International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report IR-12-072

Size-dependent mortality and competition interactively shape community diversity

Barbara Taborsky
Mikko Heino
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Pavel Kabat
Director General and Chief Executive Officer

February 2015

Size-dependent mortality and competition interactively shape community diversity

Barbara Taborsky[1,2], Mikko Heino[2,3,4], and Ulf Dieckmann[2]

[1]Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50A, CH-3032 Hinterkappelen, Switzerland; (*barbara.taborsky@iee.unibe.ch*)

[2]Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria (*dieckmann@iiasa.ac.at*)

[3]Department of Biology, University of Bergen, Box 7803, NO-5020 Bergen, Norway (*mikko.heino@bio.uib.no*)

[4]Institute of Marine Research, Box 1870 Nordnes, NO-5817 Bergen, Norway

Running title: Diversity through body size evolution

Keywords: model, body size evolution, life history, polymorphism, adaptive dynamics

Correspondence:

Barbara Taborsky, Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50A, CH-3032 Hinterkappelen, Switzerland;

e-mail: *barbara.taborsky@iee.unibe.ch*

tel: +41 31 631 9157

fax: +41 31 631 9141

Abstract

Body size is recognized as a major factor in evolutionary processes mediating sympatric diversification and community structuring. Life-history types with distinct body sizes can result from two fundamental mechanisms, size-dependent competition and size-dependent mortality. While previous theoretical studies investigated these two processes in separation, the model analyzed here allows both selective forces to affect body-size evolution interactively. Here we show for the first time that in the presence of size-dependent competition, size-dependent mortality can give rise to multiple, coexisting size morphs representing the final outcomes of evolution. Moreover, our results demonstrate that interactions between size-dependent competition and mortality can create characteristic abrupt changes in size structure and non-monotonic patterns of biological diversity along continuous and monotonic environmental gradients. We find that the two selective forces differentially affect the body-size ratios of coexisting morphs: size-dependent competition results in small and relatively constant ratios, whereas size-dependent mortality can open niches for morphs that greatly differ in body size. We show that these differential effects result in characteristic distributions of size ratios across communities, which we suggest can help detect the concurrent action and relative influence of size-dependent competition and mortality in nature.

Keywords: model, body-size evolution, life history, polymorphism, adaptive dynamics

Introduction

Community ecologists have long been interested in understanding the mechanisms underlying the formation of communities, but have only recently focused attention on the role of adaptation as one of those mechanisms (e.g., Caldarelli et al. 1998, Drossel et al. 2001, McKane 2004, Dieckmann and Ferrière 2004, Loeuille and Loreau 2005, Ito and Ikegami 2006, Dieckmann et al. 2007, Ito and Dieckmann 2007). Several evolutionary models have identified body size as a key causal factor for sympatric biological diversification and subsequent community structuring (e.g., Geritz et al. 1999, Day et al. 2002). In particular, Loeuille and Loreau (2005) and Brännström et al. (2011) found that when body size determines inter-individual interactions, complex food webs can evolve from a single ancestor through the combination of gradual adaptive evolution with adaptive radiation in body size.

In general, the coexistence of phenotypes that differ in body size can be achieved by two different mechanisms. First, body-size differences may allow interacting populations to evade competition by engaging in differential resource utilization (e.g., Wilson 1975, Robertson 1998). Furthermore, if the impact of competition diminishes sufficiently fast with increasing size difference, competition can give rise to the adaptive divergence of body sizes in communities in which size differences did not previously exist (e.g., Dieckmann and Doebeli 1999, Geritz et al. 1999, Claessen and Dieckmann 2002, Loeuille and Loreau 2005, Yoder and Nuismer 2010).

Second, it has been shown that size-dependent mortality readily induces alternative equilibria of body-size evolution (Ratner and Lande 2001, Day et al. 2002, Taborsky et al. 2003, Gårdmark and Dieckmann 2006). A life-history strategy with prolonged juvenile growth may allow individuals to reach a mortality refuge at large body size before the onset of reproduction; this involves a potentially long reproductive lifespan, but comes at the expense of a high risk of dying before attaining adulthood. Conversely, a life-history strategy with short juvenile growth period, implying a small adult body size, maximizes the chance of reaching adulthood, but does so at the expense of a short reproductive lifespan (Taborsky et al. 2003). Previous models suggest that this mechanism can explain body-size and life-history diversity among different populations (Taborsky et al. 2003, Gårdmark and Dieckmann 2006). As yet it has not been explored, however, under which conditions size-dependent mortality can result in the stable coexistence of alternative life-history strategies in a single community.

The impact of frequency-dependent competition between size morphs (e.g., Geritz et al. 1999, Loeuille and Loreau 2005) and size-dependent mortality (e.g., Ratner and Lande 2001, Day et al. 2002, Taborsky et al. 2003) on life-history diversity has so far been systematically explored only in separate models. In the present study, both selective forces are varied and affect body-size evolution jointly. This better reflects the conditions met in natural communities, where competitive and predator-prey interactions jointly determine the success of differently sized morphs (Beaugrand and Zayan 1985, Robertson 1998). We find that size-dependent competition allows for the ‘robust’ coexistence of different size morphs created by size-dependent mortality, so that these coexisting morphs represent final outcomes of community evolution. Remarkably, the interplay between these two diversity-enhancing mechanisms results in more complex patterns of phenotypic diversity along continuous ecological gradients than can be achieved by these mechanisms operating in isolation.

Model

Our goal is to explore community diversification driven by size-dependent mortality and competition. We consider life histories with linear juvenile growth and no adult growth, resulting in a determinate growth pattern. An adult individual can therefore be characterized by its adult body size s_{A}, which equals its size at maturation, and is the trait that can evolve in our model. Mortality affects both juveniles and adults, and is assumed to decline with body size according to exponential functions, whose monotonic slopes and resultant absence of inflection points ensure that size niches are not simply created by step-like changes in size-dependent mortality. We assume that competition affects only adults, which compete about resources needed for reproduction. Competition is assumed to decline with increasing differences in body size according to symmetric normal functions, whose dependence on differences alone ensures that there are no body sizes that are a priori competitively superior to others. Below, we describe in turn how we model growth, mortality, fecundity, and competition, before we evaluate the resultant lifetime reproductive success of size morphs.

Growth

Life-history models with full flexibility in how individuals allocate surplus energy between growth and reproduction often predict optimal life histories with determinate growth and the absence of energy allocation towards reproduction during the juvenile period (e.g., Taborsky et al. 2003). This allows us to simplify the model by Taborsky et al. (2003) by considering only life histories with determinate growth. The modeled life cycle thus consists of a juvenile period followed by adulthood with continuous reproduction and no further growth. In other words, all accrued surplus energy is allocated to somatic growth in juveniles and to reproduction in adults. This implies that the adult size s_A of a morph equals its maturation size**.** When analyzing an optimality model with these simplifying assumptions, we recover the same, wedge-shaped region of bistability in adult body size found by Taborsky et al. (2003), who analyzed a model with no predefined constraints on growth patterns and with pulsed reproduction.

An individual's weight w depends on its size s according to the allometric relationship $w = \alpha\, s^{\gamma}$, where α is a scaling constant and $\gamma = 3$ is the allometric exponent (changes in γ have no qualitative effect on results as long as $\gamma > 1$; Taborsky et al. 2003). The somatic growth of juveniles is linear in size and occurs at rate g. This implies maturation at age $(s_A - s_B)/g$ and a size-specific weight-production rate of $g\,\alpha\,\gamma\, s^{\gamma-1}$.

Mortality

The instantaneous mortality rate depends on body size s and is composed of a size-independent component and a negatively size-dependent component,

$$m(s) = m_\mathrm{i} + m_\mathrm{d} \exp(-s/s_0).$$

Here m_i is the size-independent (baseline) mortality, and s_0 describes how fast size-dependent mortality drops with size from its maximum m_d at $s = 0$. An individual's survival probability until maturation is given by

$$P(s_\mathrm{A}) = \exp(-\int_0^{(s_\mathrm{A}-s_\mathrm{B})/g} m(gt)\,\mathrm{d}t),$$

where s_B denotes the size at birth. Adults do not grow, and thus face a constant mortality rate $m(s_\mathrm{A})$, implying an average adult life span of $1/m(s_\mathrm{A})$.

Fecundity

An adult's effective fecundity f is the rate at which it produces offspring that survive the phase of massive mortality occurring shortly after birth. It is given by the parent's weight-production rate $g\,\alpha\,\gamma\,s_\mathrm{A}^{\gamma-1}$ divided by the initial offspring weight w_B and multiplied by the offspring's short-term survival probability S, $f(s_\mathrm{A}) = g\,\alpha\,\gamma\,s_\mathrm{A}^{\gamma-1}\,w_\mathrm{B}^{-1}\,S$.

The factor w_B^{-1} accounts for the trade-off between offspring number and offspring size (e.g., Stearns 1992, Fox and Czesak 2000), which reflects that the total amount of energy available for reproduction is limited. This means that the higher the initial offspring weight w_B, the fewer offspring a parent can produce.

The factor S accounts for the trade-off between offspring size and offspring survival (e.g., Stearns 1992). Larger, better provisioned offspring usually have a survival advantage relative to smaller, less well provisioned young, which naturally counterbalances the benefits of splitting the available energy across more, but smaller, young (reviewed in Azevedo et al. 1997 and Fox and Czesak 2000). We therefore assume that offspring survival S is proportional to initial offspring weight $w_\mathrm{B} = \alpha\,s_\mathrm{B}^{\gamma}$ according to $S = \max(1, \beta\,s_\mathrm{B}^{\gamma})$, where the parameter β scales the proportionality, and hence fecundity (so β can be interpreted as scaling the amount of energy or resources available in an environment). This reflects the well-documented finding that effects of initial body size (e.g., mediated through parental effects on egg size) affect survival only shortly after hatching, but then vanish soon afterwards

(Lindholm et al. 2006, Donelson et al. 2009, Segers and Taborsky 2011). The proportionality between S and w_B is empirically well supported for birds (Parsons 1970), reptiles (Sinervo et al. 1992), and insects (Fox and Mousseau 1996, Boivin and Gauvin 2009).

Accounting for both trade-offs, we thus obtain

$$f(s_\mathrm{A}) = g\,\gamma\,s_\mathrm{A}^{\gamma-1}\beta\,.$$

Competition

In density-regulated randomly mixing populations, two morphs cannot robustly coexist if density dependence affects them equally (Gause 1932, 1934, Hardin 1960). In contrast, if morphs experience the environment differently, and impact it differently, so that selection can be negatively frequency-dependent, they can robustly coexist (e.g., Heino et al. 1997). Here we include density dependence and frequency dependence by assuming indirect interactions between individuals competing for the same resources. Specifically, we assume that adult individuals compete for resources needed for reproduction such that the more similar they are in body size, the stronger their competition. Absence of density dependence during the juvenile stage is realistic when juveniles and adults occupy different niches, as is common among insects and for many aquatic organisms with pelagic juveniles and bottom-dwelling adults, or when adults compete for resources specifically required for reproduction, such as nest sites. In other cases, this assumption amounts to an approximation that greatly simplifies the analysis. Thus, in our model, competition in a polymorphic community with adult body sizes $(s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})$ and corresponding adult weights $(w_{\mathrm{A},1},\ldots,w_{\mathrm{A},N})$ and adult densities $(n_1,\ldots,n_N)$ reduces the fecundity of individuals with adult body size s'_A by a factor

$$F(s'_\mathrm{A}, s_{\mathrm{A},1}, \ldots, s_{\mathrm{A},N}) = \exp(-\textstyle\sum_{i=1}^{N} n_i \, w_{\mathrm{A},i} \, d(s'_\mathrm{A}, s_{\mathrm{A},i}) / k),$$

where k is a parameter scaling a community's total adult density and $d(s_{\mathrm{A},i}, s_{\mathrm{A},j})$ is a size-dependent competition function defined as

$$d(s'_\mathrm{A}, s_\mathrm{A}) = \exp(-\tfrac{1}{2}(s'_\mathrm{A} - s_\mathrm{A})^2 / (CV\, s'_\mathrm{A})^2),$$

where the coefficient of variation, CV, scales the range of relative size differences over which competition is strong. The competitive influence of large adult individuals is thus strong over a wider range of sizes than that of small ones. For convenience, we present our results in terms of $c = 1/CV$, so that larger values of c represent more strongly size-specific competition (since the resultant narrower competition functions mean that size-dependent competition significantly influences only individuals with more similar sizes). In our model, assuming competition to reduce fecundity is equivalent to assuming competition to increase the adult mortality rate $m(s_\mathrm{A})$, as can be seen from equation (1) below.

Lifetime reproductive success

The expected lifetime reproductive success R_0 of an individual with adult body size s'_A in a polymorphic community with adult body sizes $(s_{\mathrm{A},1}, \ldots, s_{\mathrm{A},N})$ is the product of its probability $P(s'_\mathrm{A})$ to reach adulthood, its competition-mediated fecundity $F(s'_\mathrm{A}, s_{\mathrm{A},1}, \ldots, s_{\mathrm{A},N})\, f(s'_\mathrm{A})$, and its average reproductive lifespan, given by the inverse $1/m(s'_\mathrm{A})$ of the adult mortality rate,

$$R_0(s'_\mathrm{A}, s_{\mathrm{A},1}, \ldots, s_{\mathrm{A},N}) = P(s'_\mathrm{A})\, F(s'_\mathrm{A}, s_{\mathrm{A},1}, \ldots, s_{\mathrm{A},N})\, f(s'_\mathrm{A}) / m(s'_\mathrm{A}), \qquad (1)$$

where the impact of $(s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})$ is limited to the competition factor F. For a monomorphic community ($N=1$) with adult body size s_A, the equilibrium condition $R_0(s_\mathrm{A},s_\mathrm{A})=1$ readily yields the equilibrium adult density $\hat{n}=k\ \ln(P(s_\mathrm{A})\ f(s_\mathrm{A})/m(s_\mathrm{A}))/(\alpha\, s_\mathrm{A}^{\gamma})$. For polymorphic communities, the equilibrium adult densities $(\hat{n}_1,\ldots,\hat{n}_N)$ follow analogously, from the equilibrium conditions $R_0(s_{\mathrm{A},1},s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})=1$ to $R_0(s_{\mathrm{A},N},s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})=1$.

The selection pressure on $s_{\mathrm{A},i}$ with $i=1,\ldots,N$ is given by the derivative $\partial R_0/\partial s'_\mathrm{A}$ evaluated at $s'_\mathrm{A}=s_{\mathrm{A},i}$.

Model parameters

At first glance, it would appear as though our model had nine relevant parameters (in order of appearance: α, g, m_i, m_d, s_0, s_B, β, k, and c). Since the exhaustive exploration of the effects of so many parameters would be a challenge, it is important to realize that five of these parameters are readily removed from further consideration.

First, the two parameters α and k have no bearing on lifetime reproductive success: once the solution for $\hat{n}$ is inserted into $F(s'_\mathrm{A},s_\mathrm{A})=\exp(-\hat{n}\ \alpha\ s_\mathrm{A}^{\gamma}\, d\,(s'_\mathrm{A},s_\mathrm{A})/k)$, both parameters drop out (this applies analogously also to polymorphic equilibria).

Second, the size s_B at birth only influences the survival probability P until adulthood. As long as s_B is small compared to the adult size s_A, P is essentially independent of s_B, so it is natural to let s_B approach 0.

Third, the four parameters m_i, m_d, s_0, and g can be combined into just two dimensionless parameters, $r_\mathrm{i} = m_\mathrm{i}\, s_0 / g$ and $r_\mathrm{d} = m_\mathrm{d}\, s_0 / g$, by choosing convenient units for time and body size, which highlights that mortality components must be assessed relative to growth rate.

We can thus fully explore our model by varying just the four dimensionless parameters r_i, r_d, c, and β.

Model analysis

To investigate the final outcomes of community evolution, we identify size-morph combinations $(s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})$ that simultaneously possess four stability properties. (1) All size morphs are at positive and stable equilibrium densities. (2) All size morphs are free from directional selection pressures. (3) All size morphs are convergence stable (so when their adult body sizes are perturbed, directional selection returns them to the original values). (4) The community of size morphs is immune to invasions by any additional size morphs (which implies that all size morphs are free from disruptive selection pressures).

All four stability properties are tested using the function $R_0(s'_\mathrm{A}, s_{\mathrm{A},1},\ldots,s_{\mathrm{A},N})$ (equation 1) and its derivatives. Specifically, we first search for a monomorphic evolutionary attractor among all feasible body sizes (i.e., those body sizes for which the equilibrium population size is positive). These attractors are characterized by the first derivative $\partial R_0 / \partial s'_\mathrm{A}$ of a mutant's fitness being 0 when evaluated at $s'_\mathrm{A} = s_{\mathrm{A},i}$. Second, we check for the existence of possible additional attractors: we test if, in the presence of a resident population with size $s_{\mathrm{A},1}$, the equality $R_0(s_{\mathrm{A},1}, s_{\mathrm{A},2}) = 1$ holds for any other body size $s_{\mathrm{A},2}$, by searching numerically for the roots of this equation. Third, if any roots are found, we search for the existence of dimorphic evolutionary attractors among pairs of body sizes for which the equilibrium population sizes are positive. These attractors are characterized by the first derivative $\partial R_0 / \partial s'_{\mathrm{A}}$ of a mutant's fitness being 0 when evaluated at $s'_{\mathrm{A}} = s_{\mathrm{A},1}$ or $s'_{\mathrm{A}} = s_{\mathrm{A},2}$. Fourth, we test whether such a dimorphism is stable against further invasions, analogously as for the case of monomorphism described above, and continue this procedure until all existing attractors have been found. In this way, we confirm that the final evolutionary attractor (be it monomorphic or polymorphic) is an evolutionarily stable strategy (ESS).

Results

In our model, stable coexistence of two or more size morphs occurs over a broad range of ecological conditions. Yet, the total number of coexisting morphs as well as their body sizes follow a relatively complex pattern caused by interactive effects of size-dependent competition and size-dependent and size-independent mortality (Fig. 1). For a better understanding of this complexity, Fig. 1a allows tracking the effects of these three ecological gradients together and in separation. Scrutinizing these results, we make three key observations as described below.

First, when size dependence of competition is very weak, so that all body sizes are affected by competition in a similar way, we never find more than a single morph to be present (results not shown). We see that stronger size-specific competition enables the coexistence of a larger number of size morphs, in line with analogous findings in classical models of species packing (e.g., MacArthur and Levins 1967, Roughgarden 1974). This mechanism alone is seen in operation when size-dependent mortality is absent ($r_\mathrm{d} = 0$), that is, along the vertical axes of panels in Fig. 1a: the number of coexisting size morphs increases from the leftmost to the rightmost panels.

Second, when size-dependent mortality is present and is of intermediate strength, diversification can originate through a different mechanism. This is best seen in the left column of Fig. 1a: for certain combinations of moderate size-dependent and size-independent mortality, two size morphs can coexist because size-dependent mortality generates a size refuge for life histories with large adult sizes that ‘outgrow’ the window of high mortality risk, while simultaneously allowing a niche for very small adult sizes that cope with high mortality by reproducing very early. This mechanism has been reported as a source of alternative life-history strategies and corresponding adult body sizes before (Taborsky et al. 2003); here we show for the first time that these strategies can coexist through frequency-dependent selection and represent final outcomes of community evolution.

Third, we see that the number of coexisting size morphs is relatively little influenced by size-independent mortality over the parameter range considered in Fig. 1 (as shown by comparing the results along the vertical axes of the panels, where $r_\mathrm{d} = 0$, across rows of Fig. 1a, b). For sufficiently high levels of size-independent mortality, however, the number of coexisting morphs slowly declines (Fig. 2).

On top of the two diversity-generating mechanisms described above, mortality influences the body sizes of coexisting morphs. As expected, increasing size-independent mortality causes body size to decrease. For size-dependent mortality, the picture is more nuanced. When size-independent mortality is low or moderate (Fig. 1a, top and middle row), adult size tends to increase with increasing size-dependent mortality. Under these conditions, it pays organisms to outgrow sizes with high size-dependent mortality by delaying maturation. However, when overall mortality is high (Fig. 1a, bottom row), adult sizes tend to decrease with increasing size-dependent mortality, because the risk of dying before first reproduction becomes too high for late-maturing strategies.

The interplay of the two diversifying mechanisms highlighted above gives rise to communities in which both the number and the adult sizes of the coexisting life-history types vary in interesting ways across the three considered ecological gradients. In particular, the two size-dependent selective forces, mortality and competition, acting on the evolution of body size give rise to abrupt changes in size structure and to non-monotonic changes of diversity along continuous and monotonic environmental gradients (Fig. 1b). This complexity results from the superposition of three diversity-enhancing conditions: (i) diminished overall mortality, resulting from reduced size-independent mortality r_{i} (panels from bottom to top) or size-dependent mortality r_{d} (right to left, within panels); (ii) more strongly size-specific competition, resulting from increased c (panels from left to right); and (iii) intermediate size-dependent mortality r_{d}, implying a strengthening of the aforementioned size-refuge mechanism.

Comparing the body sizes of coexisting morphs in pairs that are adjacent in terms of their size rank (referred to below as adjacent size morphs) reveals interesting differences between communities in which diversification is primarily driven by size-dependent competition as opposed to size-dependent mortality (Fig. 1c). When size-dependent competition is the main driver, we see the expected pattern: for a given size-specificity of competition, the size ratios of adjacent size morphs are almost invariant, and typically take values between 2 and 3. The signature of diversification driven by the size-refuge mechanism is completely different: here we see that the size ratios of adjacent size morphs are not only sensitive to size-dependent mortality, but also tend to be much larger. This is because the size refuge imposes divergent selection on body size (Taborsky et al. 2003), and thus broadens the size gaps between morphs. These gaps broaden further when size-dependent mortality r_d gets stronger, resulting in size ratios rapidly increasing with r_d (Fig. 1c). Interestingly, the size gaps caused by the size-refuge mechanism can even create niche space for the existence of an additional morph that is positioned between two divergent size morphs (Fig. 1a and c, right column, middle row, $r_\mathrm{d} = 8 \text{ to } 10$).

The non-trivial interactions between size-dependent competition and size-dependent and size-independent mortality become even more visible in a contour plot displaying the number of coexisting morphs (Fig. 2.). The top and bottom panels conform to the usual expectations: in both panels, diversity declines when competition becomes less size-specific and size-dependent mortality is increased. Also, diversity is lower in the bottom panel because of higher size-independent mortality. Considering only these two panels would suggest that size-dependent competition and size-dependent mortality show no significant interaction. However, the two middle panels exhibit a strikingly different pattern: a tongue-like positive diversity anomaly occurs at intermediate levels of size-dependent mortality. This diversity anomaly results from diversification caused by the size-refuge mechanism.

The fourth essential parameter in our model, the fecundity scale β, which reflects the energy richness of an environment, does not affect our results qualitatively (results not shown). In line with previous work by Brännström et al. (2011), we find, however, that it influences overall diversity: since fecundity scales with β, high values of β enable morphs to tolerate more mortality. Consequently, the number of coexisting morphs increases monotonically with β (Fig. 3).

Our findings suggest that (1) size-dependent mortality can give rise to the stable coexistence of different life-history strategies when size-dependent competition alone would not support diversification and that (2) where size-dependent competition gives rise to diversification, size-dependent mortality can support additional diversification. Can these predictions be tested in the field? We explore this question in two directions.

First, Fig. 1c suggests that a characteristic signature of diversification driven by size-dependent mortality is the presence of much larger body-size ratios of adjacent size morphs than is typical for diversification driven by size-dependent competition alone. If the three-dimensional parameter space in Fig. 1 were randomly sampled by natural communities, we would find the frequency distribution of body-size ratios of adjacent size morphs to be characterized by a pronounced peak at small ratios and an extended tail at large ratios (Fig. 4). This tail is the signature of diversification mediated by size-dependent mortality, as it is lacking in the absence of size-dependent mortality (as demonstrated by the distribution shown by black outline in Fig. 4).

Second, we investigate the relationship between the body masses and the equilibrium densities of morphs across randomly sampled environments, separately for communities consisting of one, two, or three different morphs. As predicted by theory (e.g., Damuth 1981, Brown et al. 2004), density and body mass are allometrically related, so logarithmic density and logarithmic body mass are approximately linearly related (Fig. 5). While these results do not yield a clear signature of diversification mediated by size-dependent mortality, they show that both community structure itself (in terms of the number of morphs coexisting in a community, Fig. 5a, b) and the mechanisms shaping community structure (in terms of the presence, Fig. 5a, or absence, Fig. 5b, of size-dependent mortality), alter the allometric exponent to an extent that is comparable to the range of exponents observed in nature.

Discussion

Our results suggest that size-dependent competition and size-dependent mortality need to be considered together to understand the number of stably coexisting life-history types. In the absence of frequency-dependent selection caused by size-dependent competition, no stable coexistence occurs at all. If size-dependent competition is present, size-dependent mortality enriches patterns of community diversity, resulting in non-monotonic changes of life-history diversity and in abrupt changes in size structure along continuous and monotonic environmental gradients. It also causes a characteristic amplification in the body-size ratios of adjacent size morphs, and hence a tell-tale tail in the in size-ratio distribution of local communities.

In the absence of size-dependent mortality, our model confirms previous results on the role of frequency-dependent competition in generating and maintaining diversity (e.g., Schluter 1994, Bolnick 2004). Reviewing theoretical evidence, Chesson (2000) identified negative frequency-dependent competition as a key mechanism for stabilizing diversity, a conclusion that has received experimental support (Harpole and Suding 2007). Negatively size-dependent mortality also enhances diversity, as organisms then need to choose between reaching relatively safe body sizes at the cost of a prolonged pre-reproductive period and maturing early at the cost of growing to only small body sizes well below the mortality refuge. This trade-off has been empirically demonstrated in a marine bivalve (Nakaoka 1998). Theoretical work showed that it can readily give rise to alternative life-history strategies (Ratner and Lande 2001, Day et al. 2002, Taborsky et al. 2003, Gårdmark and Dieckmann 2006). Here we have demonstrated for the first time that these alternative life-history strategies promoted by size-dependent mortality can robustly coexist through the latter's interplay with size-dependent competition.

Life-history diversity in our model can result from the combination of gradual adaptive evolution with adaptive radiation: we have focused on globally evolutionarily stable strategies that can be attained by these processes, and that are characterized by robust coexistence (Geritz et al. 1999). The coexisting life-history types can thus be equally well envisaged as sympatric genetically determined size morphs of a single species or as ecologically similar members of a community of species that are distinguished mainly by their adult body size.

Notably, the two considered size dependences differentially affect the dispersion of adult body sizes in our model communities, resulting in a characteristic disparity of the resultant body-size ratios. In our model, size-dependent competition gives rise to relatively constant and small size ratios of adjacent size morphs. Frequency-dependent competition and character displacement have been recognized before as likely explanations for the existence of near-constant size ratios in natural populations (Kohda et al. 2008) and species communities (Schluter 2000). In contrast, size-dependent mortality results in much broader gaps between body sizes than expected from competition alone. This happens when the resultant selection pressures favor either a very small adult size associated with a very short juvenile period, or a prolonged juvenile period allowing maturation and adulthood at a large body size conferring relative safety from mortality. When size-dependent mortality gets stronger, body sizes diverge even further as then (i) even larger adult sizes (and longer juvenile periods) are needed to reach the size refuge and (ii) increasing mortality forces the fast-living strategy to become even faster by maturing even earlier. At too high mortality, however, long initial growth periods result in very low survival until first reproduction, so that the life history that delays maturation goes extinct first.

There is an ongoing debate about the expected exponent of the allometric relationship density and body mass: e.g., the allometric exponent expected from geometric theory equals –2/3, whereas the allometric exponent expected from metabolic theory equals –3/4 (see Damuth 1981 for a review). Moreover, a substantial range of exponents is observed in nature, even within the same major taxonomic group (e.g., herbivorous mammals: –0.61; carnivorous mammals: –0.94; Peters and Wassermann 1983). Our results show that the presence or absence of size-dependent mortality, as well as a community's diversity of size morphs, can impact these exponents (Fig. 5), giving rise to a variability of exponents comparable to that observed in natural communities. Our findings also reveal a potential additional result: whether the monotonic decrease in Fig. 5a of allometric exponents with increasing morph diversity represents another characteristic signature of size-dependent mortality, requires further study.

Size-dependent mortality has been recognized as an important selective force shaping life-history evolution (e.g., Day et al. 2002) and influencing population dynamics (e.g., de Roos et al. 2003). The most important source of mortality is predation, and most often mortality rates decline with body size (Lorenzen 1996, Sogard 1997, Day et al. 2002, Gislason et al. 2010). In more than 90% of predator-prey interactions, the predator is larger than the prey, so that size-selective predation is an important organizing force of trophic hierarchies (Cohen et al.

1993). Predation has also been recognized as a potent mechanism for increasing trait divergence (Holt 1977, Doebeli and Dieckmann 2000, Vamosi 2005, Troost et al. 2008), particularly when different anti-predator strategies exist (Arendt 2009). Several empirical studies suggest the importance of size-selective predation for the evolution of prey-size dimorphisms (Griffiths and Seiderer 1980, Kenner 1992, Wellborn 1994, Chase 1999).

In conclusion, size-dependent competition and size-dependent mortality are ubiquitous adaptive forces and it is inevitable that they will frequently act simultaneously as drivers of body-size evolution. Our integrative modeling of these two processes shows that their interplay favors diversity in a complex way. Furthermore, our results suggest that the outcome of this interplay can be detected in the field: we predict that in a community shaped by size-dependent mortality and competition, the distribution of size ratios of adjacent-sized morphs is skewed with a heavy tail. While the majority of these body-size ratios are small and result from competition-mediated species packing, size-dependent mortality opens niches for life histories with intermediate to very large adult body-size ratios.

Acknowledgements

We thank two reviewers for helpful comments. BT acknowledges financial support by the Austrian Science Fund (FWF, Project 18647-B16) and by the Swiss National Science Foundation (SNF, Projects 3100A0-111796 and 31003A_133066). MH acknowledges financial support by the Bergen Research Foundation. UD acknowledges financial support by the European Commission, the European Science Foundation, the Austrian Science Fund, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund.

Literature cited

Arendt, J. D. 2009. Influence of sprint speed and body size on predator avoidance in New Mexican spadefoot toads (*Spea multiplicata*). Oecologia 159:455-461.

Azevedo, R. B. R., V. French, and L. Partridge. 1997. Life-history consequences of egg size in *Drosophila melanogaster*. Am. Nat. 150:250-282.

Beaugrand, J. P., and R. Zayan. 1985. An experimental model of aggressive dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). Behav. Proc. 10:1-52.

Boivin, G., and M. J. Gauvin. 2009. Egg size affects larval performance in a coleopteran parasitoid. Ecol. Entomol. 34:240-245.

Bolnick, D.I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution 58:608-618.

Brännström, Å., N. Loeuille, M. Loreau, and U. Dieckmann. 2011. Emergence and maintenance of biodiversity in an evolutionary food-web model. Theor. Ecol. 4:467-478.

Brown, J. H., J. F. Gillooly, V. M. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771-1789.

Caldarelli, G., P. G. Higgs, and A. J. McKane. 1998. Modelling coevolution in multispecies communities. J. Theor. Biol. 193:345-358.

Chase, J.M. 1999. Food web effects of prey size refugia: Variable interactions and alternative stable equilibria. Am. Nat. 154:559-570.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Ann. Rev. Ecol. Syst. 31:343-366.

Claessen, D., and U. Dieckmann. 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. Evol. Ecol. Res. 4:189-217.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldana. 1993. Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62:67-78.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699-700.

Day, T., P. A. Abrams, and J. M. Chase. 2002. The role of size-specific predation in the evolution and diversification of prey life histories. Evolution 56:877-887.

de Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecol. Lett. 6:473-487.

Dieckmann, U., and R. Ferrière. 2004. Adaptive dynamics and evolving biodiversity. In: Evolutionary Conservation Biology (eds. Ferrière, R., Dieckmann, U. and Couvet, D.). Cambridge University Press, Cambridge, UK, pp. 188-224.

Dieckmann, U., Å. Brännström, R. HilleRisLambers, and H. C. Ito. 2007. The adaptive dynamics of community structure. In: Mathematics for Ecology and Environmental Sciences (eds. Takeuchi, Y., Sato, K. and Iwasa, Y.). Springer Verlag, Berlin, pp. 145-177.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354-357.

Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. Am. Nat. 156:S77-S101.

Donelson, J. M., P. L. Munday, and M. I. McCormick. 2009. Parental effects on offspring life histories: When are they important? Biol. Lett. 5:262-265.

Drossel, B., P. G. Higgs, and A. J. McKane. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. J. Theor. Biol. 208:91-107.

Fox, C.W., and M. E. Czesak,. 2000. Evolutionary ecology of progeny size in arthropods. Ann. Rev. Entomol. 45:341-369.

Fox, C. W., and T. A. Mousseau. 1996. Larval host plant affects fitness consequences of egg size variation in the seed beetle *Stator limbatus*. Oecologia 107:541-548.

Gårdmark, A., and U. Dieckmann. 2006. Disparate maturation adaptations to size-dependent mortality. Proc. R. Soc. B 273:2185-2192.

Gause, G. F. 1932. Experimental studies on the struggle for existence: 1. Mixed population of two species of yeast. J. Exp. Biol. 9:389-402.

Gause, G. F. 1934. The Struggle for Existence. Baltimore: Williams and Wilkins.

Geritz, S. A. H., E. van der Meijden, and J. A. J. Metz. 1999. Evolutionary dynamics of seed size and seedling competitive ability. Theor. Pop. Biol. 55:324-343.

Gislason, H., N. Daan, J. C. Rice, and J. G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish Fish. 11:149-158.

Griffiths, C. L., and J. L. Seiderer. 1980. Rock lobsters and mussels – Limitations and preferences in a predator-prey interaction. J. Exp. Mar. Biol. Ecol. 44:95-109.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.

Harpole, W. S., and K. N. Suding. 2007. Frequency-dependence stabilizes competitive interactions among four annual plants. Ecol. Lett. 10:1164-1169.

Heino, M., J. A. J. Metz, and V. Kaitala,. 1997. Evolution of mixed maturation strategies in semelparous life-histories: The crucial role of dimensionality of feedback environment. Phil. Trans. R. Soc. B 352:1647-1655.

Holt, R. D. 1977. Predation, apparent competition, and structure of prey communities. Theor. Pop. Biol. 12:197-229.

Ito, H. C., and U. Dieckmann. 2007. A new mechanism for recurrent adaptive radiations. Am. Nat. 170:E96–E111.

Ito, H. C., and T. Ikegami. 2006. Food-web formation with recursive evolutionary branching. J. Theor. Biol. 238:1-10.

Kenner, M. C. 1992. Population dynamics of the sea urchin *Strongylocentrotus purpuratus* in a central California kelp forest – Recruitment, mortality, growth and diet. Mar. Biol. 112:107-118.

Kohda, M., J. Y. Shibata, S. Awata, D. Gomagano, T. Takeyama, M. Hori, and D. Heg. 2008. Niche differentiation depends on body size in a cichlid fish: A model system of a community structured according to size regularities. J. Anim. Ecol. 77:859-868.

Lindholm, A. K., J. Hunt, and R. Brooks. 2006. Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. Biol. Lett. 2:586-589.

Loeuille, N., and M. Loreau. 2005. Evolutionary emergence of size-structured food webs. Proc. Natl. Acad. Sci. USA 102:5761-5766.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: A comparison of natural ecosystems and aquaculture. J. Fish Biol. 49:627-647.

MacArthur, R. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101:377-387.

McKane, A. J. 2004. Evolving complex food webs. Eur. Phys. J. B 38:287-295.

Nakaoka, M. 1998. Optimal resource allocation of the marine bivalve *Yoldia notabilis*: The effects of size-limited reproductive capacity and size-dependent mortality. Evol. Ecol. 12:347-361.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in herring gull (*Larus argentatus*). Nature 228:1221-1222.

Peters, R. H., and K. Wasserman. 1983. The effect of body size on animal abundance. Oecologia 60:89-96.

Ratner, S., and R. Lande. 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. Ecology 82:3093-3104.

Robertson, D. R. 1998. Implications of body size for interspecific interactions and assemblage organization among coral-reef fishes. Austr. J. Ecol. 23:252-257.

Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. Theor. Pop. Biol. 5:163-186.

Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. Science 266:798-801.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. Am. Nat. 156:S4-S16.

Segers, F. H. I. D., and B. Taborsky. 2011. Interactive effects of egg size and food abundance on juvenile phenotype suggest adaptive maternal provisioning. Funct. Ecol. 25:166-176.

Sinervo, B., P. Doughty, R. B. Huey, and K. Zamudio. 1992. Allometric engineering – A causal analysis of natural selection on offspring size. Science 258:1927-1930.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford: Oxford University Press.

Taborsky, B., U. Dieckmann, and M. Heino. 2003. Unexpected discontinuities in life-history evolution under size-dependent mortality. Proc. R. Soc. B 270:713-721.

Troost, T. A., B. W. Kooi, and U. Dieckmann. 2008. Joint evolution of predator body size and prey-size preference. Evol. Ecol. 22:771-799.

Vamosi, S. M. 2005. On the role of enemies in divergence and diversification of prey: A review and synthesis. Can. J. Zool. 83:894-910.

Wellborn, G. A. 1994. Size biased predation and prey life histories – A comparative study of freshwater amphipod populations. Ecology 75:2104-2117.

Wilson, D. S. 1975. Adequacy of body size as a niche difference. Am. Nat. 109:769-784.

Yoder, J. B., and S. L. Nuismer. 2010. When does coevolution promote diversification? Am. Nat. 176:802-817.

Figure legends

Fig. 1: Influence of size-dependent and size-independent mortality and size-dependent competition on coexisting size morphs, in terms of (a) adult body sizes, (b) number of morphs, and (c) body-size ratios of adjacent size morphs (for reference, the dashed line shows a size ratio of 1). Notice that in (a) the vertical scales differ between the top row and the two bottom rows. Other parameters: fecundity scale $\beta = 10^3$; size-independent mortality, from top to bottom, $r_\mathrm{i} = 0.1$, $r_\mathrm{i} = 0.5$, and $r_\mathrm{i} = 0.9$; size-dependent competition, from left to right, $c = 0.25$, $c = 0.5$, and $c = 1.0$.

Fig. 2: Contour plots of the number of coexisting size morphs along gradients of size-dependent competition and size-dependent mortality. Shades of grey indicate the number of morphs, ranging from black (four morphs) to light grey (one morph). Other parameters: fecundity scale $\beta = 10^3$; size-independent mortality, from top to bottom, $r_\mathrm{i} = 0.1$, $r_\mathrm{i} = 0.5$, $r_\mathrm{i} = 0.9$, and $r_\mathrm{i} = 2.0$.

Fig. 3: Influence of the fecundity scale β on the number of coexisting size morphs. Other parameters: $r_\mathrm{i} = 0.9$, $r_d = 0.5$, and $c = 1.0$.

Fig. 4: Frequency distribution of body-size ratios of adjacent size morphs randomly sampled from 4000 model environments. Gray bars: sampling of the parameter ranges $r_\mathrm{i} = 0.09$ to 0.9, $r_\mathrm{d} = 1.2$ to 12.0, and $c = 0.1$ to 1.0. Black outline: same sampling except for $r_\mathrm{d} = 0$, i.e., without size-dependent mortality.

Fig. 5: Allometric relationship between equilibrium densities $\hat{n}$ and body masses w and the corresponding regression lines in double-logarithmic plots for communities consisting of one, two, or three size morphs. (a) Random sampling of the parameter ranges $r_\mathrm{i} = 0.09$ to 0.9, $r_\mathrm{d} = 1.2$ to 12.0, and $c = 0.1$ to 1.0; (b) same sampling except for $r_\mathrm{d} = 0$, i.e., without size-dependent mortality. The inset figure legends show the numeric values obtained as regression slopes for the allometric exponents b of the relationship $\hat{n} \propto w^b$.

Fig. 1a

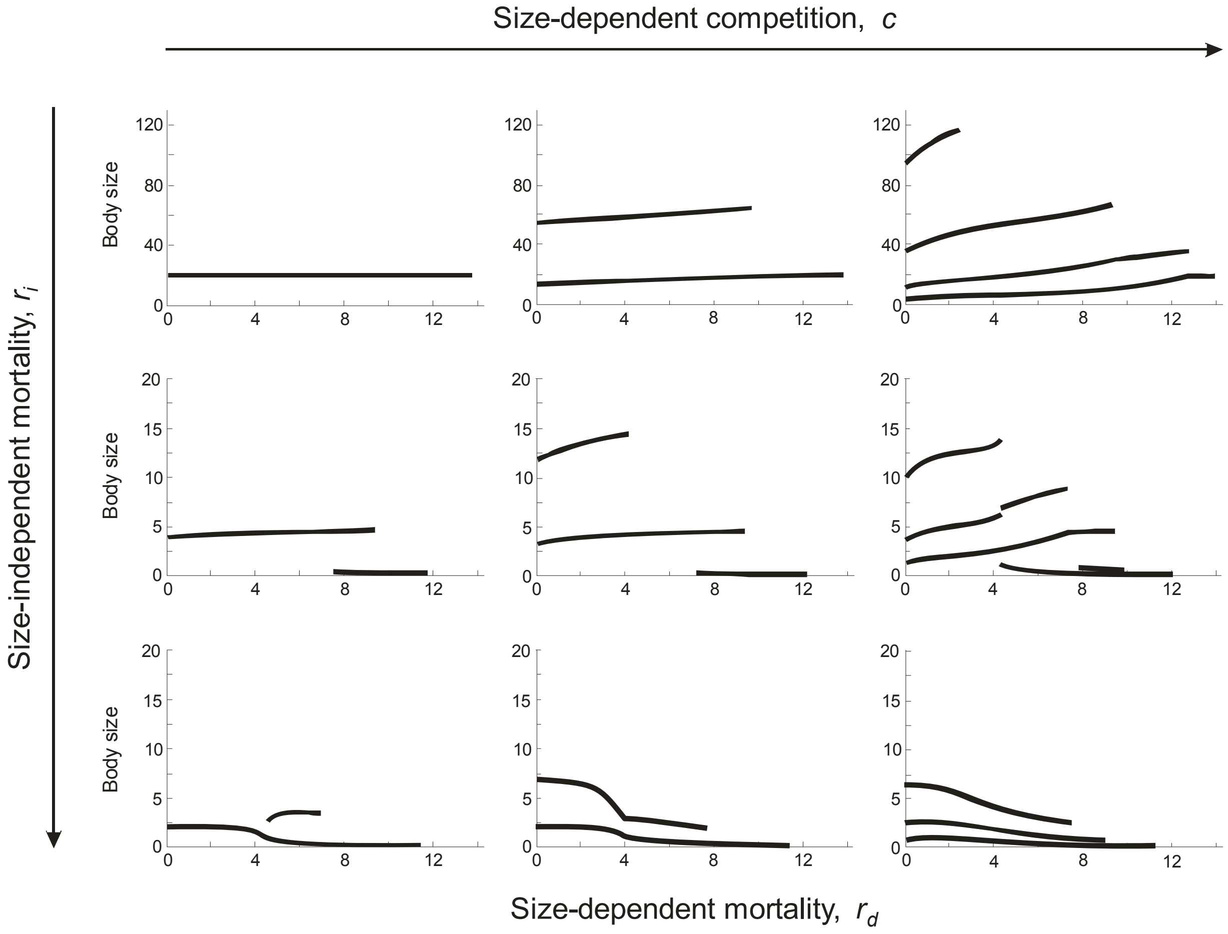
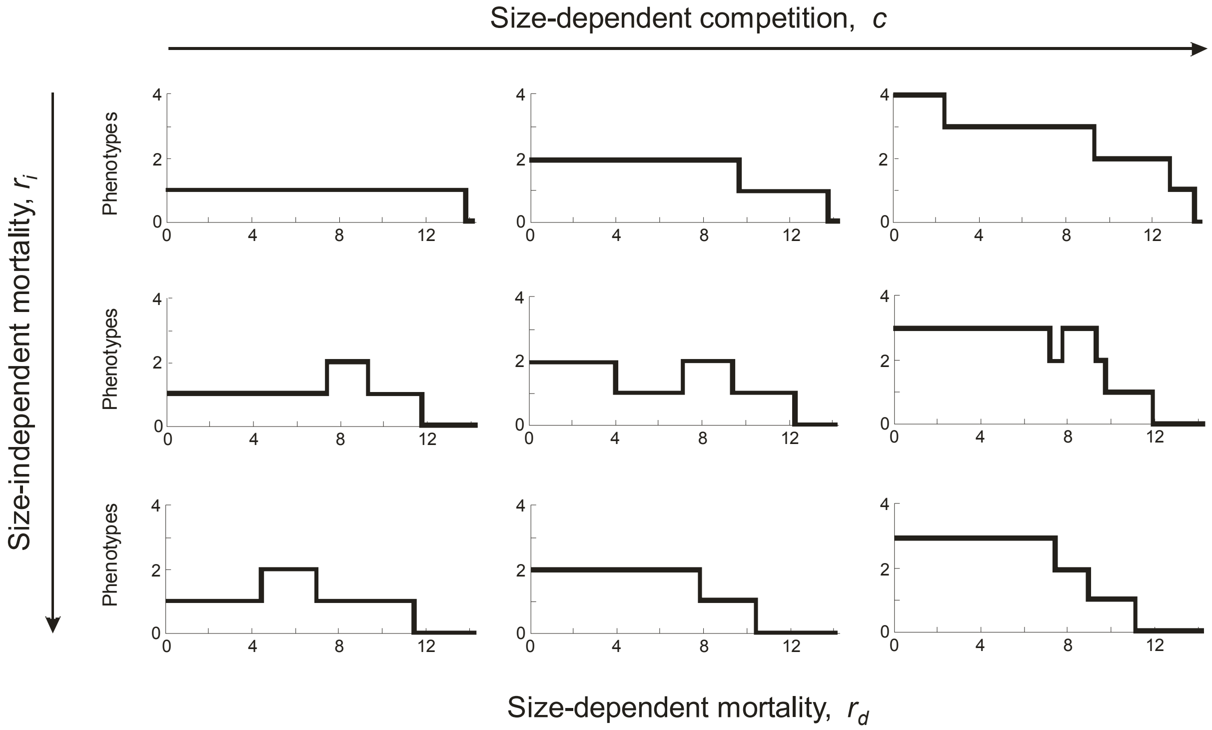

Size-dependent competition, c
Size-independent mortality, r_i
Body size
Size-dependent mortality, r_d
0
4
8
12
0
40
80
120
0
5
10
15
20

Fig. 1b



Size-dependent competition, c
Size-independent mortality, r_i
Phenotypes
Phenotypes
Phenotypes
4
2
0
0
4
8
12
Size-dependent mortality, r_d

Fig. 1c

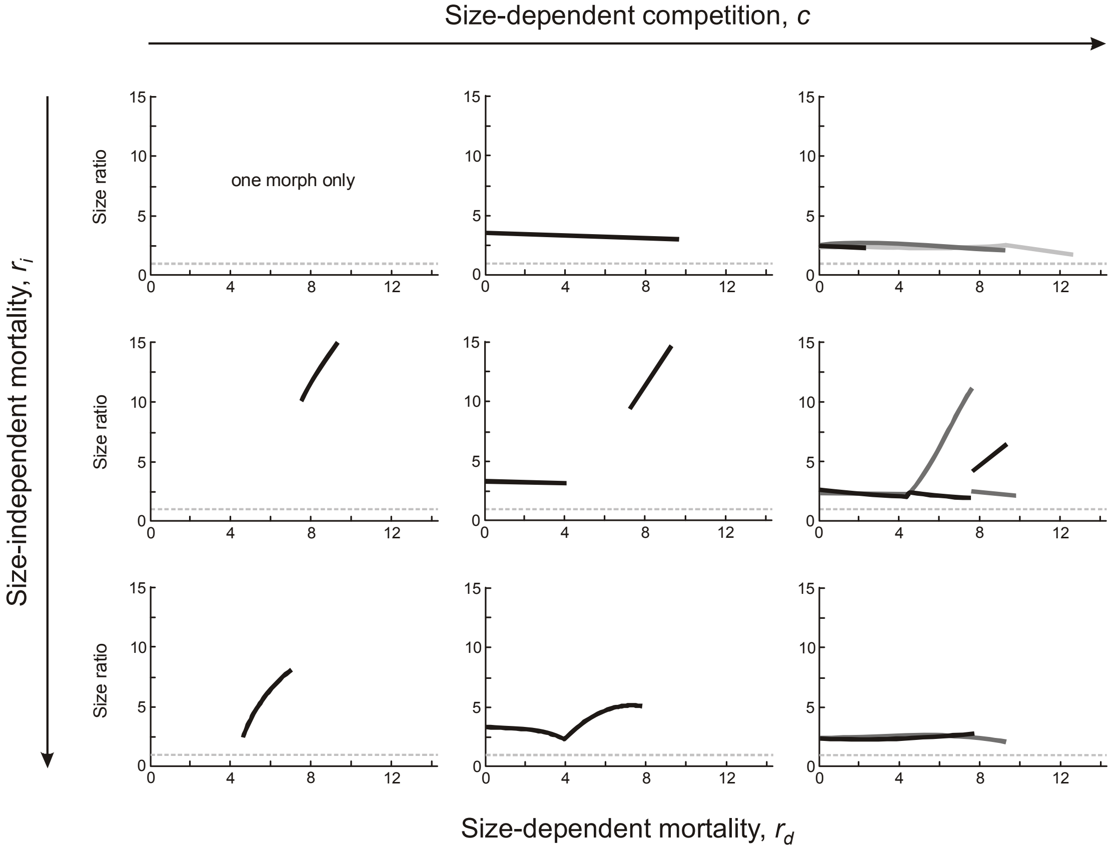

Size-dependent competition, c
Size-independent mortality, r_i
Size ratio
one morph only
15
10
5
0
0
4
8
12
Size-dependent mortality, r_d

Fig. 2

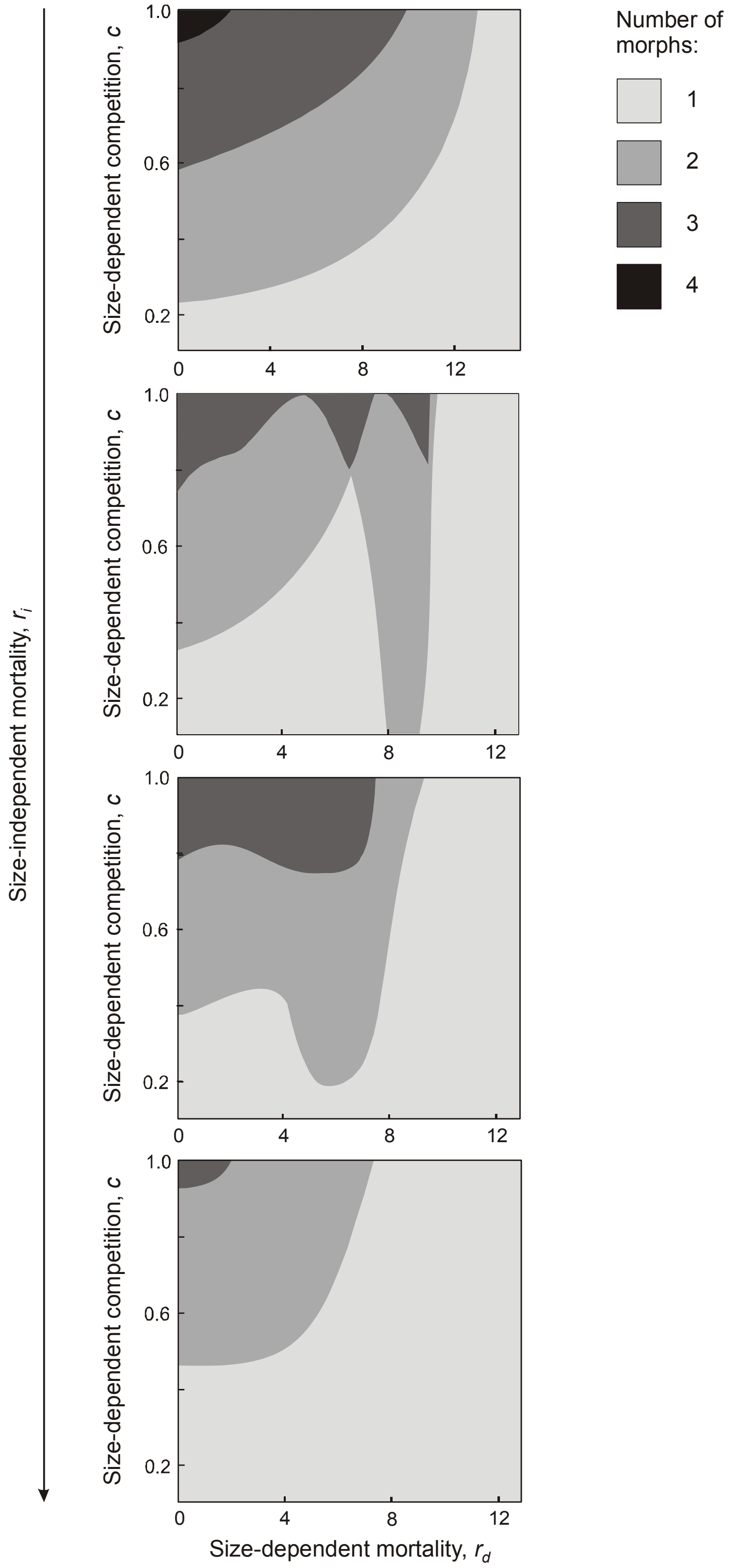
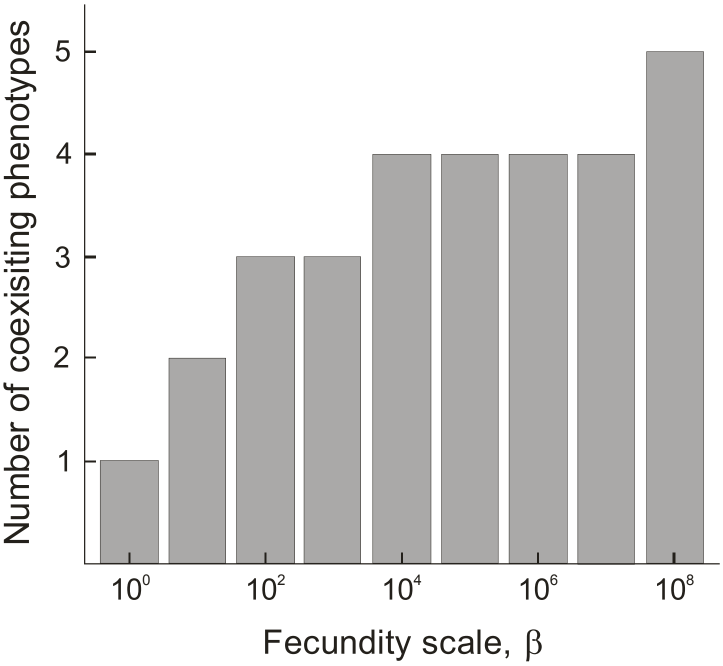

Number of morphs:
1
2
3
4
Size-independent mortality, r_i
Size-dependent competition, c
1.0
0.6
0.2
0
4
8
12
Size-dependent mortality, r_d

Fig. 3



Number of coexisiting phenotypes
5
4
3
2
1
10^0
10^2
10^4
10^6
10^8
Fecundity scale, β

Fig. 4

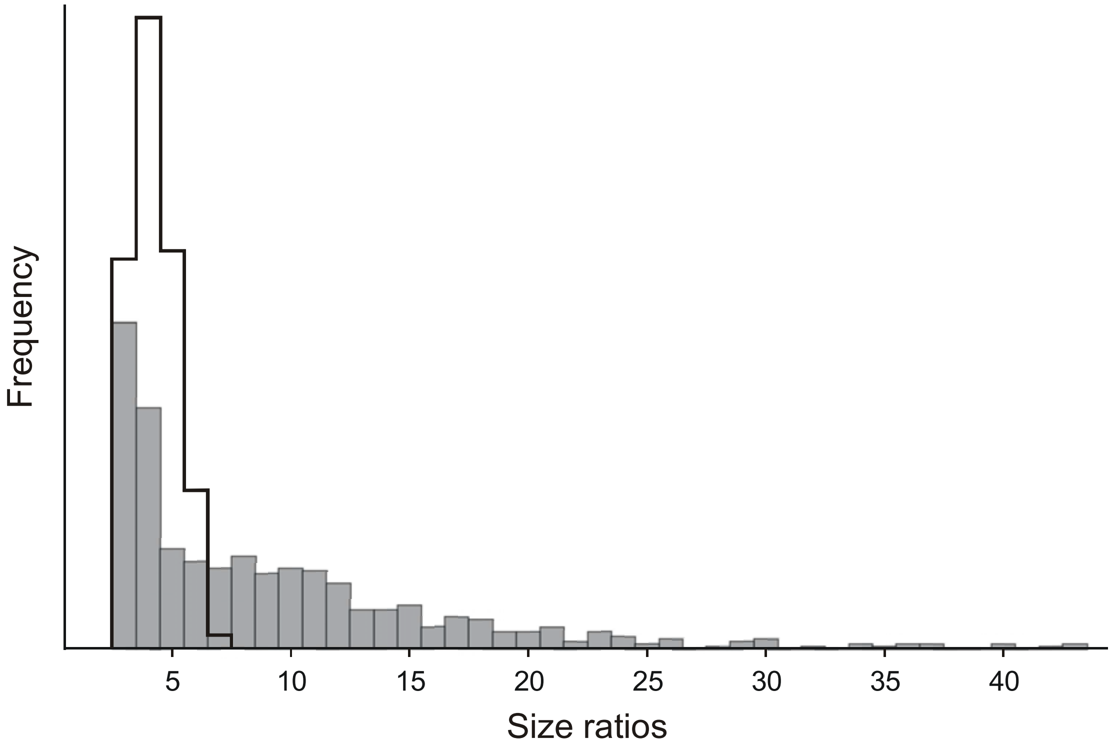
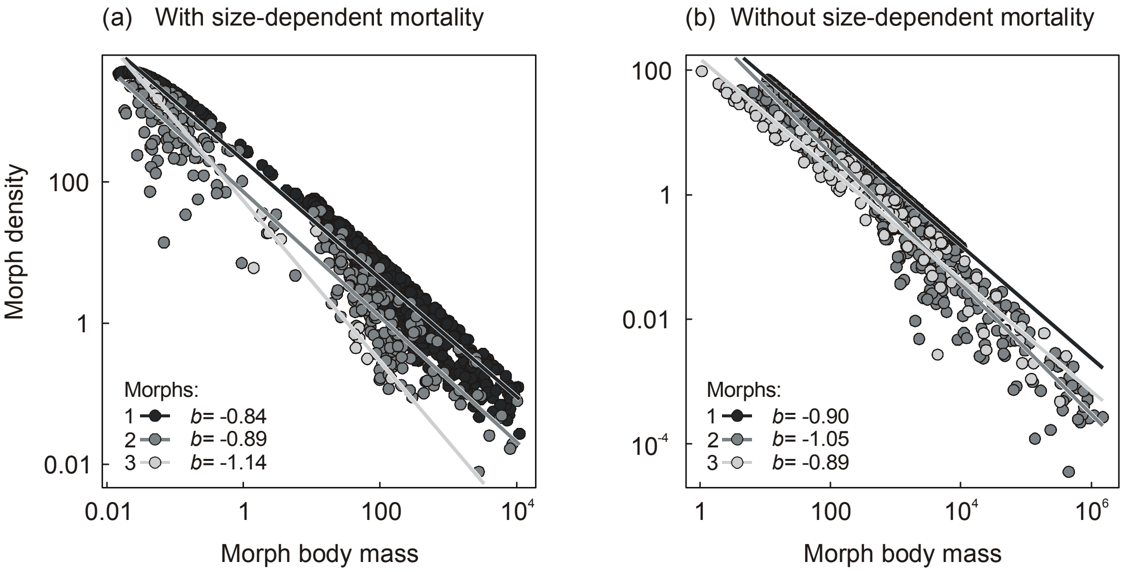


Fig. 5


(a) With size-dependent mortality
Morph density
100
1
0.01
0.01
1
100
10^4
Morph body mass
Morphs:
1 b= -0.84
2 b= -0.89
3 b= -1.14
(b) Without size-dependent mortality
100
1
0.01
10^{-4}
1
100
10^4
10^6
Morph body mass
Morphs:
1 b= -0.90
2 b= -1.05
3 b= -0.89