



ORGANISMAL COMPLEXITY AND THE POTENTIAL FOR EVOLUTIONARY DIVERSIFICATION

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We present two theoretical approaches to investigate whether organismal complexity, defined as the number of quantitative traits determining fitness, and the potential for adaptive diversification are correlated. The first approach is independent of any specific ecological model and based on curvature properties of the fitness landscape as a function of the dimension of the trait space. This approach indeed suggests a positive correlation between complexity and diversity. An assumption made in this first approach is that the potential for any pair of traits to interact in their effect on fitness is independent of the dimension of the trait space. In the second approach, we circumvent making this assumption by analyzing the evolutionary dynamics in an explicit consumer-resource model in which the shape of the fitness landscape emerges from the underlying mechanistic ecological model. In this model, consumers are characterized by several quantitative traits and feed on a multidimensional resource distribution. The consumer's feeding efficiency on the resource is determined by the match between consumer phenotype and resource item. This analysis supports a positive correlation between the complexity of the evolving consumer species and its potential to diversify with the additional insight that also increasing resource complexity facilitates diversification.

KEY WORDS: Adaptive dynamics, consumer-resource model, evolutionary branching, frequency dependence, genetic polymorphism, multidimensional trait space.

Disruptive selection due to negative frequency dependent intraspecific interactions is increasingly considered an important driver for adaptive phenotypic diversification in general (Rueffler et al. 2006b) and adaptive speciation in particular (Dieckmann et al. 2004; Bolnick and Fitzpatrick 2007; Doebeli 2011). For quantitative traits, so-called evolutionary branching points are indicative of negative frequency dependent disruptive selection (Metz et al. 1996; Geritz et al. 1998). These are points in trait

space that are attractors of the evolutionary dynamics: directional selection causes a population to evolve toward such points. However, as the population evolves, the fitness landscape gradually changes and once the population mean trait value is sufficiently close to the attractor, the fitness landscape has developed a minimum, that is, selection has turned disruptive (Metz et al. 1996; Geritz et al. 1998). Importantly, in the vicinity of evolutionary branching points similar genotypes can coexist in a protected dimorphism and experience further divergent selection. In clonal populations of sufficient size, this leads to a split of one lineage

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into two diverging lineages. In sexual populations, recombination prevents such a split and the population also contains phenotypically intermediate heterozygotes with reduced fitness. Any mechanism that prevents the production of such heterozygotes is then favored by selection, possibly resulting in speciation (e.g., Dieckmann and Doebeli 1999; Geritz and Kisdi 2000; Gavrillets 2004; Bürger et al. 2006; Pennings et al. 2008; van Doorn et al. 2009). More generally, at an evolutionary branching point, any evolutionary response resulting in increased phenotypic variation is favored by selection and the realized evolutionary outcome will strongly depend on the availability genetic variation for the various alternatives (see Rueffler et al. 2006b for a review).

Evolutionary branching points are a generic feature of eco-evolutionary models that incorporate intraspecific interactions (e.g., Metz et al. 1992; Geritz et al. 1998; Kisdi and Geritz 1999; Day 2000; Doebeli and Dieckmann 2000; Mathias et al. 2001; Day et al. 2002; Doebeli 2002; Schreiber and Tobiasson 2003; Leimar 2005; Rueffler et al. 2006c; Massol et al. 2011; Doebeli 2011; Rueffler et al. 2013; Svardal et al. 2014). The analysis in these models is usually based on the technical assumption of large population size, rare mutations of small effect, and asexual reproduction. Importantly, individual-based simulations have shown repeatedly that the phenomenon of evolutionary branching is remarkably robust against violations of these assumptions (e.g., Dieckmann and Doebeli 1999; Kisdi and Geritz 1999; Proulx and Day 2001; Claessen et al. 2007; van Doorn et al. 2009; Svardal et al. 2011, 2014). For a more technical discussion of the robustness of evolutionary branching, see Champagnat et al. (2006) and Wakano and Iwasa (2013). Importantly, also empirical evidence for negative frequency dependent disruptive selection as a driver of phenotypic diversification is accumulating. Such results come both from field (Smith 1993; Benkman 1996; Kingsolver et al. 2001; Bolnick 2004; Calsbeek and Smith 2007; Pfennig et al. 2007; Bolnick and Lau 2008; Hendry et al. 2009; Martin and Pfennig 2012) and laboratory studies (Buckling and Rainey 2002; Friesen et al. 2004; Meyer and Kassen 2007; Spencer et al. 2008; Tyerman et al. 2008; Kassen 2009; Herron and Doebeli 2013). Together, these findings suggest that evolutionary branching points are an important concept for explaining the origin of biological diversity.

The vast majority of mathematical models in which evolutionary branching points have been identified, including all theoretical studies cited in the previous paragraph, treat evolution in one-dimensional trait spaces. More recently, the phenomenon of evolutionary branching has also been investigated in multidimensional trait spaces, that is, under the premise that the phenotype of individuals is characterized by an n -dimensional trait vector (Kisdi 2002; Vukics et al. 2003; Ackermann and Doebeli 2004; Van Dooren et al. 2004; Egas et al. 2005; Leimar et al. 2006; Ito and Shimada 2007; Ravigné et al. 2009; Doebeli and

Ispolatov 2010; Nurmi and Parvinen 2011; Svardal et al. 2011; Cooper et al. 2011; Débarre et al. 2014; Doebeli and Ispolatov 2014). Some of these studies report that evolutionary branching can occur in multidimensional trait spaces in situations where it cannot occur in the embedded one-dimensional trait spaces. The reason is easily understood. In multidimensional trait spaces, at an evolutionary branching point, the steepest increase in the fitness landscape is often in a direction where several traits change simultaneously, thus, in a composite direction in trait space. In particular, in multidimensional trait spaces, it is possible that selection is stabilizing in the direction of each separate trait whereas selection is disruptive in directions where several traits change in concert. Biologically, this can occur when traits interact in their effect on fitness. For instance, a morphological structure might only be efficient in catching prey if its various parts are compatible with each other in an intricate manner. Then, it is possible to detect stabilizing selection when varying a single trait while keeping the other traits constant and detect disruptive selection when varying several traits simultaneously.

Doebeli and Ispolatov (2010) were the first to address the relationship between organismal complexity and the scope for adaptive phenotypic diversification due to negative frequency dependent selection. They suggest that more complex organisms, as manifested in the dimension of the trait space, are more likely to experience such a selective regime and are therefore more likely to undergo phenotypic diversification. Doebeli and Ispolatov derive their proposition from a numerical experiment based on a classical Lotka–Volterra competition model by Roughgarden (1979) that they adapt to accommodate organisms with an arbitrary number of quantitative traits. More recently, Débarre et al. (2014) extended this finding to a more general class of competition models.

In this article, we revisit the question how organismal complexity affects the propensity for the emergence of phenotypic diversity. In its first part, we address this question independent of any specific underlying ecological model. This approach is based on properties of the Hessian matrix of invasion fitness. This matrix describes the shape of the fitness landscape locally around a potential evolutionary branching point (Metz et al. 1996; Dercole and Rinaldi 2008; Leimar 2009; Doebeli 2011). In this part, we prove that with increasing dimension of the trait space, it becomes more likely that directions in trait space exist in which selection is disruptive, a necessary prerequisite for the existence of an evolutionary branching point.

The previous studies by Doebeli and Ispolatov (2010) and Débarre et al. (2014) as well as our own approach based on the Hessian matrix rest on assumptions whose significance is difficult to evaluate without further investigation and this is our aim in the second part. First, both Doebeli and Ispolatov (2010) and Débarre et al. (2014) derive their predictions from models of “symmetric”

competition. In these models, the strength of competition among individuals only depends on the absolute value of their phenotypic distance. For the case of a one-dimensional trait space, it has been shown that the ensuing adaptive dynamics is, irrespective of the complexity of the underlying ecology, always equivalent to the adaptive dynamics of a symmetric, logistic competition model (Doebeli and Ispolatov 2013). However, for trait spaces with more than one dimension, this is not true in general. Second, both the studies by Doebeli and Ispolatov (2010) and Débarre et al. (2014) are based on the evaluation of many Hessian matrices that are generated according to a simple recipe: all (off-diagonal) entries are drawn from the same distributions over the real numbers irrespective of the dimensionality. Biologically, this assumption means that all traits have the same potential to interact in their effect on fitness, that this potential is independent of the dimension of the trait space, and that the strength of interaction among pairs of traits is independent of each other. Our own approach based on the Hessian matrix relaxes the assumption that all matrix entries are drawn from the same distribution but still assumes that the set of distributions is independent of the dimension of the trait space. These approaches are mathematically convenient but biologically not well motivated. After all, the entries of a Hessian matrix reflect how the morphology and physiology of the individuals in an evolving population affect the interactions with, for example, their prey and predators. A priori, there is no reason to assume that the ensuing complexities at the level of the Hessian matrix are captured by the procedures just described. In particular, we cannot exclude the possibility that, if we were to derive the Hessian matrix from a detailed mechanistic model, the set of possible Hessian matrices would be constrained in a manner that affects the link between complexity and diversity. To address these issues, we derive a Lotka–Volterra competition model from an explicit consumer–resource model in which consumers are characterized by up to five quantitative traits and feed on a resource distribution with up to five dimensions. More precisely, the feeding efficiency of a consumer with a specific set of trait values for different resource items is modeled as a key–keyhole mechanism: the feeding apparatus of the consumer has to match the various properties of a resource item for the consumer to be efficient. In this version of the model, the entries of the Hessian matrix emerge from assumptions at the level of underlying mechanistic traits that can be interpreted at the level of the individual (cf. Rueffler et al. 2006a). As expected, the competition arising from this explicit model is not symmetric. Nevertheless, our analysis again suggests a positive correlation between the complexity of the individuals in the evolving consumer population and their potential for adaptive diversification. An additional insight that, due to their simplicity, cannot emerge from the previous studies is that also increasing resource complexity facilitates evolutionary branching.

Complexity, Evolutionary Branching, and the Hessian Matrix

In this section, we explore the potential link between organismal complexity and diversity independent of any specific ecological model. We start our treatment with a short methodological introduction. We are interested in the evolutionary dynamics of a population in which individuals are characterized by n quantitative traits. Thus, each individual is described by a trait vector $\mathbf{x} = (x_1, \dots, x_n)$. We follow the dynamics of the traits over evolutionary time as it results from mutations and substitutions. Specifically, we are interested in the potential for the evolution of protected polymorphism due to balancing selective forces (i.e., even in the absence of recurrent mutation or genetic constraints such as heterozygote advantage) as a function of the dimensionality of the trait space. This aspect depends primarily on properties of the (variable) fitness landscape of the underlying eco-evolutionary model. This fitness landscape can be explored effectively by assuming a simplified mutational process in a clonal population in which rare mutations of small effect change the trait values from \mathbf{x} to $\mathbf{x}' = \mathbf{x} + \delta\mathbf{x}$ (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998), where mutations can occur in all directions of the trait space. The evolutionary dynamics can then be determined by following a series of mutation–substitution events in which the trait vector \mathbf{x} of the resident population changes over time. The fundamental tool to predict this dynamics is invasion fitness $s(\mathbf{x}', \mathbf{x})$, which is defined as the expected long-term exponential growth rate of an infinitesimally small mutant subpopulation with trait vector \mathbf{x}' in an environment in which all relevant components such as prey, pathogen, and predator densities are determined by the resident population with trait vector \mathbf{x} (Metz et al. 1992; Metz 2008).

In the limit of small mutational steps and rare mutation events, the evolutionary dynamics is approximated by

$$\frac{d\mathbf{x}}{dt} = c(\mathbf{x})\mathbf{M}(\mathbf{x})\mathbf{S}(\mathbf{x}) \quad (1)$$

(Dieckmann and Law 1996; Dercole and Rinaldi 2008; Durinx et al. 2008). Here, the real-valued positive function $c(\mathbf{x})$ accounts for the rate with which new mutants appear and \mathbf{M} is the n -dimensional mutational variance–covariance matrix describing a symmetric distribution of mutations around the resident type \mathbf{x} . Finally, $\mathbf{S}(\mathbf{x})$ denotes the n -dimensional selection gradient with entries

$$S_i(\mathbf{x}) = \left. \frac{\partial s(\mathbf{x}', \mathbf{x})}{\partial x'_i} \right|_{\mathbf{x}'=\mathbf{x}}. \quad (2)$$

We note that a gradient equation for the evolutionary dynamics also results from the quantitative genetics approximation in which it is assumed that all genotypes are present at the same

time. In this case, \mathbf{x} characterizes the mean of the phenotype distribution, the variance–covariance matrix describes the distribution of the standing genetic variation, and the factor $c(\mathbf{x})$ is a constant (Lande 1979; Abrams et al. 1993; Débarre et al. 2014). Points \mathbf{x}^* where $S(\mathbf{x}^*) = 0$ are often referred to as “evolutionarily singular points.” At such points, the evolutionary dynamics as described by equation (1) comes to a halt. For a singular point to be an evolutionary branching point, it has to fulfill four requirements (Metz et al. 1996; Doebeli 2011). (1) The point \mathbf{x}^* has to be an attractor of the evolutionary dynamics. In a more technical language, this means that the point \mathbf{x}^* has to be an asymptotically stable fixed point of the dynamics given by equation (1). (2) The point \mathbf{x}^* has to be locally invadable in at least some directions. (3) In the directions of invadability, nearby mutants on opposite sides of the singular point must be able to coexist in a protected polymorphism. (4) These coexisting types have to experience divergent selection. In one-dimensional trait spaces, the former two properties imply the latter two. However, in higher dimensional trait spaces, this need not to be the case (see Chapter 5, p. 297 in Doebeli 2011 for a discussion).

Here, we focus on the question of invadability of singular points. This property can be evaluated based on the Hessian matrix of invasion fitness (Metz et al. 1996; Leimar 2009; Doebeli 2011). It describes the fitness landscape for rare mutants \mathbf{x}' locally around a singular point \mathbf{x}^* . Invadability is given if and only if the Hessian matrix H of invasion fitness evaluated at \mathbf{x}^* with entries

$$h_{ij} = \left. \frac{\partial^2 s(\mathbf{x}', \mathbf{x}^*)}{\partial x'_i \partial x'_j} \right|_{\mathbf{x}'=\mathbf{x}^*} \quad (3)$$

is not negative-semidefinite, or, equivalently, if and only if its dominant eigenvalue λ_d is positive. Note that the Hessian matrix is necessarily symmetric: $h_{ij} = h_{ji}$. If $\lambda_d > 0$, then \mathbf{x}^* is not a maximum of the fitness landscape but either a minimum or a saddle point and nearby mutants \mathbf{x}' that correspond to a higher point on this fitness landscape are able to invade the population. In this case, selection is disruptive in at least some directions in trait space. In the following, we present two results on how the structure and dimension of the Hessian matrix H affects the magnitude of its dominant eigenvalue λ_d (proofs can be found in Appendix S1):

- (1) Consider a Hessian matrix in which all off-diagonal entries equal zero, that is, H is a diagonal matrix. Biologically, this means that the traits do not interact in their effect on the fitness landscape but act purely additively. However, in organisms characterized by more than one trait we can expect that traits interact in their effect on fitness. Adding nonzero off-diagonal entries to a diagonal matrix either increases or does not affect the dominant eigenvalue. The dominant eigenvalue λ_d strictly increases if the following condition is met. Assume

H is an n -dimensional real diagonal matrix. Let $i \in \{1, \dots, n\}$ be an index such that $h_{ii} \geq h_{jj}$ for all j . Then, changing an entry $h_{ij} = h_{ji}$ to nonzero for at least one $j \neq i$ strictly increases the dominant eigenvalue. Thus, interactions between traits at the level of fitness favor invadability at a singular point. Importantly, this result is independent of the sign of the interaction.

- (2) For symmetric matrices with entries drawn from distributions over the real numbers, the average dominant eigenvalue over all such matrices strictly increases with increasing dimension. In other words, on average, the dominant eigenvalue of symmetric matrices increases with their dimension.

Result (2) is trivial if H is constrained to be a diagonal matrix. In this case, the eigenvalues of H are given by the entries on the diagonal. Then, the higher the dimension of the trait space and, therefore, the higher the dimension of H , the more likely it becomes that at least one diagonal entry h_{ii} exists that is positive. Débarre et al. (2014) refer to this phenomenon as “combinatorial effect.” Importantly, result (2) also holds when selection is stabilizing in the direction of each trait ($h_{ii} < 0$ for all i), that is, in the absence of the combinatorial effect.

Under certain restrictions stronger versions of result (2) can be obtained. Let us consider real symmetric matrices of dimension n with diagonal entries $d < 0$ and independently distributed off-diagonal entries that are drawn from distributions that are symmetric around zero, have equal variance σ^2 , and uniformly bounded higher moments. Under these conditions, Wigner (1958) showed that for very large n , the dominant eigenvalue approaches $2\sigma\sqrt{n} + d$. Thus, the dominant eigenvalue increases linearly in σ and \sqrt{n} . Furthermore, for given σ and d , a singular point becomes invadable when $n > (-d/2\sigma)^2$. These findings are reflected in Figure 1, which shows that the proportion of random matrices with positive dominant eigenvalue increases with increasing σ and n . It is worth mentioning that similar approaches are used in ecology to assess the relationship between stability and complexity in food webs (e.g., May 1972; Allesina and Tang 2012).

The Hessian Matrix and the Doebeli and Ispolatov Model

Doebeli and Ispolatov (2010) derive their results based on a Lotka–Volterra competition model of the form

$$\frac{dN(\mathbf{x}_i)}{dt} = N(\mathbf{x}_i)R(\mathbf{x}_i) \left(1 - \frac{\sum_j \alpha(\mathbf{x}_i, \mathbf{x}_j)N(\mathbf{x}_j)}{K(\mathbf{x}_i)} \right). \quad (4)$$

Here, $N(\mathbf{x}_i)$ denotes the density of individuals characterized by the trait vector \mathbf{x}_i and the summation runs over all phenotypes \mathbf{x}_j present in the population. The competition coefficient

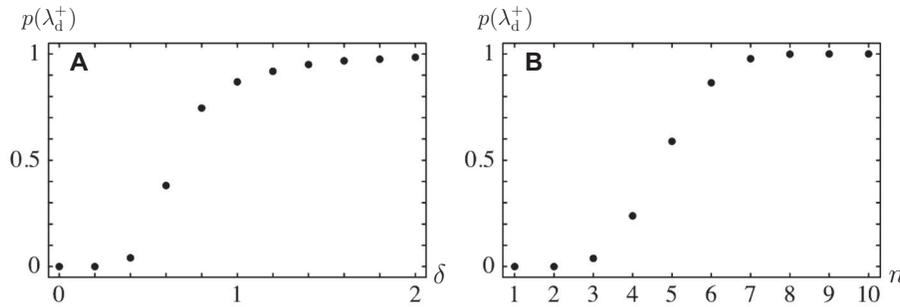


Figure 1. Dependence of the dominant eigenvalue of a symmetric matrix on its off-diagonal entries and its dimension. The y-axis shows the probability $p(\lambda_d^+)$ that the dominant eigenvalue λ_d of a symmetric matrix is positive. Probabilities are calculated as the proportion of matrices with $\lambda_d > 0$ based on 10,000 random matrices. In these matrices, diagonal entries are fixed to $d = -0.3$. Thus, selection is stabilizing in the direction of each separate trait. (A) Off-diagonal entries are drawn from an interval symmetric around zero with a size δ varied along the x-axis. The dimension of the trait space equals $n = 3$. (B) Off-diagonal entries are drawn from the interval $(-0.2, 0.2)$, that is, $\delta = 0.4$. The dimension of the trait space is varied along the x-axis.

$\alpha(x_i, x_j)$ and carrying capacity $K(x_i)$ are given by multivariate Gaussian functions with inverse variance–covariance matrices A and K , respectively. (Recall that an n -dimensional Gaussian distribution with variance–covariance matrix Σ around the mean μ is given by $f(x) = ((2\pi)^n \det \Sigma)^{-1/2} \exp(-1/2(x - \mu)\Sigma^{-1}(x - \mu)^T)$, where the superscripts -1 and T indicate matrix inversion and vector transposition, respectively.) Invasion fitness of a rare mutant with trait vector x' in a monomorphic resident population with trait vector x at its population dynamical equilibrium $K(x)$ is then given by

$$s(x', x) = R(x') \left(1 - \frac{\alpha(x', x)K(x)}{K(x')} \right), \tag{5}$$

where the intrinsic growth rate $R(x') = R$ is assumed to be trait independent. For this model, it is straightforward to show that the Hessian matrix of invasion fitness equals

$$H = [h_{ij}] = [a_{ij} - k_{ij}]2R = (A - K)2R. \tag{6}$$

Doebeli and Ispolatov (2010) evaluate a large number of random matrices A and K with the constraint that selection is stabilizing in the direction of each axis in trait space. They find that the dominant eigenvalue of H is more likely to be positive with increasing dimension of the trait space. Result (2) from the previous section constitutes a proof for this finding and an analogous argument applies to the Lotka–Volterra competition model studied by Débarre et al. (2014).

Evolutionary Branching in Multidimensional Trait Spaces Derived from an Explicit Consumer-Resource Model

In this section, we analyze the effect of organismal complexity on the potential for adaptive diversification based on an explicit

consumer-resource model. This allows us to derive the entries of the Hessian matrix from assumptions that have a mechanistic interpretation at the level of the individual (Rueffler et al. 2006a). More specifically, we choose a Lotka–Volterra consumer-resource model (MacArthur and Levins 1964, 1967) adapted to incorporate a multidimensional consumer trait space and a multivariate resource distribution. Following MacArthur (1972) and Ackermann and Doebeli (2004, see also Doebeli 2011, p. 45), we derive from this a Lotka–Volterra competition model of the form of equation (4). Importantly, the emerging functions describing the carrying capacity and competition coefficient are neither Gaussian functions (as assumed by Doebeli and Ispolatov 2010) nor is the competition function symmetric.

Consider a consumer species in which individuals are characterized by an n -dimensional vector of quantitative traits x that feed on an m -dimensional continuous resource distribution so that each resource item is characterized by an m -dimensional vector z . The density of consumer individuals with trait vector x is denoted by $N(x)$ and the density of resource items described by the vector z is denoted by $F(z)$. The dynamics of consumers and resources is described by

$$\frac{dF(z)}{dt} = F(z)r \left(1 - \frac{F(z)}{S(z)} \right) - F(z) \int e(x, z)N(x)dx \tag{7a}$$

$$\frac{dN(x)}{dt} = N(x) \left(b \int e(x, z)F(z)dz - d \right). \tag{7b}$$

Thus, in the absence of consumers, resources grow logistically with the trait-independent intrinsic growth rate r and trait-dependent carrying capacity $S(z)$. The efficiency with which a consumer of type x feeds a resource of type z is determined by the feeding efficiency $e(x, z)$. Consumer offspring production is proportional to the amount of consumed resources with constant

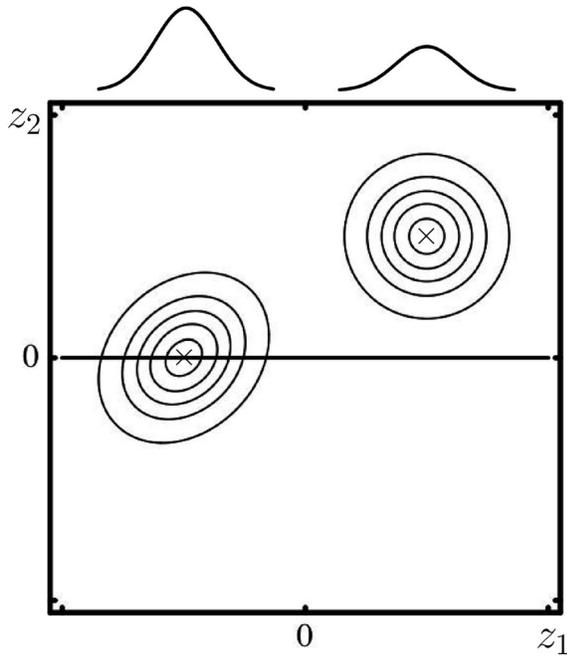


Figure 2. Feeding efficiency $e(x, z)$ as determined by equation 10 for two dimensions. The crosses indicate the trait vectors of two consumers and the contour lines visualize the feeding efficiency as a function of the resource characteristics z_1 and z_2 . The efficiency is maximal for resources with matching characteristics and gradually declines with increasing distance between consumer trait values and resource characteristics. The consumer with trait vector $x = (-0.5, 0)$ is characterized by a matrix E with positive covariance whereas the consumer with trait vector $x = (0.5, 0.5)$ is characterized by a matrix E with zero covariance. If the consumer trait space has one dimension less than the resource distribution (eq. 11c), then consumers are effectively constrained to the horizontal line $x = (x_1, 0)$ and consumers such as the second one are not possible. In this case, consumers are most efficient for resource items with $z_2 = 0$ and become less efficient with increasing deviations of z_2 from zero. In contrast, if the resource distribution has one dimension less than the consumer trait space (eq. 11a), then both consumers are possible. However, there is no resource characteristic z_2 and the feeding efficiency is given by a one-dimensional cross-section as shown above the contour plots. In this case, any deviation from $x_2 = 0$ results in a reduction of the feeding efficiency as indicated by the lower maximum of the curve on the right-hand side.

of proportionality b and consumers die at the constant rate d . From equation (7), we can derive a Lotka–Volterra model for the consumer population dynamics of the form given by equation (4) with

$$R(x) = b \int_z e(x, z)S(z)dz - d \tag{8a}$$

$$K(x) = r \frac{b \int_z e(x, z)S(z)dz - d}{b \int_z e(x, z)^2 S(z)dz} \tag{8b}$$

$$\alpha(x', x) = \frac{\int e(x', z)e(x, z)S(z)dz}{\int e(x', z)^2 S(z)dz} \tag{8c}$$

(Appendix S2). As a consequence, invasion fitness in our explicit consumer resource model is given by equation (5). We note that from the right-hand side of equation (8c), it is evident that the competition function $\alpha(x', x)$ is not symmetric with respect to its arguments.

In the following, we describe the functions $S(x)$ and $e(x, z)$. For the resource carrying capacity, we chose the following Gaussian function:

$$S(z) = s_0 \exp(-zS^T), \tag{9}$$

where s_0 is a positive scaling parameter and $S = [s_{ij}]$ is an m -dimensional inverse variance–covariance matrix. Hence, the carrying capacity of a resource characterized by z decreases with increasing Euclidean distance of z from the zero-vector $\mathbf{0}$.

How does one describe the feeding efficiency of a consumer with n traits for a resource item drawn from an m -dimensional distribution? There is no single answer to this question and here we focus on the scenario that the feeding efficiency can be viewed as depending on the match between the feeding apparatus of the consumer and the structure of the resource analogous to the fit of a key into a keyhole. More specifically, we assume that the feeding efficiency decreases with increasing Euclidean distance between x and z according to the multivariate Gaussian function

$$e(x, z) = e_0(E) \exp(-uEu^T). \tag{10}$$

Here, the matrix $E = [e_{ij}]$ is an inverse variance–covariance matrix with $\dim E = \max\{n, m\}$ and $e_0(E)$ is a positive scaling factor depending on E . The vector u is defined as

$$u = (x_1 - z_1, \dots, x_m - z_m, x_{m+1}, \dots, x_n) \quad \text{for } n > m, \tag{11a}$$

$$u = (x_1 - z_1, \dots, x_n - z_n) \quad \text{for } n = m, \tag{11b}$$

$$u = (x_1 - z_1, \dots, x_n - z_n, -z_{n+1}, \dots, -z_m) \quad \text{for } n < m. \tag{11c}$$

Thus, the i th entry in the vector u describes the distance between the i th consumer trait x_i and i th resource trait z_i . When the dimension of the consumer trait space exceeds the dimension of the resource distribution, we set $z_i = 0$ for $i > m$ (eq. 11a). Biologically, this assumption means that the feeding efficiency decreases for all items of the resource distribution with increasing distance of the “excess traits” from zero. Similarly, when the dimension of

the resource distribution exceeds the dimension of the consumer trait space, we set $x_i = 0$ for $i > n$ (eq. 11c). Biologically, this assumption means that consumers cannot specialize on items of the resource distribution with $z_i \neq 0$ for $i > n$ to the same extent as they can for items of the resource distribution with $z_i = 0$ for $i > n$. Figure 2 serves to illustrate these ideas. Three technical remarks are appropriate here. First, in Appendix S3, we show that without restricting generality, we can assume that S equals the identity matrix I ($s_{ii} = 1$ for $i \in \{1, \dots, m\}$ and $s_{ij} = 0$ for $i \neq j$). Second, equations (11a) and (11c) assume that the lower dimensional space is embedded as a linear subspace in the higher dimensional space. This assumption is required for mathematical tractability. Third, equations (11a) and (11c) imply that the lower dimensional space is embedded into the higher dimensional space such that the former can be described by as many coordinates of the latter as the former has dimensions. This embedding can be assumed without restricting generality (Appendix S3).

Our main interest is the effect of n and m on the sign of the dominant eigenvalue λ_d of the Hessian matrix H , because a positive λ_d implies that the fitness landscape has a minimum in at least some directions. To keep versions of the model that differ in n , m , and E comparable, we perform two normalizations (Appendix S2). First, the total amount of resources in the absence of consumers is normalized to be independent of m (const. = $\int S(z)dz$ for all m). Second, the total amount of resources that is consumed by a consumer individual with the singular strategy \mathbf{x}^* in the absence of competition is scaled to be independent of n and m and of the specific choice of E (const. = $\int e(\mathbf{x}^*, z)S(z)dz$ for all n , m , and E). Furthermore, it is clear that λ_d depends on the consumer's death rate: smaller values of d result in larger values of λ_d . We determine a reference death rate d^* in the following way. We choose $E = I$ and calculate the unique death rate d that results in $\lambda_d = 0$. In other words, given $E = I$ and $d = d^*$, the fitness landscape locally around the singular point \mathbf{x}^* is either flat (if all eigenvalues equal zero) or it has the shape of a crest where the fitness landscape is flat in some directions and curved downwards in others (if some eigenvalues equal zero whereas the other eigenvalues are negative). Due to our normalizations, the reference death rate is independent of m and n .

Our results are then derived from the following numerical experiment. For each combination of n and m , we generate 10,000 symmetric matrices E by drawing the diagonal entries e_{ii} independently and uniformly from the interval $(0, 2)$ and the off-diagonal entries e_{ij} from the intervals $(-\sqrt{e_{ii}e_{jj}}, \sqrt{e_{ii}e_{jj}})$. The latter assumption ensures that E is indeed an inverse variance-covariance matrix. For these matrices, we compute the average of the dominant eigenvalue of the corresponding Hessian matrices (see Appendix S4 for details), its standard error, and the proportion of matrices with positive dominant eigenvalue. The rationale is that each matrix E represents a different species with a different phe-

notypic makeup. Looking at a large set of such phenotypes allows us to determine the effect of the consumer and resource complexity on the potential for evolutionary branching. To single out the effect of interactions between traits on the feeding efficiency, we calculate the average dominant eigenvalue and the proportion of matrices with a positive dominant eigenvalue in two ways: first, after replacing all off-diagonal entries in E with zero, that is, as if E is a diagonal matrix and, second, based on the full matrix E . These results are shown in Figure 3 and discussed in the following. For symmetry reasons, it is clear that the trait value matching the maximum of the resource carrying capacity, $\mathbf{x}^* = \mathbf{0}$, is a singular point. In Appendix S4, we prove that $\mathbf{x}^* = \mathbf{0}$ is an attractor of the evolutionary dynamics described by equation (1) for all n , m , and E , and independent of the mutational variance-covariance matrix M .

Based on our numerical experiment, the following observations can be made (Fig. 3). First, for a given dimension of the consumer trait space, the expected dominant eigenvalue $\bar{\lambda}_d$ increases with increasing dimension of the resource distribution (Fig. 3 A, bars of different gray-scale for the same value of n). For E diagonal, this holds true only as long as $m \leq n$ (lower parts of the same bars). Second, for a given dimension of the resource distribution, the expected dominant eigenvalue $\bar{\lambda}_d$ increases with increasing dimension of the consumer trait space (Fig. 3 A, bars of the same gray-scale for different values of n). For E diagonal, this holds true only as long as $m \leq n$. Third, for consumers with the dimension of the trait space matching the dimension of the resource distribution, the expected dominant eigenvalue $\bar{\lambda}_d$ increases with increasing dimension (Fig. 3 A, bars marked with \diamond). Fourth, for a given n and m , the expected dominant eigenvalue $\bar{\lambda}_d$ increases when adding nonzero off-diagonal entries to a diagonal matrix E . Figure 3 B shows that the same observations hold with respect to the probability $p(\lambda_d^+)$ that the dominant eigenvalue of the Hessian matrix is positive. The only exception to this rule is the case $m = 1$ for which, independent of n , half of the Hessian matrices have a positive dominant eigenvalue. The reason is that in this case, due to our choice for the death rate d , $\lambda_d > 0$ if and only if $e_{11} > 1$. For diagonal entries e_{11} that are randomly drawn from a uniform distribution with mean 1, this condition is fulfilled in approximately half of the cases. We note that the first three observations also hold for the component of the expected dominant eigenvalue that is due to nonzero off-diagonal entries in E alone (upper parts of bars in Fig. 3 A). Thus, the effect of interactions at the level of the feeding efficiency on $\bar{\lambda}_d$ increases with increasing n and m .

The following analytical results help to understand the pattern found in the numerical experiment. We first focus on the case with no interactions between consumer traits on the feeding efficiency, that is, when E is a diagonal matrix. In Appendix S4, we prove that then also H is a diagonal matrix. Consequently, the dominant eigenvalue of H is given by the largest diagonal entry

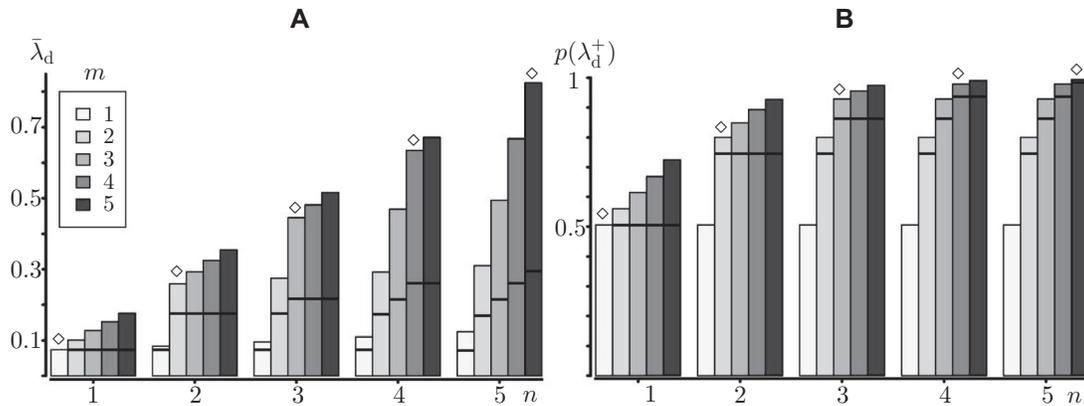


Figure 3. (A) Average dominant eigenvalue of the Hessian matrix, $\bar{\lambda}_d$ (y-axis). (B) Proportion of matrices E that result in a Hessian matrix of invasion fitness with a positive dominant eigenvalue, $p(\lambda_d^+)$ (y-axis). Results are shown for $n \in \{1, \dots, 5\}$ (x-axis) and $m \in \{1, \dots, 5\}$ (shades of gray) and are calculated from 10,000 random matrices E with $e_{ii} \in (0, 2)$ and $e_{ij} \in (-\sqrt{e_{ii}e_{jj}}, \sqrt{e_{ii}e_{jj}})$ for $i \neq j$. Bars are separated into a lower and an upper part by a horizontal line. The lower part gives $\bar{\lambda}_d$ and $p(\lambda_d^+)$, respectively, for E diagonal. The upper part gives the additional increase in $\bar{\lambda}_d$ and $p(\lambda_d^+)$ caused by nonzero off-diagonal entries in E . Thus, the total bar-height shows the effect of random matrices E on $\bar{\lambda}_d$ and $p(\lambda_d^+)$ whereas the lower part shows the effect when the matrices E are constrained to be diagonal matrices. Bars for which $n = m$ are marked with a \diamond . Standard errors in (A) are between 0.001 and 0.002 for the lower part of bars and between 0.001 and 0.004 for the full bars and omitted for clarity. Other parameter values are: $b = 1$, $d = 0.25$.

of H and the eigenvectors of H point in the direction of the coordinate axes of the trait space. Furthermore, each h_{ii} depends on e_{ii} but on no other entry in E . If $n > m$, then the diagonal entries h_{ii} with $i > m$ are negative whereas for the entries h_{ii} with $i \leq n$ the sign depends on e_{ii} . Based on these results, we can draw the following conclusions. For E diagonal, the evolutionary dynamics is determined by the dynamics along each axis of the consumer trait space, and the more such axes exist, the higher the probability that branching is possible along at least one of them. Débarre et al. (2014) refer to this as “combinatorial effect.” Importantly, increasing the number of consumer traits increases the probability for the dominant eigenvalue to be positive only as long as $n \leq m$. If $n > m$, then there are $n - m$ “excess dimensions” to which the combinatorial effect does not apply. This is intuitively clear because the “excess traits” do not interact with any dimension of the resource distribution. In Appendix S4, we prove that in the $n - m$ dimensional subspace spanned by the “excess dimensions” negative frequency dependent selection is absent and that the evolutionary dynamics in this subspace is governed by an optimization criterion sensu Metz et al. (2008). Similarly, increasing the number of resource dimensions increases the probability for the dominant eigenvalue to be positive only as long as $m \leq n$ as can be seen from equation (D11) in Appendix S4.

Next, we focus on the effect of nonzero off-diagonal entries in the matrix E on the dominant eigenvalue λ_d of the Hessian matrix. First, interactions at the level of E result in non-zero off-diagonal entries in the Hessian matrix H . Based on our earlier result that adding nonzero off-diagonal entries to H can increase but never decrease its dominant eigenvalue, it is tempting to conclude that

the same holds true when adding nonzero off-diagonal entries to E . However, equation (D4) in Appendix S4 shows that the diagonal entries of H depend both on the diagonal entries of E and its off-diagonal entries. Thus, adding nonzero off-diagonal entries to E does not correspond to simply adding nonzero off-diagonal entries to H but to changing all its entries and a priori no conclusion can be drawn for the dominant eigenvalue of H . However, in Appendix S5, we prove that locally perturbing a diagonal matrix E by adding ϵL , where L is a real symmetric matrix with $l_{ii} = 0$ and ϵ small, does introduce nonzero off-diagonal entries in H , while up to first order, the diagonal entries of H are unaffected. Thus, at least locally, result (1) from the section “Complexity, Evolutionary Branching, and the Hessian Matrix” can indeed be applied.

Discussion

Is there a relationship between the complexity of an organism as measured by the number of traits that specify its phenotype, and the potential to experience negative frequency dependent disruptive selection promoting the evolution of adaptive phenotypic diversity? Doebeli and Ispolatov (2010) recently showed that, on theoretical grounds, a positive correlation between complexity and diversity is to be expected. This prediction is derived from a symmetric Lotka–Volterra competition model in which the trait-dependent carrying capacity and competition coefficient are described by multivariate Gaussian functions. More recently, Débarre et al. (2014) generalized this finding to Lotka–Volterra competition models with arbitrary unimodal carrying capacity functions and arbitrary symmetric competition functions that only

assume that competition increases with increasing phenotypic similarity.

In the present study, we reexamine the question how organismal complexity interacts with the potential for adaptive diversification from two different angles. First, we show analytically that the potential for disruptive selection is expected to increase the more quantitative traits affect the fitness of individuals in an evolving population. This approach is based on the Hessian matrix of invasion fitness, which describes the shape of the fitness landscape locally around a stationary point of the evolutionary dynamics given by equation (1). More specifically, we show that with increasing dimension of the trait space, it becomes more likely that directions in trait space exist in which the fitness landscape has a local minimum. This is a necessary, albeit not sufficient, prerequisite for the existence of so-called evolutionary branching points (Metz et al. 1996; Geritz et al. 1998; Doebeli 2011), at which negative frequency dependent selection acts to increase phenotypic variation within the population (Rueffler et al. 2006b). This result has been reported by Débarre et al. (2014) for the special case of diagonal Hessian matrices, that is, in the absence of interactions among traits on fitness. They refer to this observation as “combinatorial effect”: the more traits determine fitness, the more likely it becomes that selection is disruptive in at least one of them. Importantly, our result also holds when selection is constrained to be stabilizing along the direction of each axis of the trait space. It therefore constitutes a proof of the numerically derived statements of Doebeli and Ispolatov (2010) and Débarre et al. (2014) that increasing the dimension of the trait space in symmetric competition models makes evolutionary branching more likely even in the absence of the combinatorial effect.

In our second approach, we investigate the interaction of organismal complexity and the potential for adaptive diversification in an explicit consumer resource model. This allows us to relax the following assumptions made by Doebeli and Ispolatov (2010) and Débarre et al. (2014): (1) competition is symmetric, that is, the strength of competitive effects among individuals only depends on their absolute phenotypic distance, (2) the potential for interactions among traits on fitness is identical for all traits, and (3) this potential is independent of the dimension of the trait space. The third assumption is also implicit on our own generalization based on the Hessian matrix. However, it is clear that the entries of a Hessian matrix reflect biology: they describe how the interaction between morphology and physiology of the individuals in the evolving population with their prey, predators, and parasites shapes the fitness landscape. It is therefore important to understand how features of the fitness landscape emerge from underlying mechanistic assumptions that can be interpreted at the level of the individual (Rueffler et al. 2006a) and this is the ultimate goal of our second approach. This mechanistic approach allows us to

include another dimension of biological realism: consumers may clearly vary in their complexity but the same applies to resources! In this analysis, we confirm the finding by Doebeli and Ispolatov and Débarre et al. that evolutionary branching points become more likely with an increasing number of traits that characterize the evolving consumer population. An additional insight is that the potential for evolutionary branching also increases with the number of dimensions that characterize the resource distribution.

Similarly to Doebeli and Ispolatov (2010) and Débarre et al. (2014), we identify the combinatorial effect and interactions between traits on fitness as causal mechanisms for the positive correlation between complexity and the potential for diversification. We discuss these two mechanisms in turn. First, our explicit consumer-resource model shows that increasing the dimension of the consumer trait space beyond the dimension of the resource distribution does not add to the combinatorial effect. Indeed, we are able to prove that for $n > m$, there exists an $n - m$ subspace in which disruptive selection is impossible. Second, based on our analysis of the Hessian matrix, we conclude that introducing interactions among traits on fitness tends to favor disruptive selection. Interestingly, the corresponding finding in our explicit consumer-resource model does not follow from this general result: interactions among traits on the consumer’s feeding efficiency that cause interactions among traits at the fitness level do not only affect the corresponding entries in the Hessian matrix but all its entries. This underpins the necessity of mechanistic models.

In the numerical experiments by Doebeli and Ispolatov (2010) and Débarre et al. (2014), the potential for interactions among traits on fitness is identical for all pairs of traits. This is due to the assumption that the interaction terms are drawn from the same uniform distribution. In our explicit consumer-resource model, we perform a similar numerical experiment but at the level of interactions among traits on the feeding efficiency and investigate the effect on the Hessian matrix. When the dimension of the consumer trait space equals the dimension of the resource distribution, it is clear for symmetry reasons that the distribution of values taken by the off-diagonal entries of the Hessian matrix is identical (but not uniform) for all entries. However, when the dimension of the consumer trait space does not equal the dimension of the resource distribution, the distribution of values taken by the off-diagonal entries of the Hessian matrix differs among entries.

Evolutionary branching requires that a fixed point of the evolutionary dynamics, here called singular point, is both an attractor of the evolutionary dynamics described by equation (1) and invadable by nearby mutants. Doebeli and Ispolatov (2013) show that the first property is always fulfilled in symmetric Lotka–Volterra competition models and is therefore in particular fulfilled in the Lotka–Volterra competition models studied by Doebeli and Ispolatov (2010) and Débarre et al. (2014). We also confirm this

property in our explicit consumer-resource model. Thus, in these models, whether a singular point is invadable does not affect whether it is an attractor of the evolutionary dynamics. However, in principle, these two properties can occur in any combination. One can even argue that increasing the dominant eigenvalue of a Hessian matrix should make it less likely that a singular point is an evolutionary attractor. To see this, note that for a singular point \mathbf{x}^* to be an attractor, it is sufficient that the Jacobian matrix $J = [h_{kl} + q_{kl}]$ of the fitness gradient (eq. 2) is negative definite (Leimar 2009). Here, h_{kl} is given by equation (3) and $q_{kl} = \partial^2 s(\mathbf{x}', \mathbf{x}) / \partial x'_k \partial x_l |_{\mathbf{x}' = \mathbf{x} = \mathbf{x}^*}$. In contrast, if the Jacobian matrix J is not negative semidefinite, then a singular point \mathbf{x}^* can be a repeller of the evolutionary dynamics and evolutionary branching is impossible. From the condition for an evolutionary attractor, one might expect that increasing the dominant eigenvalue of a Hessian matrix makes it less likely that J is negative semidefinite. This point has been investigated more systematically by Débarre et al. (2014) and they show for the Levene model (Levene 1953) that increasing the dimension of the trait space indeed tends to destabilize singular points.

A related issue can arise when modelers decide which parameters in a particular model are considered evolutionary labile and which are considered fixed. Let us assume we are studying the evolutionary dynamics of a single quantitative trait and have established the conditions under which an evolutionary branching point exists for this trait. As a modeler, we could now decide that a previously fixed model parameter should also be subject to evolutionary change, increasing the dimensionality of the trait space from 1 to 2. In this extended trait space, we might find that the previously attracting singular point has turned into an evolutionary saddle point. This means that it is an attractor of the evolutionary dynamics in some directions and a repeller in other directions. Thus, by increasing the complexity of the model, the potential for evolutionary branching has been diminished. Several published models have identified this situation (Ackermann and Doebeli 2004; Van Dooren et al. 2004; Leimar 2005; Svardal et al. 2011). Thus, increasing complexity in this sense can actually decrease the potential for evolutionary branching.

In our consumer-resource model, the traits of the evolving consumer species determine its feeding efficiency for the different resource items according to a key–keyhole mechanism. The obvious example is a complex feeding apparatus that, depending on its size and proportions, is most efficient in consuming a resource item of a specific size and with specific proportions. We suggest that it is scenarios of this kind for which we have good theoretical evidence that more complex structures facilitate evolutionary branching. It is clear, however, that many traits characterizing complex organisms mediate interspecific interactions in other ways and therefore might have a different effect on the potential for evolutionary branching. For instance, traits can act

sequentially during food processing, resulting in a rather different functional form for the feeding efficiency, or different traits can mediate interactions with different prey or pathogen species. In conjunction with the issues raised in the previous two paragraphs, these considerations suggest that a lot remains to be learned about evolutionary diversification in multidimensional trait spaces.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Correlations in fitness and the dimension of the Hessian matrix.

Appendix S2. The Lotka–Volterra consumer resource model.

Appendix S3. The resource and consumer coordinate system.

Appendix S4. Singular point, convergence stability, and invadability.

Appendix S5. Local analysis of the effect of interactions in E on fitness.