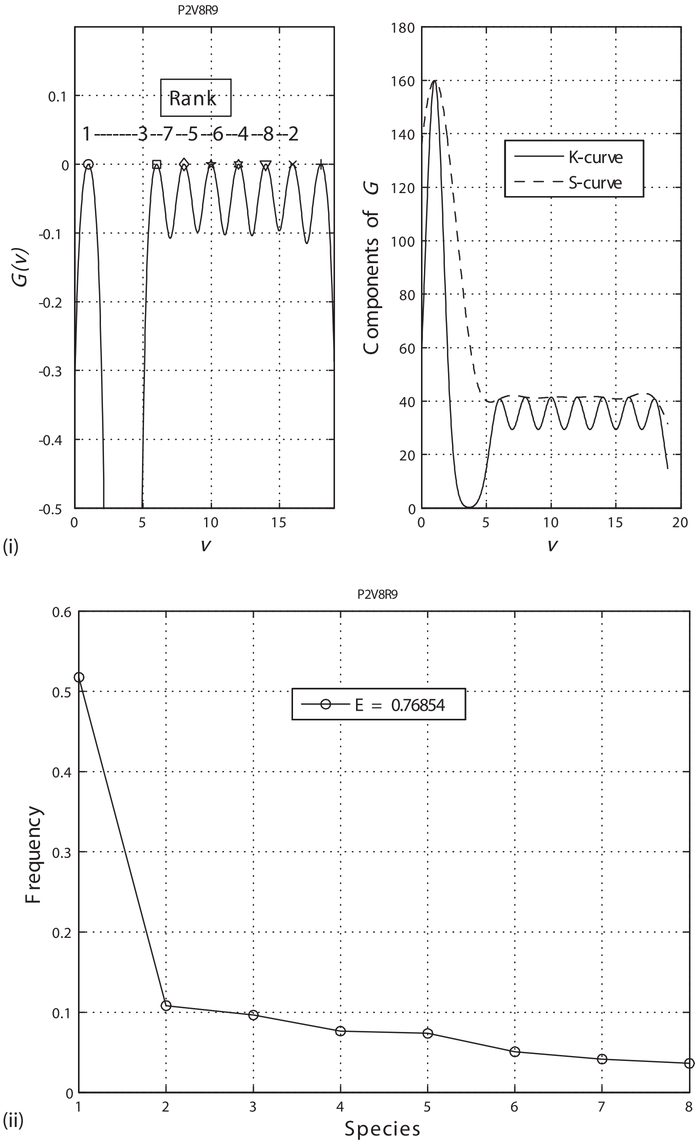

Fig. 8. (i) A disproportionately high peak in the *K*-curve results in (ii) strong dominance by one strategy in the community.

Table 3. Figure 8 results obtained by setting parameters given by (8) and (9) ($E = 0.7685$)

Rank	1	3	7	5	6	4	8	2
x^*	159.50	29.73	12.80	22.67	15.61	23.46	11.14	33.31
u	1.00	6.01	8.01	9.99	12.00	14.01	15.97	18.04

Table 4. Results obtained (not illustrated) by setting $\beta = 0.5$, with all other parameters given by (8) and (9) ($E = 0.7420$)

Rank	1	4	6	5	7	3	8	2
x^*	164.52	28.31	12.53	25.17	11.07	29.99	3.98	39.51
u	1.08	6.02	8.00	10.01	11.98	14.03	15.95	18.08

Table 5. Results obtained (not illustrated) by setting $\beta = -0.5$, with all other parameters given by (8) and (9) ($E = 0.7542$)

Rank	1	2	8	4	6	5	7	3
x^*	165.33	32.69	8.85	25.89	13.80	23.46	13.09	29.66
u	0.92	6.02	8.02	9.98	12.01	13.99	16.00	18.01

The Shannon index of evenness does not vary much between each of these communities (see Tables 3–5). Note, however, that evenness is much lower overall than in a 'fair' environment. These results indicate that unfair environments can have a strong influence in creating dominant species and also shows that asymmetric strategy effects can have a strong influence on the ordering of rarer species. In all cases, the alternating dominant–rare rule of thumb still works for species that have equivalent amounts of resources in the environment.

Consequences of species removal

Removal experiments can indicate whether a particular species has a large or small effect on other species in a community. We can explore our models in more depth by asking: What happens to a community in ecological time (that is, if evolution is not allowed to occur) if we remove a dominant or rare species? Starting with the case where *K*-curve peak heights are equal but competitive interactions are not symmetric (Fig. 7), with parameters

$$\mathbf{K}_m = [81.5 \quad 80 \quad 80 \quad 80 \quad 80 \quad 80 \quad 80 \quad 81.5] \tag{10}$$

$$\beta = 0.5,\ \alpha_{\text{comp}} = 0,\ \sigma_k = 0.7071,\ R = 0.25,\ \sigma_\alpha = 2.1, \tag{11}$$

we first remove the biggest magnitude strategy (most dominant species), then remove the second-to-smallest strategy (rarest species) by setting their respective densities equal to zero. (Recall the bigger magnitude strategies have the advantage over the smaller, and that the rarest species is not going to be the smallest magnitude strategy because the smallest strategy has no competitors on one side of the trait spectrum.) Rerunning the simulation gives us the following results that can be compared with Table 1:

- Removing the most dominant species results in $E = 0.73219$

Table 6. All parameters given by (10) and (11)

Rank	2	6	4	5	3	Missing	1	Removed
x^*	68.70	2.77	54.36	9.77	56.30	0	79.24	—
u	4.01	6.01	8.00	10.00	12.00	13.97	16.12	—

- Removing the rarest species results in $E = 0.81918$

Table 7. All parameters given by (10) and (11)

Rank	2	Removed	4	5	6	3	Missing	1
x^*	72.3292	—	45.3386	31.819	20.9553	51.5371	0	79.5568
u	4.0233	—	7.9835	10.008	11.9938	14.0006	15.9656	18.0572

Removing the most dominant species allows the formerly extinct rarest species ($u \approx 16$; Table 1) to become the most dominant species because it no longer has competition from a dominant neighbouring trait. Such an extreme advantage causes the extinction of $u \approx 14$ and the resulting shift in alternating rare–common ranking for the rest of the species. However, if evolution were allowed to occur, the system would shift back to the solution found in Table 1. Removing the rarest species ($u \approx 6$; Table 6) essentially leaves the community unchanged (compare with Table 7) in the ranking of the remaining species, as might be expected from its small competitive effect on other species.

Consider the flip side of the coin: What happens to a community when the highest peak in the *K*-curve is unoccupied (again, in ecological time)? Using parameters from (8) and (9) and removing the dominant species off the highest peak results in Fig. 9 with a Shannon index of evenness $E = 0.89409$. In this case, removing the dominant species creates a more even community that follows a ranking pattern that one might expect of a community with a uniform *K*-curve.

Table 8. Results obtained by setting $\beta = 0$, with all other parameters given by (8) and (9)

Rank	Removed	2	7	3	5	4	6	1
x^*	—	33.36	11.02	23.73	15.08	23.73	11.02	33.36
u	—	5.95	8.02	9.99	12.00	14.01	15.97	18.04

If we compare the community with the highest *K*-curve peak occupied (Table 3) with the community where we remove the dominant species off the peak (Table 8), neither ranking nor absolute abundance change much for the rest of the community. This reflects the

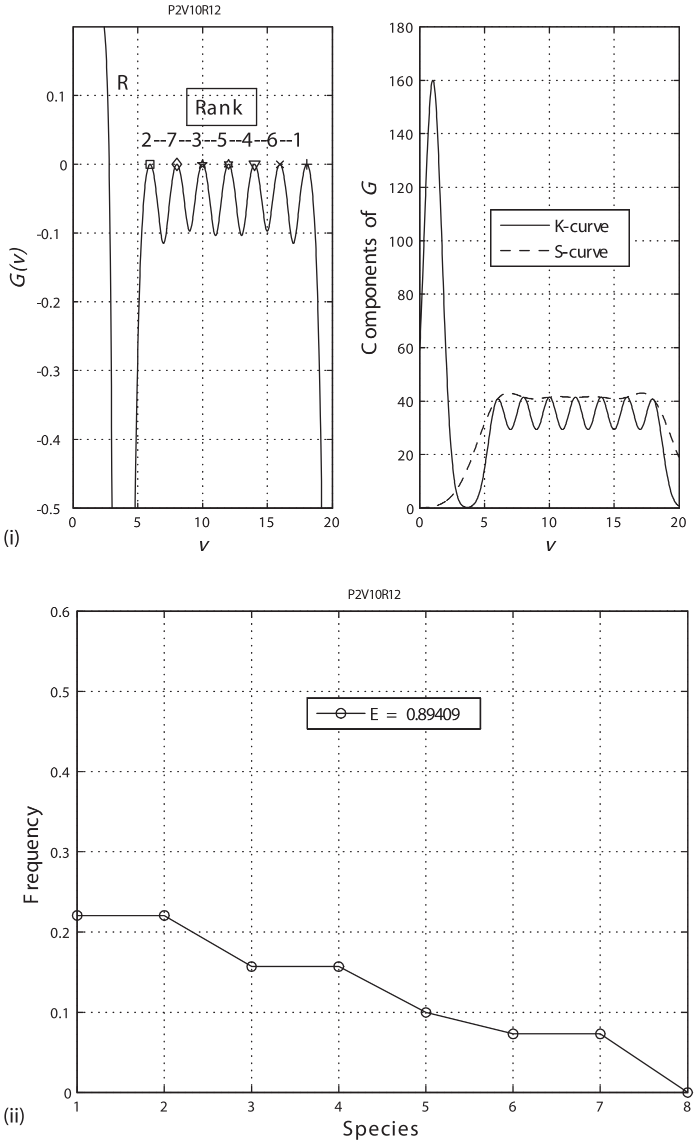

Fig. 9. (i) The dominant strategy is artificially removed. (ii) The resulting community is more even.

importance of *K*-curve peaks in setting absolute abundance but not necessarily rank. As stated before, if evolution (or invasion) were allowed to occur, the system would evolve to Table 3 values and the unoccupied *K*-curve peak would become occupied.

Brown and Vincent (1992) performed similar species removals with a predator–prey community to see what would happen when a prey or predator is removed. They referred to a species as being ecologically keystone if its removal results in the extinction of other species on an ecological time scale, and evolutionarily keystone if its removal causes the extinction of another under Darwinian dynamics. Both scales are relevant here. In some cases, a species that would otherwise go extinct can co-exist while other species go extinct.

DARWIN'S FINCHES

Can our models of relative abundance distributions be applied to real systems? Examining relative abundance in a real system requires data from which the *K*- and *S*-curves can be constructed. Such data are rare in the literature, although one data set does exist. Schluter and Grant (1984) collected the relevant data from communities of Darwin's finches (*Geospiza*) on the Galapagos Islands, a group of species arguably characterized by competition for food resources and natural selection on morphological characters via this competition (Lack, 1947). Our modelling approach can be used to study relative abundance in *Geospiza* because this is a group of evolutionarily identical individuals (they most likely share the same *G*-function) and the strategy of importance is a scalar variable (log beak depth). Schluter and Grant (1984) estimated the abundance of hypothetical finch species (designated by beak depth) in the absence of inter-specific competition for 15 Galapagos islands. They did this by determining the range of seeds that a hypothetical species may consume on a particular island (range determined by beak strategy), determining the abundance of all available food for each particular strategy, and finally calculating the number of individuals of a species that may be supported by this quantity of food. In each step, they based their calculations on measured relationships (see Schluter and Grant, 1984, for details). The graphs that they created from these three steps (expected population density vs. log beak depth) are essentially carrying-capacity functions with respect to strategy. They constructed these '*K*-curves' for 15 Galapagos islands and most of them can be considered polymodal distribution functions (see Schluter and Grant, 1984, Figure 4).

In their paper, Schluter and Grant give details for their calculations for only one island [Isla Wolf (see Table 1 in Schluter and Grant, 1984)]. From this table, we are able to closely approximate construction of the *K*-curve using the five exponential functions defined below:

$$K(v) = K_{m_1} \exp\left[-\frac{(v-u_{p_1})^2}{2\sigma_{k_1}^2}\right] + K_{m_2} \exp\left[-\frac{(v-u_{p_2})^2}{2\sigma_{k_2}^2}\right] + K_{m_3} \exp\left[-\frac{(v-u_{p_3})^2}{2\sigma_{k_3}^2}\right]$$

$$+ K_{m_4} \exp\left[-\frac{(v-u_{p_4})^2}{2\sigma_{k_4}^2}\right] + K_{m_5} \exp\left[-\frac{(v-u_{p_5})^2}{2\sigma_{k_5}^2}\right],$$

where

$$\mathbf{K}_m = [-4.1 \quad 11 \quad 1.9 \quad 3.0 \quad 6.0],$$

$$\mathbf{u}_p = [1.8 \quad 1.9 \quad 2.4 \quad 2.595 \quad 2.8],$$

$$2\boldsymbol{\sigma}_k^2 = [0.0024 \quad 0.0600 \quad 0.0200 \quad 0.0032 \quad 0.0200].$$

Figure 10 illustrates the *K*-curve approximation.

In addition, we can also use their table to construct an *S*-curve, albeit much less directly than the *K*-curve. The *S*-curve is made up of two components: $\alpha(v, u_j)$ and x_j^*. The latter is determined by the model at equilibrium, but we need a way of generating the former. Recall that $\alpha(u_i, u_j)$ is the competitive effect of type j using strategy u_j on the fitness of individuals of type i using strategy u_i. We can construct an α-function with respect to a focal strategy v if we construct a table of competitive effects of one strategy upon another (see Appendix for details). From Table 1 in Schluter and Grant (1984), we can calculate the percent overlap in diet for each strategy with respect to other strategies. If we assume that diet overlap is a

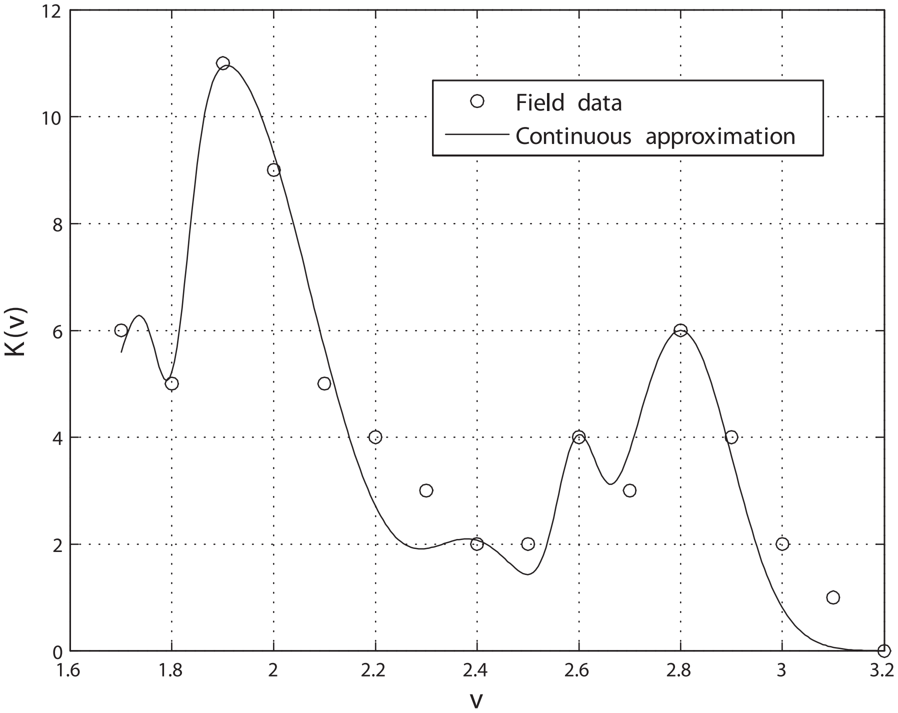

Fig. 10. The solid line represents the continuous approximation to the 16 data points obtained from Schluter and Grant (1984). The three significant peaks are closely approximated.

good estimate of competitive effect on fitness, then discrete points for $\alpha(v, u_j)$ can be calculated (see Appendix). Using this information, we can estimate a continuous α-function (see Appendix):

$$\alpha(v, u_j) = \exp\left[-\frac{(v-u_j)^2}{2\sigma_a^2 + \left(\dfrac{v}{a_1}\right)^{a_2}}\right], \qquad (12)$$

where

$$2\sigma_a^2 = 0.31,\ a_1 = 3.2,\ a_2 = 10. \qquad (13)$$

Using Darwinian dynamics, this function can then be used in conjunction with our penta-modal *K*-curve to create an ESS solution. For Isla Wolf, we predict an ESS coalition of two as illustrated in Fig. 11. We also predict that the abundance of the smaller-beaked finch species will be close to its carrying capacity, and the abundance of the larger-beaked finch species will be nearly half its carrying capacity at equilibrium. This is due to an overlap in the use of one seed type. For the small-beaked finch strategy, the diet overlap is small (25%) compared with the diet overlap for the large-beaked finch strategy (50%) (see Schluter and Grant, 1984, Table 1).

Although our *K*-curve is penta-modal, this does not necessarily mean that one can assume the evolution of five species to match those peaks. Because of the interplay between the *K*-curve and the *S*-curve, only two species can reach an evolutionarily stable

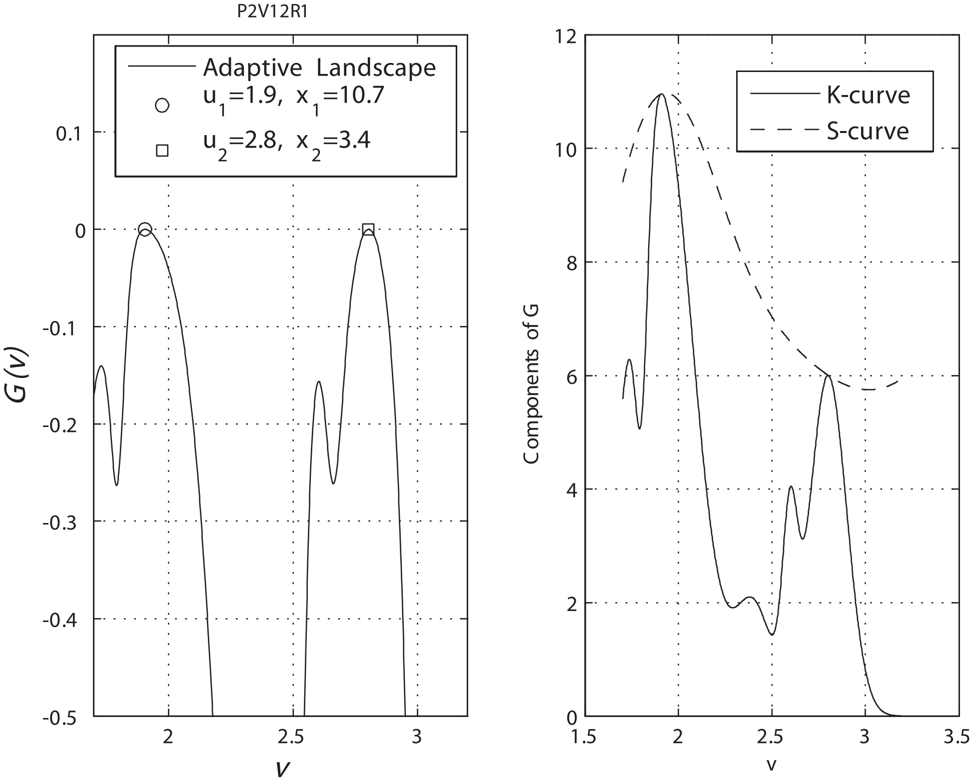

Fig. 11. With three and perhaps four peaks, only two finches are evolutionarily stable on this island, as illustrated in the left-hand panel. The right-hand panel shows why this must be the case. The smaller peaks in the *K*-curve cannot supply sufficient resources to maintain co-existence of additional species.

equilibrium. As Schluter and Grant (1984, Figure 4) show, only two species of Galapagos finches co-existed on Isla Wolf when they conducted their study: a large-beaked finch ($u \approx 2.7$) and a small-beaked finch ($u \approx 2.0$). These strategy values are close, but not exactly our predictions (i.e. $u = 2.8$ and $u = 1.9$). Schluter and Grant (1984) do not have data on the abundance of these species, so we cannot test our relative abundance predictions here. However, this exercise does demonstrate that our model can be adapted for use in predicting relative abundance in natural systems if the correct data are available.

DISCUSSION

Using an evolutionary approach to modelling patterns of relative abundance in biological communities, we have discovered several new and interesting implications. With our method, we take the classic Lotka-Volterra competition equations and the *K*- and α-functions from Roughgarden (1983) and use a *G*-function and strategy dynamics to determine the outcome of competitive interactions between species within a community (Vincent and Brown, 2005). Because the Lotka-Volterra competition equations do not produce evolutionarily stable communities [‘ESS coalitions’ *sensu* Vincent and Brown (2005)] containing more than one species (Vincent *et al.*, 1993), we examine modifications of this model that produce multispecies communities for their effect on relative abundance distributions.

We began with the assumption that a 'community' is a group of evolutionarily identical individuals that all share the same rules of ecological engagement – share the same *G*-function (Vincent and Brown, 2005) – including the same intrinsic growth rate, living in the same local area, and competing for the same or similar resources. Thus our predictions apply to ecological communities like *Geospiza* finches on the Galapagos Islands (Schluter and Grant, 1984), filter-feeding dabbling ducks (Gurd, 2007), subspecies of crossbills (Benkman, 2003), stickleback fish (Schluter, 2003), and lacustrine fish (Mason *et al.*, 2008), to name but a few examples. The assembly of more inclusive communities, such as 'North American breeding birds', potentially could be modelled using multiple *G*-functions (Vincent and Brown, 2005, Ch. 4.6), but we leave out such an analysis here.

We also assumed that individual traits (strategies) are important, and could influence the outcome of the 'ecological engagement' in the manner of an evolutionary game. We defined a species by the mean value of all strategies used in a population and we allowed new species to arise via evolutionary dynamics. In our model, we assume that an individual's strategy is a scalar value, like, for example, the depth of a beak in *Geospiza* finches (Schluter and Grant, 1984). For some communities, ecologically important strategies may be multi-dimensional – for example, gape width and lamellar separation in dabbling ducks (Gurd, 2007), bill depth and palate groove width in crossbills (Benkman, 2003), body depth, snout width, and gill raker number in sticklebacks (Schluter, 2003). The incorporation of multi-dimensional traits (vector strategies) into a single *G*-function model is possible (see Vincent and Brown, 2005, Ch. 4.4), but we do not address such an analysis here.

We modified the competition equations so that communities with more than one species could be evolutionarily stable. As we showed (Vincent and Vincent, 2007), this can be accomplished by adding a fixed competitive cost $\alpha_{\mathbf{comp}}$, or by creating a polymodal relationship between carrying capacity and strategy (polymodal *K*-curve). We began with a form of the Lotka-Volterra competition model that assumes competition to be strongest when strategies are most similar. This assumption is not unrealistic (see, for example, Fargione *et al.*, 2003). Adding a fixed competitive cost is analogous to having some sort of cost of competition no matter how different strategies are to one another, with the consequence that a population can never reach carrying capacity. This might work for a community in which all individuals take up space no matter how differently they garner other resources. It turns out that models with a fixed competitive cost and unimodal *K*-curves, with or without competitive asymmetries β, do not result in communities with typical relative abundance distributions. Unimodal *K*-curves create very even communities with many abundant species and few rare species (the relative abundance curve bows outward).

Our model shows that when environments have only one peak in carrying capacity with respect to strategy, only frequency dependence allows there to be more than one strategy that can take advantage of that peak. Perhaps there is only one kind of resource in the environment (one species of pine nut) and only one optimal strategy (say, beak width) that is best at opening that pine nut. Other strategies manage to co-exist in this community because they can open the pine nut (though slightly less efficiently) and because there are frequency-dependent effects and a fixed competitive cost. To add more species to this community, we can decrease the competitive effect by increasing the value of σ_K. This produces flatter and flatter *K*-curves (strategies farther and farther from the optimal strategy find it easier to open the pine nut), and more and more even communities.

In modelling terms, it becomes more difficult to add more species as the community grows because it becomes harder and harder to seek out small differences between the *S*- and *K*-curves. This, and the outward-bowed relative abundance curves, make it unlikely that these conditions exist for most natural communities.

Most biological communities can be characterized by few abundant species, some common species, and many rare species (Fisher *et al.*, 1943) (the relative abundance curve bows inward). Thus, we turn to polymodal *K*-curves. By incorporating polymodal *K*-curves into our model, we eliminate the need for a fixed competitive cost α_{comp} to give us evolutionarily stable communities of more than one species. When we allow several peaks in carrying capacity with respect to strategy, we create an environment where only particular strategies, on their own, can exploit these peaks. Perhaps there are several kinds of a resource in the environment (say, four species of pine nuts), and only that number of optimal ways of garnering those kinds (say, four widths of beak). In addition, we assume that carrying capacity drops off rapidly away from the optimal strategies that can exploit these peaks. We find that models with polymodal *K*-curves produce relative abundance curves that bow inward with fewer abundant species and more rare species. Thus, we can infer from our models that natural communities are more likely to have environmental conditions that create polymodal *K*-curves rather than unimodal *K*-curves. Indeed, we would argue that one study that actually estimated the distribution of *K* with respect to strategy for finch communities on 15 Galapagos islands found at least 13 islands to be polymodal (Schluter and Grant, 1984). We note here that *n* peaks in the *K*-curve do not necessarily produce *n* evolutionarily stable species in a coalition. Moreover, the ordering of the relative abundance of these species does not necessarily follow the ordering of the heights of the peaks, nor do the EES strategies necessarily lie at the top of each peak. This is due to frequency-dependent competitive interactions.

We began with a form of the Lotka-Volterra competition model that assumes competition to be strongest when strategies are most similar. This competition is also assumed to be symmetric such that for a given individual's strategy, the effect of competition is symmetric with respect to the virtual variable v. We added the term β to the competition equation to make competition asymmetric. This allows one strategy to have more or less of an effect on the fitness of a second strategy than the second strategy has on the first. The value of β shifts the value of v required for maximum competitive effect (Brown and Vincent, 1987). This kind of competitive asymmetry might exist in cases where competitors with a larger trait (like beak depth) have a greater competitive effect on individuals with a smaller trait than vice versa (like, for example, if body size scales with beak width and larger birds can physically exclude smaller birds). This scenario is not unrealistic (see, for example, Morris *et al.*, 2000). We found that adding β to our models had two effects. First, β eliminated stair-step-like patterns in relative abundance distributions. Thus, we might expect to find competitive asymmetries in the shorebird community depicted in Fig. 1(i) but not in the duck community depicted in Fig. 1(ii). Second, we found from our removal experiments that β can influence which end of the strategy spectrum (small or large) is likely to have the highest ranked (most dominant) species. However, we also found that the effects of β do not necessarily overwhelm an environment that strongly favours strategies that can potentially achieve large carrying capacities. Thus, if large-beaked finches have a greater competitive advantage in interactions with small-beaked finches, this advantage could be outweighed by substantially more resources (higher peak in the *K*-curve) that are best garnered by a smaller-beaked finch.

We also found that our models predict an underlying pattern to relative abundance distributions. That is, species at the ends of the strategy spectrum (smallest or largest of some trait) will be dominant in a community (all else being equal) and that species with strategies closest to the dominant species will be the rarest (all else being equal). Thus, we can expect an alternation of dominant and rare species as we move towards the median strategy value of the community and that the median strategies will hold near-median rankings. However, we also found that the carrying capacity of the environment, as well as β, can mask this underlying pattern. Therefore, we might predict that species at the ends of trait distributions should have higher abundance unless the K-curve peak heights are small or competition is greatly asymmetric. For example, Bowers and Brown (1982) show that body mass might be the strategy of importance in determining the assembly of North American desert rodent communities. Figure 1 in Bowers and Brown (1982) shows the strategy distributions in three communities containing four species each. We would expect from the results of our models that the smallest and largest species should have the greatest relative abundance. However, a true test of the results of our models would require estimating the K-curve peak heights and competitive interactions, as discussed below.

The beauty of the G-function analysis of our models is that if we can generate an S-curve and a K-curve for a particular community of interest, we can predict the evolutionarily stable assembly of that community. Generating a K-curve is fairly straightforward (with a great deal of careful fieldwork). The K-curve can be estimated by calculating the abundance of hypothetical strategies in the absence of inter-specific competition. Depending on the community of interest, one might determine the limits to resource use inherent to each strategy, determine the amount of particular resources available for each strategy, and, finally, calculate the number of individuals that could be supported by this quantity of resources (as done in Schluter and Grant, 1984). The S-curve is made up of two components: the strength of competition by a strategy u_j on focal strategy v multiplied by the population size of u_j. Strength in competition might be measured in terms of diet overlap, as we have done here using Schluter and Grant's (1984, p. 30) data (see Appendix for generation of the α-function). Once we have generated an α-function with respect to strategy, we can use our model and strategy dynamics to arrive at ESS values for $\mathbf{x}$, and the number of co-existing strategies.

Some might argue that an 'equilibrium' analysis of relative abundance distributions could not predict the state of natural communities, which might not be at equilibrium, let alone evolutionarily stable equilibrium. However, we note that evolution of strategies can be quite rapid [as is the case for finches on the Galapagos Islands (Grant and Grant, 2008)]. Also, our theory allows strategy dynamics to 'chase' the fitness peaks and thus capture the trends in evolutionary movement. If the environment changes the K-curve, it is no problem to plug a new curve into the model and watch where the community is headed next. The flexibility of the G-function approach, and its potential for empirical applications, make this a valuable tool in the study of relative abundance distributions.

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APPENDIX

We generate an α-function by first creating a table (Table A1) of percent diet overlap based on Table 1 in Schluter and Grant (1984). Table A1 represents the proportional diet overlap (which we consider competitive effect α) that a particular strategy v has with all other strategies u_j.

Recall that the S-curve is $\Sigma\alpha(v, u_j)\ x_j^*$. This is a continuous function, thus we need to approximate the α matrix with a continuous function. Using (12) and selected parameter values, we generated tables comparable to Table A1. We manipulated the parameters to try and minimize percent error between Table A1 and the new tables. This resulted in Table A2 and the values given in (13). Percent error between these two tables is 0.185.

Thus, for a particular strategy v we can approximate the effect of u_j on v with a low average error rate at the values given in the matrix Table A1. The continuous function and parameters given in (12) and (13) may not be the best fit function for the matrix in Table A1, but it is a good approximation and does show that it is possible to apply such data to our modelling technique.

Table A1. Top row is the strategy u_j [ln(beak depth)]. The remaining rows gives the value for $\alpha(v, u_j)$

Strategy u_j	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2
$\alpha(1.7, u_j)$	1.0	1.0	0.6	0.6	0.2	0	0	0	0	0	0	0	0	0	0	0
$\alpha(1.8, u_j)$	1.0	1.0	0.6	0.6	0.2	0	0	0	0	0	0	0	0	0	0	0
$\alpha(1.9, u_j)$	0.75	0.75	1.0	1.0	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
$\alpha(2.0, u_j)$	0.75	0.75	1.0	1.0	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
$\alpha(2.1, u_j)$	0.5	0.5	1.0	1.0	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
$\alpha(2.2, u_j)$	0	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.3, u_j)$	0	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.4, u_j)$	0	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.5, u_j)$	0	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.6, u_j)$	0	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.7, u_j)$	0	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0
$\alpha(2.8, u_j)$	0	0	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	1.0	1.0	1.0	1.0	1.0
$\alpha(2.9, u_j)$	0	0	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	1.0	1.0	1.0	1.0	1.0
$\alpha(3.0, u_j)$	0	0	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	1.0	1.0	1.0	1.0	1.0
$\alpha(3.1, u_j)$	0	0	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	1.0	1.0	1.0	1.0	1.0
$\alpha(3.2, u_j)$	0	0	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	1.0	1.0	1.0	1.0	1.0

Table A2. Modification of Table A1 according to text

Strategy u_j	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2
$\alpha(1.7, u_j)$	1.0	0.97	0.88	0.75	0.61	0.47	0.35	0.26	0.2	0.16	0.13	0.12	0.12	0.13	0.15	0.18
$\alpha(1.8, u_j)$	0.97	1.0	0.97	0.88	0.76	0.62	0.49	0.37	0.29	0.23	0.19	0.17	0.17	0.18	0.2	0.22
$\alpha(1.9\ u_j)$	0.88	0.97	1.0	0.97	0.88	0.76	0.63	0.51	0.40	0.32	0.27	0.24	0.23	0.23	0.25	0.28
$\alpha(2.0, u_j)$	0.75	0.88	0.97	1.0	0.97	0.89	0.77	0.65	0.53	0.44	0.37	0.33	0.31	0.30	0.31	0.33
$\alpha(2.1, u_j)$	0.6	0.75	0.88	0.97	1.0	0.97	0.89	0.78	0.67	0.56	0.48	0.43	0.39	0.38	0.38	0.4
$\alpha(2.2, u_j)$	0.45	0.6	0.75	0.88	0.97	1.0	0.97	0.9	0.8	0.69	0.6	0.53	0.49	0.46	0.46	0.47
$\alpha(2.3, u_j)$	0.32	0.45	0.6	0.75	0.88	0.97	1.0	0.97	0.9	0.81	0.72	0.65	0.59	0.56	0.54	0.54
$\alpha(2.4, u_j)$	0.21	0.32	0.45	0.61	0.76	0.89	0.97	1.0	0.97	0.91	0.83	0.76	0.69	0.65	0.62	0.61
$\alpha(2.5, u_j)$	0.13	0.21	0.32	0.46	0.61	0.76	0.89	0.97	1.0	0.98	0.92	0.85	0.79	0.74	0.71	0.69
$\alpha(2.6, u_j)$	0.07	0.13	0.21	0.32	0.46	0.62	0.77	0.9	0.97	1.0	0.98	0.93	0.88	0.83	0.79	0.76
$\alpha(2.7, u_j)$	0.04	0.08	0.13	0.22	0.33	0.47	0.63	0.78	0.9	0.98	1.0	0.98	0.94	0.9	0.86	0.83
$\alpha(2.8, u_j)$	0.02	0.04	0.08	0.13	0.22	0.34	0.49	0.65	0.8	0.91	0.98	1.0	0.99	0.95	0.92	0.89
$\alpha(2.9, u_j)$	0.01	0.02	0.04	0.08	0.14	0.23	0.35	0.51	0.67	0.81	0.92	0.98	1.0	0.99	0.96	0.93
$\alpha(3.0, u_j)$	0	0.01	0.02	0.04	0.08	0.15	0.24	0.37	0.53	0.69	0.83	0.93	0.99	1.0	0.99	0.97
$\alpha(3.1, u_j)$	0	0	0.01	0.02	0.05	0.09	0.16	0.26	0.40	0.56	0.72	0.85	0.94	0.99	1.0	0.99
$\alpha(3.2, u_j)$	0	0	0	0.01	0.02	0.05	0.10	0.17	0.29	0.44	0.60	0.76	0.88	0.95	0.99	1.0