



The shape of the competition and carrying capacity kernels affects the likelihood of disruptive selection [☆]

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ABSTRACT

Many quantitative genetic and adaptive dynamic models suggest that disruptive selection can maintain genetic polymorphism and be the driving force causing evolutionary divergence. These models also suggest that disruptive selection arises from frequency-dependent intraspecific competition. For convenience or historical precedence, these models assume that carrying capacity and competition functions follow a Gaussian distribution. Here, we propose a new analytical framework that relaxes the assumption of Gaussian competition and carrying capacity functions, and investigate how alternative shapes affect the likelihood of disruptive selection. We found that the shape of both carrying capacity and competition kernels interact to determine the likelihood of disruptive selection. For certain regions of the parametric space disruptive selection is facilitated, whereas for others it becomes more difficult. Our results suggest that the relationship between the degree of frequency dependence and the likelihood of disruptive selection is more complex than previously thought, depending on how resources are distributed and competition interference takes place. It is now important to describe the empirical patterns of resource distribution and competition in nature as a way to determine the likelihood of disruptive selection in natural populations.

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1. Introduction

In many models of quantitative genetics and adaptive dynamics intraspecific competition is the driving force causing disruptive selection (Bürger et al., 2006; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003; Doebeli et al., 2007; Rosenzweig, 1978; Taper and Case, 1985; reviewed in Bolnick and Fitzpatrick, 2007; Turelli et al., 2001). For instance, in the model of Dieckmann and Doebeli (1999), a monomorphic asexual population evolves by directional selection to an optimal phenotype, where intraspecific competition induces disruptive selection. Disruptive selection occurs because competition is frequency dependent, so that nearby phenotypes suffer little competition interference from the crowded optimal phenotype. As a consequence, evolutionary branching occurs, with the emergence of two coexisting descendent lineages (Ackermann and Doebeli, 2004; Dieckmann and Doebeli, 1999). If the degree of frequency dependence is sufficiently high, the ancestral lineage may split into several daughter lineages in one single burst, producing adaptive radiations (Bolnick, 2006).

Most of adaptive dynamic models of sympatric speciation have assumed the carrying capacity and the competition interference functions (K and C , respectively) to be Gaussian (Ackermann and Doebeli, 2004; Bolnick, 2006; Bolnick and Doebeli, 2003; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003). For example, in Dieckmann and Doebeli's (1999) model, one of the most relevant results is that evolutionary branching will occur only when the curvature of C is higher than that of K ($\sigma_C < \sigma_K$). The use of Gaussian functions, however, has been based either on arguments of mathematical tractability or on the historical precedence of models (MacArthur, 1970; MacArthur and Levins, 1967) with questionable biological assumptions (Ackermann and Doebeli, 2004; Abrams et al., 2008a). In fact, a couple of recent models have shown that non-Gaussian carrying capacity, resource utilization, or competition functions can affect evolutionary dynamics (Abrams et al., 2008b; Doebeli et al., 2007; Leimar et al., 2008). For example, box-like kernels have been shown to facilitate evolutionary branching as compared to Gaussian kernels (Doebeli et al., 2007; Leimar et al., 2008).

Here, we propose a set of non-Gaussian competition and carrying capacity kernels and investigated the likelihood of disruptive selection under these kernels, using the Dieckmann and Doebeli model as a framework. These kernels have a parameter that turns it more or less box-like (Fig. 1). This box-like

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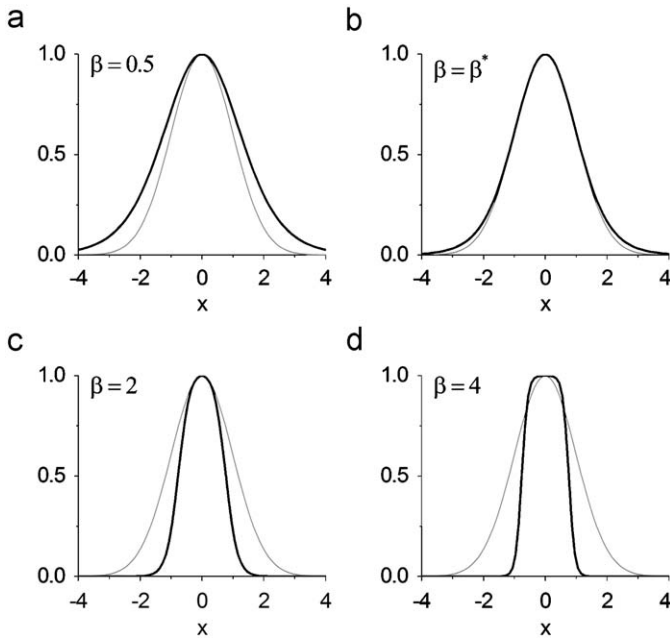


Fig. 1. Comparison between Gaussian $G(x, \sigma)$ (gray line) and hyperbolic tangent $H(x, \beta, \zeta)$ (black line) functions for several values of β . The larger the β , the more box-like the function: (a) $\beta < \beta^* = 0.658$ and H is more spread out than G , (b) $\beta = \beta^*$ and H is approximately G , and (c, d) $\beta > \beta^*$ and H is more box-like than G . $\sigma = 1$ for both functions in all plots.

function is inspired by the fact that many natural populations rely on resources that are not continuously distributed, but instead fall into discrete functional groups corresponding to distinct habitats or taxa. In natural populations, individuals may sometimes specialize on only a single prey group even when their population as a whole uses a number of prey groups (Bolnick et al., 2003). Individuals thus form trophic clusters, and compete strongly with other members of their cluster, but little or not at all with conspecifics that are in other clusters (Araújo et al., 2008). This clustered diet variation means that intraspecific competition may fall off very abruptly with phenotypic distance, rather than declining gradually. More box-like competition functions are meant to better approximate this abrupt change in competition intensity. We found that the competition and carrying capacity functions interact in complex ways, so that the likelihood of disruptive selection changes depending on the shape of both functions. For certain regions of the parametric space, disruptive selection becomes more likely whereas for other regions it becomes more difficult than in the Gaussian case.

2. Analytical model

We adopted the asexual model proposed in Dieckmann and Doebeli (1999), in which we consider an initial species whose individuals have an ecological trait x associated with the use of resources. The carrying capacity function, $K(x)$, determining the resource distribution of a consumer with phenotype x is assumed to be a positive unimodal function of $x - x_0$ with maximum at $x = x_0$. A simple example of such a function is $K(x) = K_0 G(x - x_0, \sigma_k)$, where

$$G(z, \sigma) = e^{-z^2/2\sigma^2} \quad (1)$$

is a Gaussian.

In the present paper, we propose a general family of such functions with two parameters, β and ζ , controlling their shape and width, respectively, that is simple enough to allow the explicit

derivation of several analytical results. The functions are given by

$$H(z, \beta, \zeta) = A[\tanh[\beta(z/\zeta + 1)] - \tanh[\beta(z/\zeta - 1)]], \quad (2)$$

where $A^{-1} = 2 \tanh(\beta)$ is a normalization constant so that $H(0, \beta, \zeta) = 1$ and \tanh is the hyperbolic tangent.

This function is convenient because it can assume Gaussian-like or box-like shapes depending on the value of β (Fig. 1). For the sake of comparison with previous models, we want to relate H with G . In order to do that, we must look for the value of β for which H is as close as possible to G . Expanding both functions to fourth order around $z = 0$ and equating the coefficients we find that $\cosh(2\beta) = 2$ or $\beta = \beta^* = 0.5 \ln(2 + \sqrt{3}) \approx 0.658$, where \cosh stands for the hyperbolic cosine. This is the critical β for which H assumes the shape of an approximately Gaussian function for all values of ζ (Fig. 1b). For $\beta > \beta^*$, H assumes a box-like shape and for $\beta < \beta^*$ it becomes more spread out than a Gaussian function (Fig. 1). We also find it useful to rewrite ζ in terms of a new parameter σ as $\zeta(\sigma) = \sqrt{2}\beta^*\sigma / \cosh \beta^*$, so that $H(z, \beta^*, \zeta(\sigma))$ is similar to $G(z, \sigma)$. This allows us to rewrite H in terms of σ , which is useful because we can investigate the conditions for the establishment of disruptive selection in terms of σ_c and σ_k (Dieckmann and Doebeli, 1999) for different values of β . We must note that, however similar $H(z, \beta^*, \sigma)$ is to the Gaussian $G(z, \sigma)$, G is not a particular case of H , which is a price to pay to work with such a simple analytical function. Even so, for the practical purposes of this paper we assume that, for $\beta = \beta^*$, H can be compared with previous results using Gaussian functions.

Bearing these considerations in mind, we choose the distribution of resources as $K(x) = K_0 H(x - x_0, \beta_k, \sigma_k)$ and consider an initially homogeneous population, where all individuals have the same trait x . The ecological dynamics of the population is given by

$$\frac{dN(x, t)}{dt} = rN(x, t) \left[1 - \frac{N(x, t)}{K(x)} \right], \quad (3)$$

where $N(x, t)$ is the population size at time t and r is the intrinsic growth rate. The equilibrium is reached at $N(x, t) = K(x)$. If a rare mutant with trait value $y = x + \delta x$ is introduced in the resident population, the mutant population might invade or become extinct, depending on the values of x , on the properties of $K(x)$ and on the degree of competition interference between individuals of different trait values. We model the competition interference between individuals of trait values x and y by the function

$$C(x, y) = H(y - x, \beta_c, \sigma_c).$$

The dynamics of the mutant population is given by

$$\frac{dN(y, t)}{dt} = rN(y, t) \left[1 - C(x, y) \frac{K(x)}{K(y)} \right] \equiv R(x, y)N(y, t), \quad (4)$$

where $R(x, y)$ is the effective growth rate of $N(y, t)$ in the presence of x . Note that $C(x, y)K(x)$ is the effective population competing for the same resources with individuals of phenotype y . Since δx is assumed small, it suffices to expand $R(x, y)$ to first order around $y = x$. The solution is then

$$N(y, t) = N(y, 0) e^{R'(x)(y-x)t}, \quad (5)$$

where $R'(x) = dR(x, y)/dy|_{y=x}$. Invasion by the mutants occurs if the exponent is positive, and extinction if it is negative. Using the definitions of $C(x, y)$ and $K(x)$ we find

$$R'(x) = -(x - x_0)f(x), \quad (6)$$

where $f(x)$ is a positive function. Therefore, R' is negative for $x > x_0$ and positive for $x < x_0$, which follows directly from the fact that $K(x)$ is a positive, unimodal function with maximum at $x = x_0$. This simple result shows that invasion occurs for $y > x$ if $x < x_0$ and for

$y < x$ if $x > x_0$. As a consequence, x_0 is the equilibrium phenotype for an evolving population.

The stability of the population at $x = x_0$, however, is not determined by the linear analysis, since $R'(x_0) = 0$. The solution of Eq. (4) for $x = x_0$ requires the expansion of $R(x, y)$ to second order around $y = x = x_0$, resulting in

$$N(y, t) = N(y, 0) e^{R''(x_0)(y-x_0)^2 t/2}. \quad (7)$$

The stability depends only on the sign of the second derivative of R , given explicitly by

$$R''(x_0) = -r \left[C''(x_0, x_0) - \frac{K''(x_0)}{K(x_0)} \right], \quad (8)$$

where the double prime means the second derivative with respect to y calculated at $y = x = x_0$. Dieckmann and Doebeli (1999) have shown that the instability of this equilibrium solution leads to disruptive selection and to the split of the population into two lineages.

The condition for disruptive selection is $R'' > 0$. Therefore, the relevant feature of the competition and resource functions for inducing disruptive selection is their second derivative, i.e., their curvature, calculated at the maximum. For Gaussian functions, the curvature coincides with the variance. For general functions, however, curvature and variance are independent quantities and should not be confused (see Appendix A). The variance of these functions is actually totally irrelevant for our purposes.

Calculating the derivatives, the condition $R'' > 0$ becomes

$$\frac{\beta_c^2}{\sigma_c^2 \cosh(\beta_c)} - \frac{\beta_k^2}{\sigma_k^2 \cosh(\beta_k)} > 0$$

or

$$\sigma_c < \sigma_k \frac{\beta_c \cosh(\beta_k)}{\beta_k \cosh(\beta_c)} \equiv \sigma_k h(\beta_c, \beta_k). \quad (9)$$

Therefore, as long as the competition and carrying capacity functions have the same shape (same β), Dieckmann and Doebeli's (1999) simple condition for speciation, $\sigma_c < \sigma_k$, is recovered. If the 'weight function' $h(\beta_c, \beta_k)$ multiplying σ_k is larger than 1, disruptive selection occurs for a wider range of σ_c values, i.e., for stronger competition interference. On the other hand, if it is smaller than 1, disruptive selection will be restricted to a smaller range of σ_c values (Fig. 2a).

As an illustration, let us take the case in which the carrying capacity function is Gaussian ($\beta_k = \beta^*$), but the competition function is allowed to vary from a Gaussian to more box-like shapes. In this case Eq. (9) reduces to

$$\sigma_c < h(\beta_c, \beta^*) \sigma_k \approx \frac{\sqrt{2} \beta_c}{0.76 \cosh \beta_c} \sigma_k. \quad (10)$$

If we start with $\beta_c = \beta^*$, in which case we have both competition and carrying capacity Gaussian functions, the coefficient $h(\beta_c, \beta^*) = 1$ and the condition for disruptive selection is $\sigma_c < \sigma_k$ (Fig. 2a). As β_c increases (recall that $\beta > \beta^*$ implicates box-like kernels), $h(\beta_c, \beta^*)$ initially increases, reaching a maximum of ~ 1.22 for $\beta_c \sim 1.146$. After that point, $h(\beta_c, \beta^*)$ decreases steadily, reaching 1 again at $\beta_c \sim 1.976$ and then becoming increasingly smaller than 1 (Fig. 2). As a consequence, disruptive selection is facilitated in relation to the Gaussian case for $\beta^* < \beta_c < 1.976$, and becomes increasingly more difficult for $\beta_c > 1.976$ (Fig. 2a).

We remark that other families of box-like functions can be defined. Although it is hard to prove that our results generalize to any such family, we also consider here, as a second example, the family of functions generated by convoluting a Gaussian with a

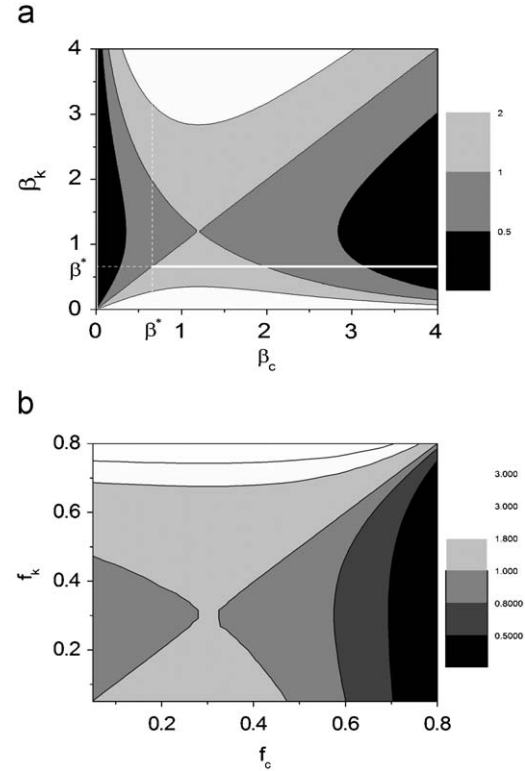


Fig. 2. Contour plot of the 'weight function' h as a function of: (a) β_c and β_k , and (b) f_c and f_k . In the diagonal line, $\beta_c = \beta_k$, $f_c = f_k$, $h = 1$, and disruptive selection occurs if $\sigma_c < \sigma_k$. For $h > 1$ (light gray, beige, and white) disruptive selection is facilitated, and for $h < 1$ (dark gray and black) disruptive selection becomes more difficult with respect to the Gaussian case: (a) the white dotted lines indicate the critical β ($\beta^* = 0.658$) where the function is Gaussian. The horizontal white line represents competition kernels ranging from Gaussian ($\beta_c = \beta^*$) to box-like ($\beta_c = 4$), with a Gaussian carrying capacity function ($\beta_k = \beta^*$). In this case, disruptive selection is initially facilitated and becomes more difficult as β_c increases (see Fig. 3) and (b) functions are Gaussian for $f = 0$ and become increasingly more box-like as f approaches 1. As in the previous case, for a Gaussian carrying capacity function ($f_k = 0$) disruptive selection is initially facilitated (up to $f_c \sim 0.5$) and then becomes increasingly more difficult. (For interpretation of the references to the color in this figure legend, the reader is referred to the web version of this article.)

box-shaped kernel (Leimar et al., 2008):

$$L(z, f, \sigma) = A_L \int_{-2f\sigma}^{+2f\sigma} e^{-(u+z)^2/2(1-f)\sigma^2} du, \quad (11)$$

where σ is the width and $0 < f < 1$ determines how much box-like is the function, $f = 0$ corresponding to Gaussian and $f = 1$ to completely box-like. Examples of L for $\sigma = 1$ and $f = 0.7, 0.9$ and 1 can be found in (Leimar et al., 2008). The disadvantage of this particular family is its implicit form as a definite integral. The normalization constant is chosen such that $L(0, f, \sigma) = 1$. The mathematical details are given in Appendix B.

We also investigated the conditions for disruptive selection under the alternative family of functions $L(z, f, \sigma)$. As discussed in Appendix B, the condition for disruptive selection in this case can also be written in the form $\sigma_c < \sigma_k h(f_c, f_k)$, with $h(f_c, f_k)$ given by Eq. (B.1). Although the details of $h(f_c, f_k)$ are different from those displayed by $h(\beta_c, \beta_k)$, the general features are clearly very similar (Fig. 2b).

3. Numerical simulations

We further explored a small part of the analytical parametric space with an individual-based asexual model, where each

individual is characterized by a trait value x ranging from -1.0 to $+1.0$ that determines its phenotype. Simulations were started with all individuals in the population having phenotype $x = +1.0$. Generations are discrete and individuals experience frequency-dependent competition for a unimodal resource distribution. At each time step t , each individual survives with probability

$$P(x) = \frac{1}{1 + \frac{r-1}{K(x)} n_{\text{effz}}(t)} \quad (12)$$

where r is the per capita number of offspring, $K(x)$ is the carrying capacity of phenotype x , $n_{\text{effz}}(t)$ is the effective population size that the individual experiences at time t

$$n_{\text{effz}}(t) = \sum_y C(x, y) n_y(t) \quad (13)$$

and $C(x, y)$ is the competition function (Bolnick and Doebeli, 2003). The sum runs over all possible trait values y and $n_y(t)$ is the number of individuals with trait value y . Survivors then reproduce and the number of offspring produced by each individual is given by a Poisson distribution with mean $r = 5$. The offspring's phenotype can differ from its parents phenotype with probability $\mu = 0.001$ and the amount of change is given by a Normal distribution with $\sigma = 0.05$. Evolutionary branching occurs when

the population evolves in two or more subgroups with different phenotypes.

The analytical results were confirmed by two sets of simulations. First, we fixed $K(x)$ as a Gaussian ($\beta_k = \beta^* = 0.658$) and varied $C(x, y)$ from Gaussian to increasingly more box-like shapes. As expected, when both functions are Gaussian speciation occurs when $\sigma_c < \sigma_k$ (Fig. 3a), further confirming Dieckmann and Doebeli's (1999) numerical results. For $\beta_c = 1.146$ speciation is facilitated as compared to the Gaussian case (Fig. 3b). As β_c increases further from this value it becomes increasingly more difficult to speciate (Fig. 3c,d). The linear behavior predicted by Eq. (9) is well reproduced by small values of σ_c and σ_k , although deviations are clearly seen for larger values, specially in Fig. 3b. This may indicate that the quadratic approximation used in the stability analysis of the equilibrium at $x = x_0$ [see Eq. (7)] is not sufficiently accurate, and that higher order corrections may be important. By increasing $\mu = 0.003$, however, branching occurred even for the higher values of σ_c and σ_k (simulations not shown), yielding a better approximation to the analytical results. Second, we verified that the condition $\sigma_c < \sigma_k$ for speciation also holds when both functions are box-like provided that $\beta_k = \beta_c$ (Fig. 4), showing that Dieckmann and Doebeli's (1999) result is a particular case of our model when both K and C are Gaussian.

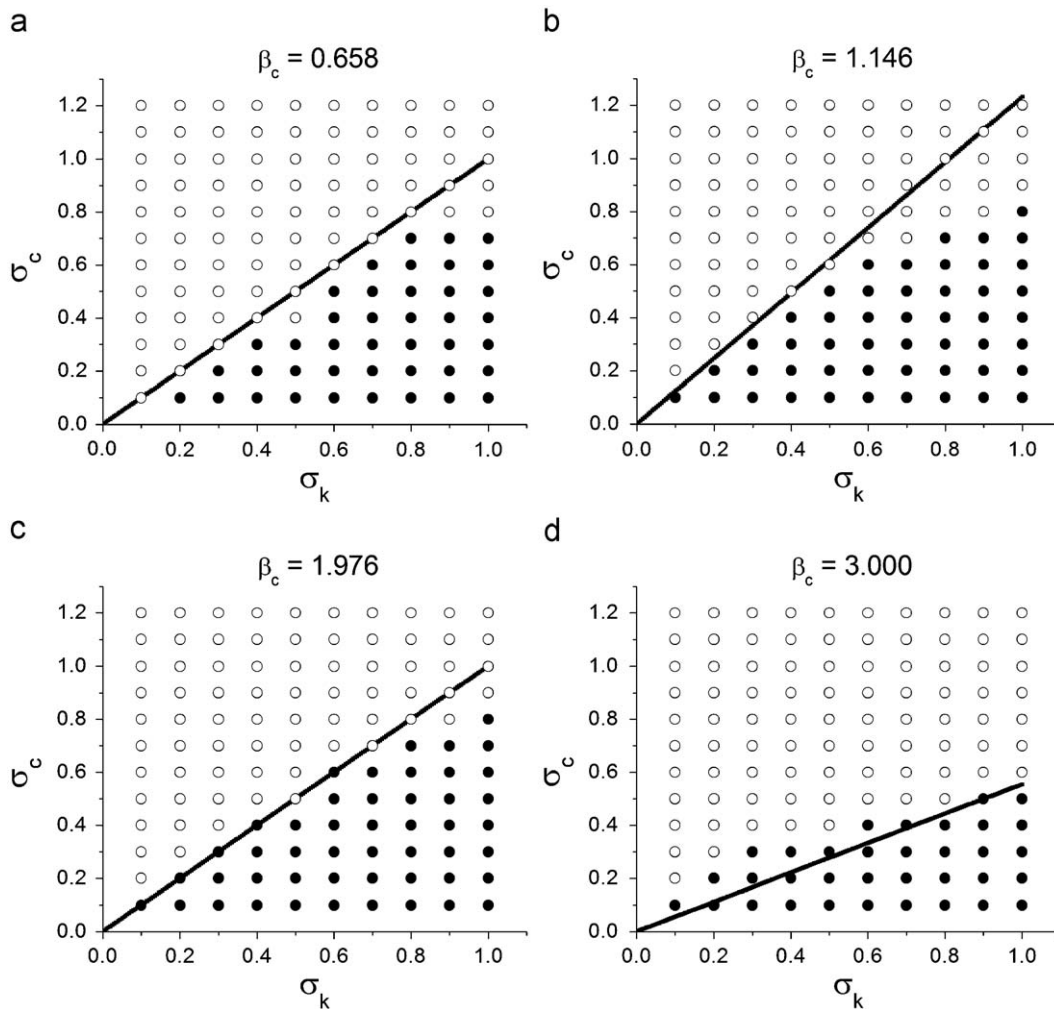


Fig. 3. Numerical simulations for a Gaussian-like carrying capacity function ($\beta_k = \beta^* = 0.658$) and different shapes of the competition function. As β_c increases the competition function becomes more box-like. (a) Gaussian competition function. Disruptive selection is first facilitated (b) and then becomes less likely as β_c increases (c, d). Filled circles indicate values of σ_c and σ_k where evolutionary branching occurred; empty circles indicate no branching (after 100,000 generations). Each circle represents the results of three simulations. The straight line shows the analytical prediction. Parameter values in simulations were $\mu = 0.001$, $K_0 = 500$, $r = 5$ and $\sigma = 0.05$.

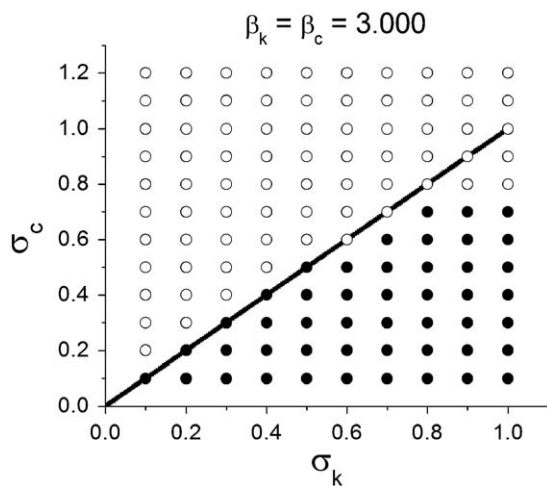


Fig. 4. Numerical simulations for $\beta_c = \beta_k = 3$. Filled circles indicate values of σ_c and σ_k where branching occurred, whereas empty circles indicate no branching (after 100,000 generations). Each circle represents the results of three simulations. The straight line shows the analytical prediction. Parameter values are the same as in Fig. 3.

4. Discussion

We found evidence that the occurrence of disruptive selection can be greatly affected by the shape of both the carrying capacity and competition kernels. If for example resources are normally distributed and the competition function is extremely box-like, disruptive selection will depend on very high levels of frequency dependence (very low σ_c). On the other hand, the likelihood of disruptive selection is also affected by the shape of the carrying capacity function. Extreme box-like resource functions coupled with Gaussian competition functions actually facilitate evolutionary branching (Fig. 2). It is thus the interaction between the shapes of the resource and the competition function that will ultimately determine the likelihood of disruptive selection. Our results, therefore, add to the growing literature showing that the shape of the resource and competition kernels can substantially affect the outcome of evolutionary models (Abrams et al., 2008b; Doebeli et al., 2007; Leimar et al., 2008).

Our findings seem to be general and not to depend on the particular family of box-like functions chosen. This is indicated by the fact that we found qualitatively similar results by investigating two different classes of box-like kernels (Fig. 2). We note that the class of kernels we propose here allows totally analytical solutions and offers an advantage in terms of mathematical simplicity as compared to the kernels used by Leimar et al. (2008). At first glance, however, there seems to be a contradiction between our results and those of Leimar et al. (2008). One of the main conclusions of their study was that when the carrying capacity function is Gaussian, box-like competition kernels induce phenotypic clustering, whereas our results indicate that evolutionary branching will be hindered in this scenario. This contradiction becomes even more striking if we notice that the values of the parameter f used by Leimar et al. (2008) to generate box-like kernels ($f = 0.7$ and 0.9) fall into the region in which disruptive selection is actually hindered (Fig. 2b). This apparent contradiction can be resolved if we note that Leimar's et al. (2008) is a spatially explicit model, in which individuals are distributed along an environmental gradient. In their model, the strength of intraspecific competition is determined both by phenotypic and spatial distance. Such spatial gradients are known to greatly facilitate pattern formation, because the emerging correlation between spatial location and phenotype increases the degree of

frequency dependence in the system (Doebeli and Dieckmann, 2003). Additionally, it is well known that kernels with sharp boundaries (e.g. box-like), whose Fourier transforms display negative regions, promote pattern formation in space (Sayama et al. 2002; de Aguiar et al. 2003). In the spatially explicit adaptive dynamic models, local adaptation leads to a correlation between geographical space and phenotype (Doebeli and Dieckmann, 2003; Leimar et al., 2008). Thus we posit that it is the clustering in geographical space caused by box-like spatial competition kernels that promotes clustering in phenotypic space via the correlation between geographical space and phenotype. Therefore, we conclude that extreme box-like competition kernels indeed facilitate evolutionary branching in spatially explicit models (Leimar et al., 2008), but will hinder it in the absence of spatial gradients (this study). It should also be mentioned that Leimar et al. (2008) investigated the parametric region in which selection acting locally was stabilizing— $\sigma_k < \sigma_0$, where σ_0 represents the width of the phenotypic competition kernel and is analog to our σ_c —, so that pattern formation can only occur along the spatial gradient. It would be interesting to extend their treatment to the case where local selection is disruptive ($\sigma_k > \sigma_0$) and investigate the effects of the shape of the kernels. We hypothesize that for low degrees of boxing, pattern formation would be greatly facilitated by the joint action of disruptive selection acting locally (recall that low degrees of boxing facilitate disruptive selection; Fig. 2) and clustering across the spatial gradient. In this case, each spatial cluster would be subdivided into two or more phenotypic clusters, each with a different phenotypic mode. Additionally, the phenotypic clusters would be scattered randomly over space within each spatial cluster. However, as the kernels became increasingly more box-like, disruptive selection will be hindered and a single spatial population should be found in each cluster.

There is now empirical evidence that intraspecific competition can cause diet variation so that individuals with different phenotype resort to different resources (Araújo et al., 2008; Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007; Swanson et al., 2003). In this scenario, competition is frequency dependent, which may drive disruptive selection in natural populations (Bolnick, 2004; Bolnick and Lau, 2008; Calbeek and Smith, 2007; Pfennig et al., 2007). Diet variation within populations seems to be a widespread phenomenon (Bolnick et al., 2003). How often this diet variation will lead to disruptive selection will depend, as shown by our study, on the shapes of carrying capacity and competition kernels.

Disruptive selection is known to be unstable on theoretical grounds (Roughgarden, 1979) and as a consequence has been downplayed as a transient and infrequent evolutionary phenomenon (Endler, 1986). However, if intraspecific competition is frequency dependent, disruptive selection may be stable (Abrams et al., 1993; Rosenzweig, 1978; Rueffler et al., 2006; Wilson and Turelli, 1986). Stable disruptive selection in turn may be an important evolutionary force in maintaining or increasing quantitative genetic variation (Bürger, 2002; Polechová and Barton, 2005; Roughgarden, 1972), causing sexual dimorphism (Bolnick and Doebeli, 2003) or even speciation (Bolnick, 2006; Bürger et al., 2006; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003; Doebeli et al., 2007). Regardless of the consequences of disruptive selection for natural populations, it is important to understand the ecological settings promoting or hindering it in the first place.

By investigating more box-like functions, we hope to approximate more realistic competition functions that reflect the more discrete structure of many resources. To the extent that intraspecific diet variation occurs as distinct dietary groups, with strong diet overlap within groups and weak overlap between groups

(Araújo et al., 2008), box-like functions may be more appropriate. The choice of Gaussian functions in most models of quantitative genetics and adaptive dynamics so far (Ackermann and Doebeli, 2004; Bolnick, 2006; Bolnick and Doebeli, 2003; Bürger et al., 2006; Dieckmann and Doebeli, 1999; Roughgarden, 1972; Taper and Case, 1985) has been based either on mathematical convenience or historical precedence of some classical models (MacArthur, 1970; MacArthur and Levins, 1967) whose stringent assumptions and biological realism have been object of criticism (Ackermann and Doebeli, 2004; Abrams et al., 2008a). It is now a task for empirical biologists to investigate the patterns of resource distribution and competitive interactions in natural populations that should dictate the kernels to be used in future models. These empirically motivated kernels, in turn, would help us to predict what populations are more prone to disruptive selection.

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Appendix A

The variance of $H(z, \beta, \xi(\sigma))$ given by

$$\text{var} = \frac{\xi^3(4\beta^2 + \pi^2)}{6\beta^2 \tanh(\beta)} = \frac{\sqrt{2}\beta^3\sigma^3(4\beta^2 + \pi^2)}{3\beta^2 \cosh^3(\beta^*) \tanh(\beta)} \quad (\text{A.1})$$

and its second derivative at $z = 0$ by

$$H''(0, \beta, \xi(\sigma)) = -\frac{2\beta^2}{\xi^2 \cosh^2(\beta)} = -\frac{\beta^2 \cosh^2(\beta^*)}{\sigma^2 \beta^{*2} \cosh^2(\beta)}. \quad (\text{A.2})$$

Notice that, for σ fixed and $\beta \rightarrow \infty$, the variance goes to a constant (proportional to σ^3) whereas the second derivative goes to zero. Here $\beta^* = 0.5 \ln(2 + \sqrt{3}) \approx 0.658$ (see text).

Appendix B

The normalization constant for $L(z, f, \sigma)$ is given by $(A_L)^{-1} = \sigma \alpha(f)$ where

$$\alpha(f) = \int_{-2f}^{+2f} e^{-u^2/2(1-f)} du.$$

The variance of L is given by $\sigma^2(1-f+4f^2/3)$ and varies only slightly from 1 to 4/3 as f is varied from 0 (Gaussian) to 1 (totally box-like). We also define the auxiliary function

$$\beta(f) = \frac{1}{1-f} \int_{-2f}^{+2f} u^2 e^{-u^2/2(1-f)} du$$

in terms of which the second derivative of L with respect to z calculated at $z = 0$ is given by

$$L''(0, f, \sigma) = -\frac{1}{(1-f)\sigma^2} \left(1 - \frac{\beta(f)}{\alpha(f)} \right).$$

Setting the competition function as $C = L(y-x, f_c, \sigma_c)$ and the resources kernel as $K = K_0 L(x-x_0, f_k, \sigma_k)$ the condition for

disruptive selection $R'' > 0$ [see Eq. (8)] can also be written in the form $\sigma_c < \sigma_k h(f_c, f_k)$ with

$$h(f_c, f_k) = \left[\frac{(\alpha(f_c) - \beta(f_c))}{(\alpha(f_k) - \beta(f_k))} \frac{(1-f_k)\alpha(f_k)}{(1-f_c)\alpha(f_c)} \right]^{1/2}. \quad (\text{B.1})$$

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