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Interim Report **IR-05-050**

Limiting Similarity Revisited

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Contents

Limiting similarity revisited

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ABSTRACT

We reinvestigate the validity of the limiting similarity principle via numerical simulations of the Lotka-Volterra model. A Gaussian competition kernel is employed to describe decreasing competition with increasing difference in a one-dimensional phenotype variable. The simulations are initiated by a large number of species, evenly distributed along the phenotype axis. Exceptionally, the Gaussian carrying capacity supports coexistence of all species, initially present. In case of any other, distinctly different, carrying capacity functions, competition resulted in extinction of all, but a few species. A comprehensive study of classes of fractal-like carrying capacity functions with different fractal exponents was carried out. The average phenotype differences between surviving species were found to be roughly equal to the competition width. We conclude that, despite the existence of exceptional cases, the classical picture of limiting similarity and niche segregation is a good rule of thumb for practical purposes.

KEY WORDS: limiting similarity, niche segregation, interspecific competition, Lotka-Volterra

INTRODUCTION

Limiting similarity is a central, but controversial tenet of community ecology. The seminal paper of MacArthur and Levins (1967) was among the most influential theoretical papers in ecology. It stated that phenotype difference on the scale of the competition width is required between coexisting species. Since then, the assertion and the related figure became an indispensable part of any ecology textbook (Begon et al. 1996, Case 2000, Krebs 2001).

While the empirical relevance of limiting similarity was clearly demonstrated in several studies (see e.g. Schluter 2000a,b), its wider context, “competition theory”, has gradually fallen out of favor since its inception in the sixties. It has become the prevailing view that importance of competition, and henceforth of limiting similarity, was originally overestimated; other types of interaction, like predation and disturbance, has a non-negligible role in shaping communities (Begon et al. 1996). On the other hand, even more recently, other researchers stress that the effect of predation is very analogous to resource limitation; an attempt to revival of niche theory as a “central organizing aspect of ecology” was made on this basis (Leibold 1995).

Decline of competition theory overshadows the fact that the real prediction of it has never been made sufficiently clear. Competitive exclusion (Gause 1934, Hardin 1960) is often interpreted in the narrow, but mathematically clear, sense as a statement that the number of coexisting species cannot be larger than the number of resources, or “limiting factors” (e.g. Levin 1970, Armstrong and McGehee 1980). Partitioning of a resource continuum cannot be discussed this way, as the continuum represents an infinite number of different resources. Then, we either have a limiting similarity type statement, or competitive exclusion predicts nothing (cf. Rosenzweig 1995).

MacArthur & Levins (1967) used the Lotka-Volterra competition model for demonstrating limiting similarity in resource partitioning. However, the more detailed analysis of the model by May and MacArthur (1972) established no clear lower bound of similarity. While May (1973) rescued the principle by referring to environmental fluctuation as a necessary ingredient of the limiting similarity argument, the very same result signaled the end of the road for limiting similarity according to Rosenzweig (1995): "… the result (limiting similarity) was quicksand that trapped the energies of community ecologists for more than ten years and nearly killed the subdiscipline".

Surprisingly, the most powerful mathematical counterexample for limiting similarity is not widely recognized in the ecological literature. Roughgarden (1979) demonstrated, that even a *continuum* of species is able to coexist in the Lotka-Volterra model. While this effort was intended to describe polymorphism within a species, it can be interpreted also in a community ecology context, as recognized by Maynard Smith and Szathmáry (1995).

Investigations going beyond the Lotka-Volterra model leaded to no firm conclusion, either (Abrams 1983, 1988). On the one hand, it seems to be clear that some kind of limit of similarity must exist in any model. On the other hand, no general result of this type has emerged.

More recently, following the lead by Sasaki and Elner (1995), Gyllenberg and Meszéna (2004) showed that any model, which allows continuous coexistence, is necessarily structurally unstable, i.e. an arbitrarily small modification of the model might be able to destroy the continuous coexistence. The continuous coexistence in Roughgarden's model will not survive a small perturbation of the carrying capacity curve. Meszéna et al. (submitted) showed that similarity of coexisting species decreases the tolerance of the assemblage towards the external environmental parameters. That is, similarity decreases the chance of coexistence. While these qualitative analytical results are very general, they do not predict any specific lower bound of similarity.

After many pros and cons, the single most important question, i.e. whether limiting similarity has any practical relevance, has remained unsolved. Here we intend to check the expectation that coexisting species should differ roughly according to their competition width. More specifically, assuming Gaussian competition functions with a standard deviation σ, can we generally expect , as a rule of thumb, 2σ distances between coexisting species? We resort to a comparative study to answer this question. We investigate the cases, which support limiting similarity, and the cases, which defy it, in the same context. As both the existence and the non-existence of limiting similarity were originally demonstrated in the Lotka-Volterra model, we use this framework also. We repeat the same numerical experiment with different choices for the carrying capacity function. The Gaussian one, corresponding to Roughgarden's counter-example with the continuous coexistence, will be considered as the reference case.

MODEL DEFINITION

We start from the familiar Lotka-Volterra competition model for several species, which we write in the form

$$\frac{dn_i}{dt} = \alpha_i n_i \left(K_i - \sum_{j=1}^{L} a_{ij} n_j \right), \tag{1}$$

where L stands for the number of species, $i \in \{1,2,\ldots,L\}$ and n_i denotes the density of the i^{th} one. The elements of the competition matrix are denoted by a_{ij}; $a_{ii} = 1$ is assumed for all i. K_i is the carrying capacity for species i. As the constant α_i is unimportant for our purpose, $\alpha_i = 1$ will be chosen for each species.

Each species is characterized by a phenotype variable x_i. Then, K_i and a_{ij} are determined by the phenotype and the difference between phenotypes, respectively. Eq. (1) takes the form

$$\frac{dn_i}{dt} = n_i \left(K(x_i) - \sum_{j=1}^{L} a(x_i, x_j) n_j \right). \tag{2}$$

We suppose decreasing competition with increasing phenotype difference, according to the usual Gaussian form

$$a(x,y) = \exp \frac{-(x-y)^2}{2\sigma^2}. \tag{3}$$

The twice standard deviation 2σ of this Gaussian will be referred to as competition width. The carrying capacity function $K(x_i)$ will be specified in each example separately.

When the number of species is large and the difference between neighboring phenotypes is small, we use the continuous approximation

$$\frac{dn(x)}{dt} = n(x)\left(K(x) - \int a(x,y)n(y)dy\right), \tag{4}$$

where $n(x)$ stands for the density of species with phenotype x. Then the equilibrium condition reads as

$$K(x_i) = \sum_{j=1}^{L} a(x_i, x_j) n_j \, , \tag{5}$$

or

$$K(x) = \int a(x, y) n(y) dy \, . \tag{6}$$

In equilibrium, these equations should hold for all species present in non-zero density.

For each choice for the carrying capacity function $K(x)$, we integrated Eq. (2) numerically with time steps of $\Delta t = 0.1$. Simulations were initiated with 1001 species, evenly distributed within the phenotype interval $[-1,1]$ with equal densities of 0.01. The outcome of competition was evaluated at $t = 10000$. At this time point the growth rates were wery close to zero. The number of coexisting species was assessed by counting species that were present and exhibited nonnegative growth at $t = 10000$. This criteria was applied to exclude populations which were bound to extinction, but eventually existed at that time.

RESULTS

Roughgarden's example for continuous coexistence

Roughgarden's (1979) example employs the Gaussian carrying capacity function

$$K(x) = \exp\frac{-x^2}{2\omega^2} \tag{7}$$

where ω denotes the half-width of this curve. Then the Gaussian species distribution

$$n(x) = \frac{\omega/\sigma}{\sqrt{2\pi\left(\omega^2 - \sigma^2\right)}}\exp\frac{-x^2}{2\left(\omega^2 - \sigma^2\right)} \tag{8}$$

is an equilibrium solution of Eq. (4), provided that $\omega > \sigma$. In this case, infinitely many arbitrarily similar species may coexist along the phenotype axis.

We reproduced this analytical result numerically (Fig. 1). All of the populations, that were present initially, survived. In agreement with Eq. (8), the equilibrium distribution of the population densities followed a Gaussian curve. Increased competition width σ led to a narrower distribution of densities. Obviously, when $\omega < \sigma$, i.e. when the carrying capacity is narrower than the competition width, only the species $x = 0$ survives (not shown).

Other simple carrying capacity functions: no continuous coexistence

The rectangular function

$$K(x) = \begin{cases} c, & if \quad x \in (-b; b) \\ 0, & if \quad x \notin (-b; b) \end{cases} \tag{9}$$

which is zero outside an interval, is the next simple choice for the carrying capacity curve. In contrast to Roughgarden's case, most of the populations go extinct. Only a very limited number of species coexist at equilibrium (Fig. 2).

The average phenotype difference between adjacent survivors can be calculated by dividing the total phenotype interval with the number of coexisting species. As plotted on Fig. 3, this difference increased with σ linearly with great accuracy. The steepness of the linear regression line was found to be 1.82. That is, in agreement with the classical expectation, the coexisting species were spaced roughly by the competition width 2σ.

It is easy to interpret this result in qualitative terms. The two species, which are located at the two ends of the livable range, gain advantage from the lack of competitors on one of their sides. Then, competition by these high-density species causes extinction within their range of competition. Two empty ranges emerge which, in turn, give advantage to two species, located at the inner ends of the empty ranges. And so on, a discrete distribution emerges.

The perturbation, that renders the coexistence of infinitely many strategies impossible does not have to be so abrupt. We get similar results if $K(x)$ is a sum of two Gaussian functions as

$$K(x) = \exp\frac{-x^2}{2\omega_1^2} + \alpha\exp\frac{-(x-\mu)^2}{2\omega_2^2} \tag{10}$$

with $\omega_1 > \sigma > \omega_2$. The first Gaussian, when alone, would maintain a continuous coexistence. In contrast, the second one supports a single phenotype, namely $x = \mu$. Fig. 4 demonstrates the emerging species distribution. The second term of Eq. (10) gives an advantage to species $x = \mu$. The high density of this species causes extinction of each species within its range of competition. Then, the empty ranges on both sides of species $x = \mu$ give advantage to the two species next to these ranges. And so on, the competitive advantages and disadvantages build up gradually and a discrete species distribution emerges.

The realistic case: Fractal-like carrying capacity functions

While the smooth Gaussian function in the role of the carrying capacity curve leads to continuous coexistence, a function with abrupt changes seems to result in limiting similarity in the usual sense. These extremes cannot tell us, however, what is the *typical* situation.

As a representative of a more natural function, we investigate fractal-like perturbation of the Gaussian carrying capacity. We chose

$$K(x) = \exp\frac{-x^2}{2\omega^2}\left(1 + f(x)\right) \tag{11}$$

where the perturbation term

$$f(x) = k\sum_{i=1}^{L}\beta_i \cos(\gamma i x + \varphi_i) \tag{12}$$

consists of periodic components with random phases. The parameters k and γ are constants. The amplitude of the i^{th} periodic component is

$$\beta_i = 1/i^{\nu} \; . \tag{13}$$

The phases φ_i were chosen randomly for each simulation run. The exponent η characterizes the fractal properties. $\eta=0$ for a white noise; Brownian motion is characterized by $\eta=1$.

We stress that, since φ_i s remain constant during a single run of the simulation, the random choice of them does not introduce stochasticity into the dynamics. Instead, this randomization ensures that each simulation uses a different carrying capacity curve, characterized by a common fractal exponent. Accordingly, each data point in Figures 5 and 6 represents an average over a class of models.

Fig. 5 shows the results with $\eta=0, 1, 1.5$ respectively. All simulations ended up with survival of a limited number of species. The number of species at equilibrium and, consequently, average phenotype distances change with η. The number of coexisting species was averaged over 50 simulations, differing in the random phases, for each η and σ combination (Fig. 6).

Distances increase with σ in all cases and the slope of the fitted line remains in the range $1.9\sigma - 2.6\sigma$. The departure from the linear dependence on Fig. 6 is related to the fact that σ is not small, compared to the total phenotype interval, at the right end of the horizontal scale.

DISCUSSION

In this paper we have reconsidered the age-old problem of limiting similarity in a Lotka-Volterra model context. The need for this re-evaluation came from the fact that in different investigations the very same model was used for both the justification and falsification of this principle. Initiating the simulations with many equally abundant species, closely packed along the phenotype variable, we observed whether a limiting similarity type of species distribution shows up. In line with theoretical predictions, a yes-and-no picture emerged. As the issue seemed to be related to the smooth-or-not nature of the carrying capacity function, we investigated “natural”, i.e. fractal-like, functions with different fractal exponents. We conclude that, in spite of the existence of exceptional cases, the classical picture of limiting similarity prevails, by and large. Especially, as a rule of thumb, the typical distance between coexisting species is near to the competition width 2σ. This result seems to be quite robust: We tested very different carrying capacity functions, including families of fractal-like ones.

Nevertheless, the details of the final distribution of the species in a specific simulation do not seem to be very regular. The surviving species are not exactly equidistant. Their abundances apparently depend on the exact shape of the carrying capacity curve as well as on which species survived. In most of the cases, the initial distribution is so far from the final one, that there is no reason to suppose that the limiting-similarity-type outcome depends on the initial distribution. On the other hand, in a specific simulation there is no reason to expect the exactly same final distribution for a different initial one.

In a specific simulation run, any species either equilibrates with a finite abundance, or dies out. Its growth rate converges to zero in the first case, but remains negative in the second one. That is, in the final state the growth rates of all extinct phenotypes are negative. Consequently, the resulting species assemblage is stable against invasion when any phenotype, which is not present, is (re)introduced in small density (cf. Jansen and Mulder 1999, Bonsall et al. 2004). On the other hand, the evolutionarily stable community/assemblage needs not be unique, i.e. it may depend on the initial conditions.

Obviously, our initial condition is far from being realistic. In the real life, there is no such supply of an almost continuous set of species. Our point exactly is that limiting similarity emerges even from starting so irrealistically far from that outcome.

Our simulation results are consistent with the empirical findings. On the one hand, character displacement studies (Schluter 2000a,b) demonstrated segregation of coexisting species in resource related traits. Note, that similarity in the environmental requirements is also necessary for coexistence (cf. Leibold 1995, Chase and Leibold 2003), so investigations based of phylogenetic relationships (e.g. Webb 2000) will not necessarily demonstrate any correlation between coexistence and dissimilarity. On the other hand, the specific arrangement of species of a community is influenced by many factors, including the initial conditions, and is not predictable via simple rules.

Limiting similarity is not without exceptions. In some sense the non-existence of an absolute and model-independent lower bound of similarity is trivial; in a parameter-rich model one can always adjust the parameters to equalize the growth rates of the species. Consequently, any set of strategies may be able to coexist, irrespective of their similarity. The real issue of coexistence starts when one refuses to fine-tune parameters. That is, the real question is whether the coexistence is robust against parameter changes.

This triviality was noted first by May and MacArthur (1972), May (1973). They varied the carrying capacities of two, or three, species. The smaller the interspecific competition, the wider the range of the carrying capacities, which enabled coexistence, was. As interpecific competition is supposedly related to the ecological difference between species, this result means that the coexistence becomes more robust with increasing difference. That is, limiting similarity is a quantitative issue. Similarity does not exclude coexistence, but makes it less likely. This conclusion has been generalized beyond the Lotka-Voltarra context by Meszéna et al. (submitted).

Decreased competition between dissimilar species has a regulating effect on their coexistence. Suppose that a perturbation affects species *A* adversely, but not *B*. Then the population size of *A* starts to decline. If the intraspecific competition is larger than the interspecific one, the decreased population size of *A* improves the living conditions of *A* in a larger extent, than that of *B*. This, in turn, compensates species *A* for the relative disadvantage it has gained by the original perturbation. Large niche overlap reduces this regulatory effect as both species gain roughly the same advantage from the decline of one of them.

The problem of continuous coexistence is a related issue. For *any* given form of the competition kernel $a(x, y)$ and for *any* prescribed species distribution $n(x)$, the equilibrium condition (Equ. (6)) determines a carrying capacity function $K(x)$, which allows the coexistence with this specific species distribution. However, as coexistence of similar strategies is possible only for a narrow range of parameters, one may reasonably presume that coexistence of a continuum of species should be sensitive to an arbitrarily small perturbation. In fact, this is the case.

Structural instability of Roughgarden's example for continuous coexistence was essentially noted already by Sasaki and Ellner (1995). Their context was entirely different; they considered mixed strategies in a fluctuating environment. Nevertheless, their criterion for an ESS mixing distribution was identical to the equilibrium condition for coexisting strategies in the Lotka-Volterra model. Consequently, their proof of the structural instability of any ESS, which mixes a continuum of pure strategies, translates to the structural instability of any Roughgarden’s type of continuous coexistence. Geritz (1995, 1999) and Meszéna and Szathmáry (2001) provided additional models in which continuous coexistence appears, but only under structurally unstable circumstances. Gyllenberg and Meszéna (2004) generalized these results be proving the structural instability of *any* model, which allows continuous coexistence.

Haccou and Iwasa (1995, 1998) demonstrated a kind of smoothness in the abrupt loss of the continuous solution for the mixed strategy problem of Sasaki and Ellner (1995). For small perturbations, the emerging discrete distribution follows closely the original continuous one. No similar general analysis is available for the coexistence problem. Still, it is sensible to suspect that the transition from continuous to discrete coexistence is smooth, again. That is, small perturbation of Roughgarden's model probably allows coexistence of discrete, but very similar, strategies. One may conjecture that the minimal distance between coexisting species grows up from zero continuously with the increasing departure from the strictly Gaussian carrying capacity function. We did *not* attempt to follow this transition. Instead, we compared the strictly Gaussian case with the distinctly different ones and studied, what determines the lower bound of similarity. In all cases we tried, we found that the minimal phenotype difference is of the order of the competition width.

The mechanism leading to limiting similarity is transparent in the simple cases we presented. Local maxima of the carrying capacity curve gives advantage to some phenotypes. In turn, these favored phenotypes impose competitive burden on the neighboring types along the phenotype axis via competition. That is, the not-very-smooth nature of the carrying capacity curve is essential for limiting similarity. In this context, it was essential to study choices somewhere in between the very smooth and the sharply changing: the fractals.

We employed fractal functions to mitigate a serious problem of mathematical ecology. In the “strategic” level of modeling (cf. Czárán 1998) the model ingredients are chosen according to their simplicity, instead of their empirical fidelity. The expectation here is, that the simpler the choice is, the lesser the danger of introducing artefactual details. Unfortunately, the ingredient functions, which are the simplest choices from mathematical point of view, are often very artificial. For instance, they are either unnaturally smooth, like a Gaussian function, or unnaturally discontinuous, like a step function.

Fractals and fractal-like functions are ubiquitous in nature (Mandelbrot 1983). If a shape is influenced by many processes, probably the system will not be dominated by a single, or a few, characteristic scales (Beran 2004). A scale-independent, self-similar pattern may emerge as a result. Such shape is represented by an autocorrelation function, which decays according to a power law. The “fractal” exponent of the power law characterizes the relative strength of the shorter and longer correlations. Self-similar patterns have been reported in many biological systems at all level of the organization (Burrough 1981, Liebovitch and Sullivan 1987, Shlesinger and West 1991, Gunnarsson 1992, Harte et al. 1999). The carrying capacity function is a result of a complicated interplay between the ecological interactions and the physiological constraints, i.e. the genotype-phenotype map. The process is likely to involve many random components acting on multiple time scales, leading to multiscaled randomness (Hausdorff 1996). As there is no reason to expect any characteristic scale in such a carrying capacity function, it is reasonable to endow it with fractal-like properties, instead.

The fractal exponent ν characterizes the relative contributions of the different scales. The larger the exponent is, the smaller the amplitude of small scale perturbations. That is, a smaller ν represents a more rugged carrying capacity curve, while a larger one represents a smoother one. Varying the fractal exponent and choosing different phases in Eq. (12) allows us to sweep through a representative variety of possible carrying capacity functions. It is remarkable that our findings were essentially independent of the fractal exponent; fractal-like carrying capacity functions with different exponents have uniformly led to limiting similarity with roughly $(2.3 \pm 0.3)\sigma$ distance between coexisting species, i.e. slightly higher than competition width.

The Lotka-Volterra model is often criticized as “phenomenological”, as opposed to the mechanistic models. Notwithstanding the success of mechanistic level of modeling (cf. Tilman 1982), it did not lead any consistent understanding on the issue of limited similarity. In particular, investigations hinted mechanism-dependence neither for the validity of the limiting similarity principle nor for the specific lower bound of similarity.

In the contrary, the universality across different mechanisms (e.g. competition and predation) was stressed by Leibold (1995), Chase and Leibold (2003). Moreover, no principal difference between the phenomenological and mechanistic model is expected because the Lotka-Volterra model can be derived from a mechanistic underpinning (Yodzis 1989). Moreover, in any model one can locally linearize the density-dependence, which leads to a Lotka-Volterra model. Consequently, any issue, like linear stability and robustness, which can be studied via small perturbations, should be the same in the original model and in its Lotka-Volterra approximation.

While Abrams (1983), Yodzis (1989) stress the model dependence of limiting similarity, analytic investigations (Gyllenberg and Meszéna 2005, Meszéna et al. submitted) testify for the generality of some basic issues. First, simple counter-examples for limiting similarity exist already in the very model, which was used to demonstrate the principle. Second, both structural instability of continuous coexistence and decreasing robustness of coexistence for increasing similarity is proven generally. This is the context, in which detailed numerical investigations make sense: We have reasons to hope for the general relevance of our conclusions.

In particular, competition kernels, other than the Gaussian, are not expected to lead to essentially different results. It is clear, that the carrying capacity curve, which allows continuous coexistence, can be constructed for any competition function via the equilibrium equation (Eq. (6)). An infinitesimal perturbation of this carrying capacity will destroy the continuous coexistence, again (Gyllenberg and Meszéna 2004). Note that the standard deviation is not necessarily a good measure of the competition width for competition functions other than the Gaussian (Yodzis 1989).

The misleading exceptionality of Roughgarden's model exhibits a serious methodological problem of ecological modeling. Nevertheless, the careful investigation of the Lotka-Volterra model in the context of analytical investigations provides a strong case for the practical relevance of the principle of limiting similarity.

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FIGURE LEGENDS:

FIGURE 1. Species distribution with Gaussian carrying capacity function for different competition widths 2σ. On each plot, dashed line depicts the shape of the carrying capacity curve, normalized to a given height. Black region denotes the population distribution. Variance of the bell-shaped species distribution decreases with increasing competition width. Parameters: ω=0.3; σ=0.04, 0.08, 0.16 in sub-figures a, b, c, respectively.

FIGURE 2. Species distribution with rectangular carrying capacity function for different competition widths 2σ. Only a finite number of species coexist. The number of coexisting species decreases with increasing σ. Parameters: b=0.6, c=5, σ=0.04, 0.08, 0.16 in sub-figures a, b, c respectively.

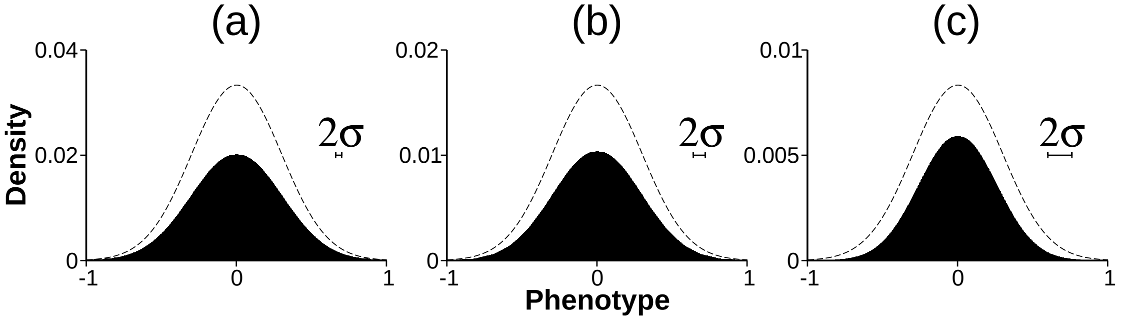
FIGURE 3. Phenotype difference between adjacent survivors as a function of σ and the fitted linear regression line (solid line) for rectangular carrying capacity. Phenotype difference values are calculated as the number of species at equilibrium divided by the length of the phenotype interval. The steepness of the linear regression line is 1.82.

FIGURE 4. Species distribution for different competition widths 2σ, when the carrying capacity function is composed from two Gaussians. Competition width increases from left to right; σ=0.04, 0.08, 0.16 in subfigures a, b, c respectively. Other parameters: ω_1=0.3, ω_2=0.03, α=0.1, μ=-0.3.

FIGURE 5. Species distribution with fractal-like carrying capacity function for different fractal dimensions η and competition widths 2σ. The η value increases from the top down: (a-c) η=0, (d-f) η=1.0, (g-i) η=1.5. σ increases from left to right for each η value; (a, d, g) σ=0.02, (b, e, h) σ=0.04, (c, f, i) σ=0.08. ω=0.3 in all cases.

FIGURE 6. Average phenotype differences between adjacent survivors p as a function of σ with fractal-like $K(x)$. Difference values were averaged over 50 simulations with different random choices for the phases. Other parameters: ω=0.3, (a) η=0, (b) η=1.0, (c) η=1.5. A linear regression line (solid line) was calculated for each η (data points, denoted by empty circles, were ignored). Slopes of regression lines are 2.64, 1.97, 1.99, respectively.

Figure 1.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(b)
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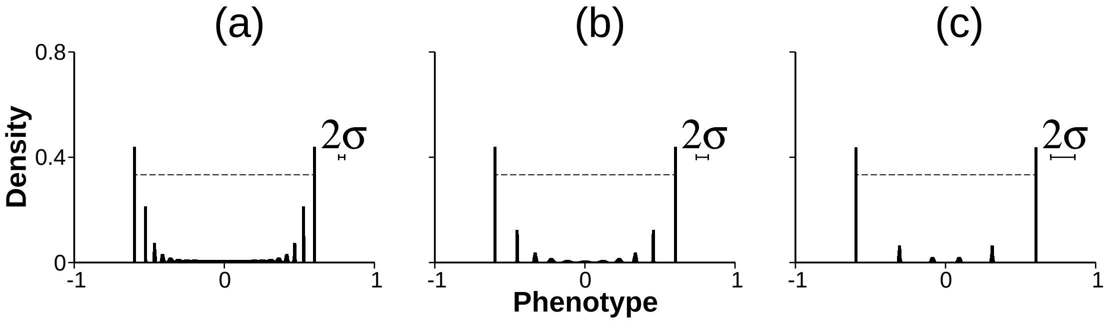
Figure 2.



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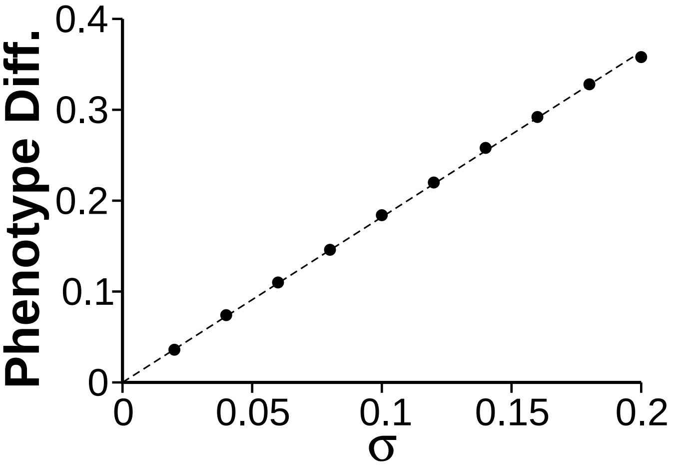

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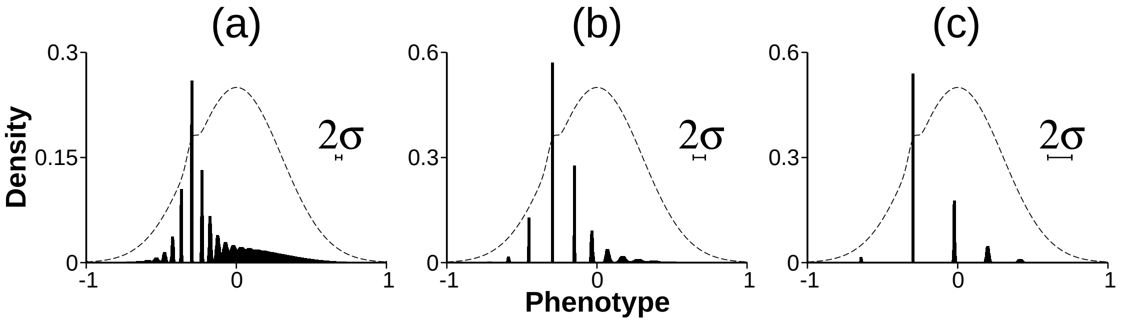
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(b)
(c)
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2σ
2σ
2σ

Figure 5.

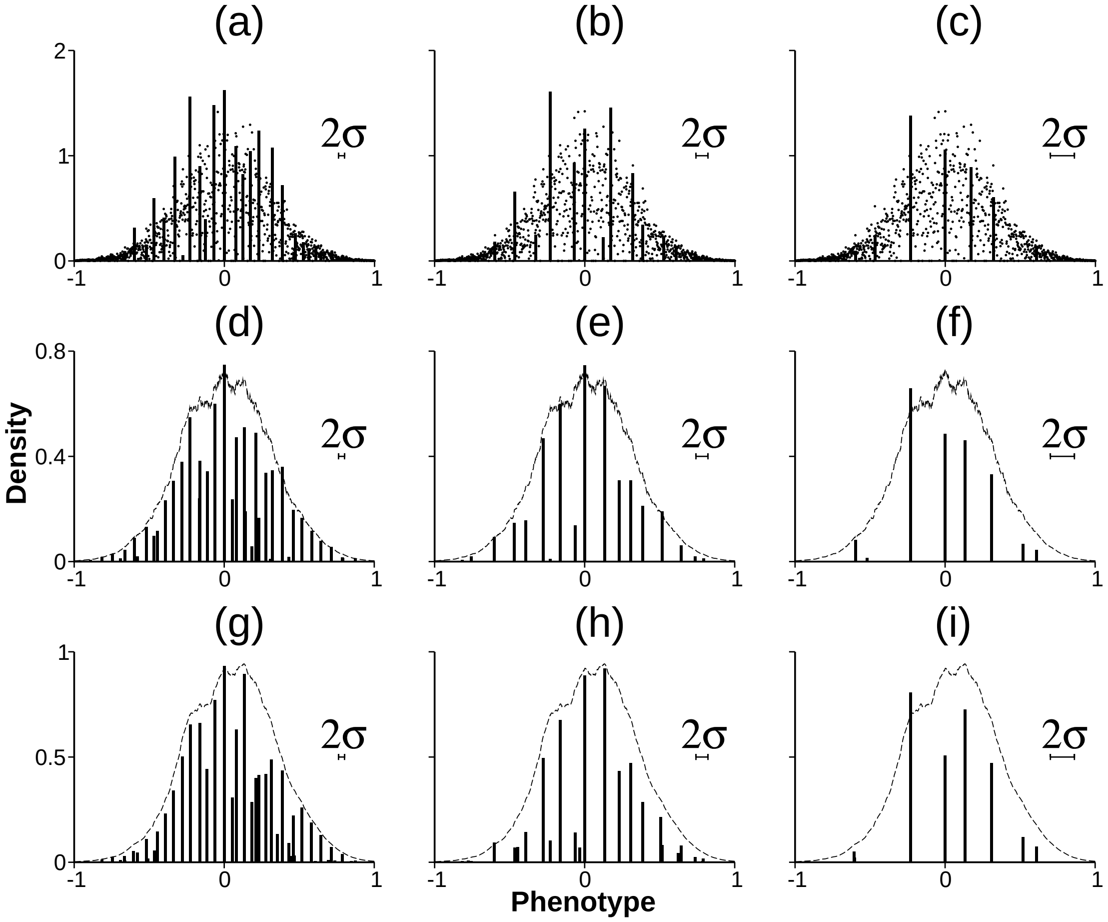

Figure 6.