
Dynamics of clade diversification on the morphological hypercube

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Understanding the relationship between taxonomic and morphological changes is important in identifying the reasons for accelerated morphological diversification early in the history of animal phyla. Here, a simple general model describing the joint dynamics of taxonomic diversity and morphological disparity is presented and applied to the data on the diversification of blastozoans. I show that the observed patterns of deceleration in clade diversification can be explicable in terms of the geometric structure of the morphospace and the effects of extinction and speciation on morphological disparity without invoking major declines in the size of morphological transitions or taxonomic turnover rates. The model allows testing of hypotheses about patterns of diversification and estimation of rates of morphological evolution. In the case of blastozoans, I find no evidence that major changes in evolutionary rates and mechanisms are responsible for the deceleration of morphological diversification seen during the period of this clade's expansion. At the same time, there is evidence for a moderate decline in overall rates of morphological diversification concordant with a major change (from positive to negative values) in the clade's growth rate.

Keywords: evolution; speciation; extinction; diversification, morphological and taxonomic; blastozoans; mathematical models

1. INTRODUCTION

Rapid morphological diversification early in a clade's history, at relatively low taxonomic diversity, with an apparent slowdown afterwards, represents a commonly observed pattern of radiation of animal life. Among the best known examples are Palaeozoic blastozoans (Foote 1992; Wagner 1995a), bryozoans (Anstey & Pachut 1995) and gastropods (Wagner 1995b), Palaeozoic and Mesozoic crinoids (Foote 1994, 1995, 1996b), Cambrian marine arthropods (Briggs *et al.* 1992; Wills *et al.* 1994) and Ordovician trilobites (Miller & Foote 1996). The pattern of rapid initial increase in morphological disparity, which remains unsurpassed during the history of the clade afterwards, has often been interpreted as evidence for major secular changes in evolutionary rates and mechanisms (Valentine 1969, 1980). Different explanations for these secular changes have been proposed. It has been argued that ecological opportunities were greater in the early history of many clades, that genetic and developmental systems were less canalized early on, and that the nature of adaptation on a 'rugged' adaptive landscape results in a slowdown of the rate of adaptation (e.g. Erwin 1994; Erwin *et al.* 1987; McShea 1993; Valentine 1969, 1980; Valentine *et al.* 1994; Kauffman 1993). Each of these factors can potentially cause a reduction in the probability and/or size of morphological changes with time, which will translate into a decline in the rate of clades' diversification.

In spite of the well-recognized potential importance of the pattern and extensive discussions of its generality and

possible explanations, there have been only few attempts to use formal mathematical models to identify a minimum set of factors sufficient to explain the pattern and to test hypotheses about underlying mechanisms. Existing time-homogeneous models have predicted a linear increase in morphological variance (Slatkin 1981; Foote 1991, 1996a; Valentine *et al.* 1994), reinforcing the belief that something has to change significantly in time to result in the observed patterns. However, some difficulties arise when one tries to apply these dynamical models to data. One reason is that while the models consider single traits that vary continuously and whose evolution is unconstrained, the empirical studies of morphological disparity are typically based on a large number of discrete characters that are always subject to some morphological constraints (geometric, structural, or functional limits on possible trait values). Another reason is that previous modelling frameworks did not include some of the factors that can significantly affect the dynamics of morphological disparity (such as subclade extinction or origination events that do not result in large differences between sister species). Here, I extend the previous work by constructing a more detailed model of the dynamics of clade diversification specifically designed for treating discrete characters, and by applying it to the data on the diversification of blastozoans.

2. MODEL

I consider the evolution of a monophyletic clade driven by extinction, speciation and anagenetic changes. Let us

assume that each lineage in the clade is characterized by L binary morphological traits. A lineage α can be described by a sequence of 0s and 1s of length L : $l^\alpha = (l_1^\alpha, l_2^\alpha, \dots, l_L^\alpha)$ where $l_k^\alpha = 0$ or 1 ($k = 1, \dots, L$). The morphological space is mathematically equivalent to a binary hypercube. In discussing the clade's diversification, it is useful to visualize each lineage as a point on a vertex of the morphological hypercube. Accordingly, a clade will be a cloud of points. Speciation, extinction and anagenesis change the size, location and structure of this cloud. Let us define a morphological 'distance' between lineages α and β as the number of traits at which the lineages are different:

$$d^{\alpha\beta} = \sum_{i=1}^L (l_i^\alpha - l_i^\beta)^2. \quad (1)$$

Distance $d^{\alpha\beta}$ is the standard Hamming distance. I will be interested in the joint dynamics of the number of lineages in the clade N , and the average pairwise distance within the clade $D = \sum_{i < j} d^{ij} / (N(N-1)/2)$. Distance D is a measure of morphological disparity characterizing the spread of the clade in the morphological space.

The dynamics of the clade's size and the morphological disparity have been the focus of previous work (e.g. Slatkin 1981; Foote 1991, 1996a; Valentine *et al.* 1994). Here in addition to N and D , I will consider the average distance of the members of the clade from its species-founder, d . Let ϵ denote the species-founder of the clade. Then $d = \sum_i d^{i\epsilon} / N$. Distance d characterizes the net evolution of the clade from its ancestral state. Below this measure will prove to be very informative and convenient to use in analysing real data. I will model clade evolution as a random walk on the morphological hypercube with births and deaths. That is, I will assume that origination and extinction events, together with morphological changes, can be considered as random (cf. Raup *et al.* 1973; Raup & Gould 1974; Slatkin 1981; McKinney 1990; Foote 1991, 1996a; Valentine *et al.* 1994). This represents a null hypothesis, which must be rejected before introducing additional factors to explain the observed patterns of taxonomic and morphological diversification.

It is convenient to formulate the model in discrete time. I consider two types of morphological changes: anagenetic and cladogenetic. Anagenetic changes are modelled by assuming that during a unit time-interval each trait in a lineage may evolve to an alternative state with a small probability μ_1 . I assume that there are two types of origination events, having probabilities σ_1 and σ_2 , respectively. The origination events of the first type do not result in any immediate differences between two (or more) new lineages into which the old lineage has split. This might be the case when different large parts of a subdivided population become completely isolated by geographical (as in the vicariance speciation scenario, e.g. Lynch (1989)) or reproductive (as in the parapatric speciation scenario, e.g. Gavrilets (1999) and Gavrilets *et al.* (1998)) factors. The origination events of the second type are accompanied by (significant) morphological changes (Eldredge & Gould 1972). This might be the case when speciation takes place in a small (peripheral) population that has undertaken significant morphological evolution before emerging as a new species (as in the peripatric

speciation scenario, e.g. Mayr (1942, 1963)). During such speciation events each trait in a new lineage can evolve to an alternative state with probability μ_2 . I assume that there are two types of extinction events. A lineage can become extinct individually (with probability δ_1) or as a member of a ' T -subclade' simultaneously with all other members (with probability δ_2). Following Derrida & Peliti (1991), I say that two lineages belong to the same T -subclade if their last common ancestor existed T years ago. Extinction of a subclade might happen when some traits that are shared by the members of the subclade 'promote' extinction (McKinney 1997) (say, after a change in the environment). I will assume that all rates defined above are small ($\mu_i, \sigma_i, \delta_i \ll 1$, $i = 1, 2$).

The changes in N , D and d between subsequent time-intervals are described by a system of difference equations (see Appendix A for details):

$$\Delta N = (\sigma - \delta)N, \quad (2a)$$

$$\Delta D = -\left(4\mu + \frac{2\sigma_1}{N} + \delta_2\phi\right)D + 2\mu L, \quad (2b)$$

$$\Delta d = -2\mu\left(d - \frac{L}{2}\right). \quad (2c)$$

Here $\sigma = \sigma_1 + \sigma_2$ and $\delta = \delta_1 + \delta_2$ are the overall rates of speciation and extinction (per unit time-interval per lineage), and ϕ is the proportion of the clade represented by a T -subclade that goes extinct. In general, these rates can change in time and/or with the clade's size. With fossil data, in practice, it will be very difficult to distinguish the two types of speciation events and distinguish anagenetic from cladogenetic morphological change (Wagner & Erwin (1995) discuss some ways to do it), but the overall rates of extinction and origination can be estimated. Parameter $\mu = \mu_1 + \sigma_2\mu_2$ is the overall probability of a morphological change (per trait per unit time-interval per lineage), which incorporates both morphological and taxonomic rates of evolution. Below I describe a simple method for estimating μ from fossil data.

The system of difference equations (2) describing the joint dynamics of N , d and D , can be easily solved numerically. Below I consider several specific cases where solutions can be found analytically. There are also some general qualitative features of the dynamics of morphological evolution which can be deduced from the form of equations (2). The right-hand side of equation (2b) has three negative terms and one positive term. The latter, which is twice the expected number μL of new traits per unit time-interval per lineage, gives the maximum possible rate of increase in morphological disparity D . Each of the three negative terms is proportional to D , meaning they are negligible initially when the clade is confined to a small volume on the hypercube (when D is small), but become increasingly important as the clade diversifies morphologically (when D becomes larger). The first negative term in the right-hand side of equation (2b) is related to the geometric structure of the morphospace: as the clade expands in the morphospace, it becomes less and less probable that a random morphological change will lead outside the volume of the morphospace already occupied by the clade. The second term describes the reduction in

D because of the splitting of lineages into independent units without immediate and significant morphological changes. The third term specifies the reduction in D due to the extinction of subclades. Thus, equation (2b) predicts rapid initial increase in D with a slowdown coming afterwards because of the geometric structure of the morphospace and the effects of extinction and speciation on morphological disparity. The slowdown is expected even when all underlying processes are time-homogeneous.

Let us turn now to variable d . The general solution of equation (2c) can be approximated as

$$d = \frac{L}{2} \left(1 - \exp\left(-\int_0^t 2\mu dt\right) \right). \quad (3)$$

This shows that provided $\mu > 0$, the average distance d of the clade from its ancestral state is always expected to increase monotonically towards the asymptotic value $L/2$. In particular, this dynamical feature is not affected by changes in the rates of extinction, origination and morphological changes.

To illustrate the dynamics of the clade's diversification let us assume that all parameters of the model are constant and that the rate of origination exceeds that of extinction. Let $R = \sigma - \delta$ be the clade's growth rate. In this case, the clade's size increases exponentially:

$$N(t) = \exp(\tau), \quad (4a)$$

the average pairwise distance within the clade tends to $L/(2 + \delta_2\phi/2\mu)$:

$$D(t) = Le^{-a\tau} \exp(b\tau) c b^a [\Gamma(-a, b\tau) - \Gamma(-a, b)], \quad (4b)$$

whereas the average distance from the founder approaches $L/2$:

$$d(t) = \frac{L}{2} [1 - \exp(-c\tau)]. \quad (4c)$$

Here $\tau = Rt$, $a = (4\mu + \delta_2\phi)/R$, $b = 2\sigma_1/R$, $c = 2\mu/R$ and $\Gamma(x, y)$ is the incomplete gamma-function (e.g. Gradshteyn & Ryzhik 1994). The dynamics effectively depend on only three parameters, μ/R , $\delta_2\phi/R$ and σ_1/R , characterizing the probabilities of a morphological change, subclade extinction and speciation of the first type relative to the clade's growth rate. Figure 1 illustrates the patterns of diversification predicted by equations (4). The numerical values used for the overall extinction and origination rates δ and σ are the same as in Foote (1996a) where the estimate of δ was based on Raup's (1991) data, whereas the origination rate σ was set to produce an increase in diversity to about 1000 lineages in 100 million years. The numerical value used for μ was estimated from the blastozoan data (see below). Depending on parameter value, disparity D can increase faster or slower than d . Note that even in the case of exponential increase in the clade's size, the clade's disparity D will approach $L/2$ asymptotically only if there is no subclade extinction ($\delta_2 = 0$). In other situations, the asymptotic value of D will be smaller than $L/2$. For instance, if on average every 50th time-step a subclade representing 50% of the clade goes extinct, then $\delta_2 = 1/50 \times 1/2 = 0.01$, $\phi = 1/2$, and if $\mu = 0.0025$, then D will approach $L/3$. Appendix A lists several other specific cases where equations (2) can be solved analytically. In general, if the clade increases in size

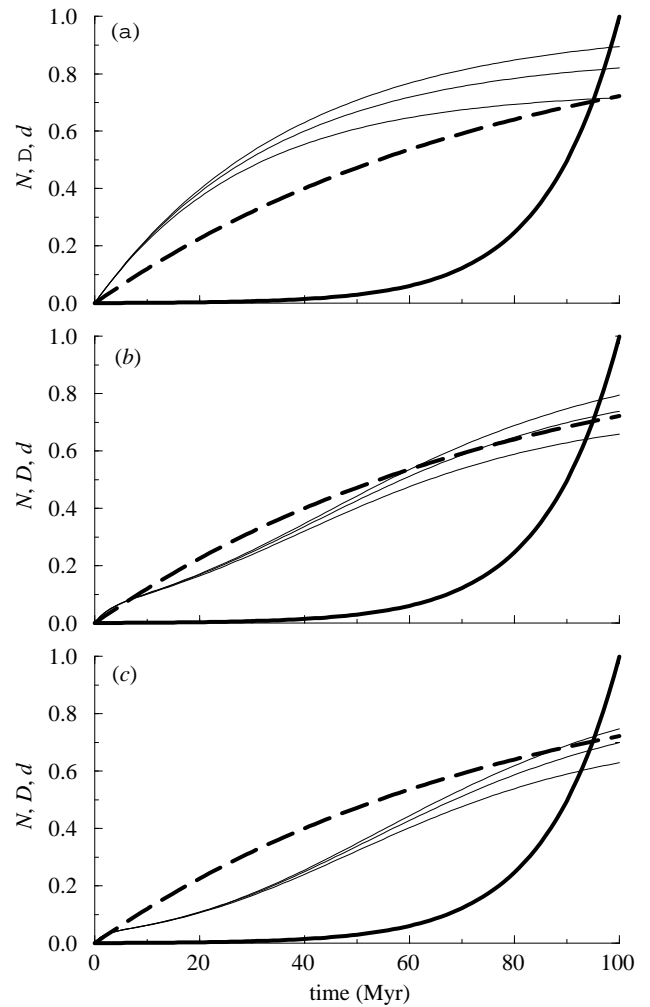


Figure 1. Dynamics of diversification as predicted by equations (4) with $\sigma = 0.32$, $\delta = 0.25$, $\mu = 0.0025$ and the unit time-interval corresponding to one million years (cf. Foote 1996a). (a) Zero probability of speciation of the first type ($\sigma_1 = 0$, $\sigma_2 = 0.32$). (b) Equal probabilities of speciation of the first and second type ($\sigma_1 = 0.16$, $\sigma_2 = 0.16$). (c) Zero probability of speciation of the second type ($\sigma_1 = 0.32$, $\sigma_2 = 0$). Thick lines represent clade size N relative to the size achieved by the end of iterations, $N_{\max} = 1096$. Dashed lines represent the average distance of the clade from the founder relative to the asymptotic value $L/2$. Thin lines show disparity D (normalized relative to $L/2$) corresponding to the extinction every tenth time-step of a subclade representing 10% (top lines), 20% (middle lines) and 30% (lower lines) of the clade.

(if $R > 0$), its morphological diversification is the fastest initially and slows down afterwards. The dynamics of D are close to that in the exponential case, especially during initial stages. If the clade decreases in size (if $R < 0$), its loss of morphological disparity is delayed relative to the loss in the number of lineages (cf. Foote 1993, 1996a).

3. APPLICATION OF THE MODEL

The model presented above provides a framework for studying the complex processes of clade diversification. It can be used to train our intuition about these processes, to identify key components, and to suggest hypotheses that

can be tested against fossil data. Can one use the observed dynamics of D and d for making quantitative inferences about the underlying processes? Using disparity D is complicated because both its dynamics and asymptotic value depend on a number of parameters that may change in time and be difficult to extract from fossil data, such as the relative importance of clade versus species—extinction, the relative importance of phyletic versus cladogenetic change, and the proportion of speciation events that involve significant morphological change. In a wide variety of circumstances, however, distance d is expected to increase regularly towards a fixed asymptotic value $L/2$. Equation (3) implies that $-\ln(1 - 2d/L) = \int_0^t 2\mu dt$. If the overall probability of a morphological change μ does not change (significantly) in time, the integral is simply $2\mu t$ and the dependence of $q = 1 - 2d/L$ on time should be a linear function on the semilog scale. (In statistical physics variable q is known as the average ‘overlap’ between binary sequences, e.g. Derrida & Peliti (1991).) This provides a simple test for approximate constancy of μ . The constancy of μ during a certain period would suggest the constancy of evolutionary rates and mechanisms. Thus, if the rate of increase of disparity D declines over time while the rate of increase of $-\ln(q)$ remains approximately constant, then the explanation of the deceleration of morphological diversification as a consequence of a change in evolutionary rates should be rejected. If $-\ln(q)$ changes as a linear function of time, the slope of the regression line gives an estimate for 2μ . In our model, the overall probability of a morphological change μ is a sum of the phyletic component μ_1 and the cladogenetic component $\mu_2\sigma_2$. Given some information about the patterns of origination in a clade, it should be possible to help constrain the relative importance of phyletic and cladogenetic change. For example, a reduction in σ_2 is supposed to translate into a comparable reduction in μ unless the phyletic component is much larger than the cladogenetic component. Thus, if there is evidence for a change in speciation rate (σ) without a proportional change in the rate of morphological evolution (μ), this suggests a greater role for phyletic evolution than would be suggested by concordant changes in μ and σ . The methods of extracting various information about μ from the clade level data proposed above are potentially useful in general, but especially in those cases in which the phylogenetic information needed to measure ancestor–descendant differences is unavailable.

4. DIVERSIFICATION OF BLASTOZOANS

In the light of the foregoing discussion, I use the model described above to reanalyse the data on the morphological diversification of blastozoans (Foote 1992, 1996a). Subphylum Blastozoa is a monophyletic group of Lower Cambrian to Permian echinoderms (Sprinkle 1973). Foote’s data provide one of the best illustrations of the pattern of accelerated early morphological diversification. The data represent 65 discrete characters measured for 147 species spanning across 12 stratigraphic levels from the Lower Cambrian to the Permian. The data included 49 binary, 11 ordered multistate, and five unordered multistate characters. For binary and unordered multistate characters the distance in a character was zero for

matches and unity for mismatches. Following Foote, to give equal weight to all characters, ordered multistate characters were scaled so that the maximum difference in a character is unity. Morphological distances between species were measured as the total number of differences divided by the number of characters compared, corresponding to d/L and D/L in the notation of the model. The time-scale used was that of Tucker & McKerrow (1995) (with the exception of the Carboniferous and Permian, which are not covered by Tucker & McKerrow and for which I used the Harland *et al.* (1990) scale). The data points were placed in the middle of the intervals. Morphological disparity (D) increases more rapidly than taxonomic diversity (N), reaching one-half of the maximum observed level by the late Cambrian and the maximum observed level by the Middle Ordovician (figure 2a,b). As emphasized earlier (Foote 1992, 1996a), during the period of this clade’s expansion the rate of increase of D apparently declines in time (figure 2b). The taxonomic diversity N grows through the Caradocian and decays after it, suggesting a major change in the pattern of origination and extinction somewhere near the Caradoc–Ashgill boundary. This change coincides with apparent drops in both d and D . A drop in morphological disparity D can be caused by an increase in subclade extinction rates, an increase in the rate of speciation of the first type, the selective extinction of morphologically ‘peripheral’ (relative to the founder) lineages, or the selective proliferation of morphologically ‘central’ lineages, among other factors. A drop in d can be caused by extinction of morphologically ‘peripheral’ lineages and/or by intensive speciation of ‘central’ lineages. The overall decrease in taxonomic diversity N between the Caradocian and Ashgillian suggests the possibility that it may have been increased extinction of morphologically peripheral lineages that caused the drop. Note that the decrease in morphological disparity is delayed relative to the decrease in taxonomic diversity. Distance d continues to increase after the Ordovician, while D declines. The fact that D is low and d is high later in the clade’s history means that the clade forms a compact group evolving far away from the founder. (In this case it is the Blastozoa (M. Foote, personal communication).) This does not necessarily imply directionality in the processes governing clade evolution or species selection. Such behaviour is expected for a completely random walk in a multidimensional space (cf. Charlesworth 1984; Bookstein 1987).

As indicated by the apparent linearity on the semilog scale (figure 2c), the dynamics of d appear to be time-homogeneous from the Lower Cambrian through the Middle Ordovician, and from the Upper Ordovician through the Upper Carboniferous, with the drops in d near the Middle Ordovician–Upper Ordovician boundary and in the Permian. I used this as a justification for splitting the data set into two parts (for computing separate regression lines) and excluding the Permian point. The estimates of μ for the periods from the Lower Cambrian through the Middle Ordovician, and from the Upper Ordovician to the Upper Carboniferous, are $(5.8 \pm 0.4) \times 10^{-3} \text{ Myr}^{-1}$ and $(3.6 \pm 0.2) \times 10^{-3} \text{ Myr}^{-1}$, respectively. For exponential processes, the time-scale is usually characterized in terms of a half-life $T_{1/2}$. The half-life for d is $\ln(2)/(2\mu)$. With

$\mu = 0.0058$ and $\mu = 0.0036$, $T_{1/2}$ is about 60 Myr and 96 Myr, respectively. The linear regressions provide an excellent fit (the r^2 coefficients are 0.983 and 0.986); the slopes are significantly different from zero ($p < 0.001$) and from each other ($p < 0.01$). The increase in the quality of fit gained by fitting two separate lines rather than just one line is significant at $p < 0.01$ (the Snedecor test). The numerical values reported above should be taken with some degree of caution for some of the assumptions underlying the regression methods might be violated. The regression estimates are obviously sensitive to details of time-scale and resolution. The appearance of more precise stratigraphic data would probably require parameter estimates to be re-evaluated but is not expected to change our qualitative conclusions about the diversification of blastozoans.

Overall, the data are compatible with a moderate (38%) reduction in μ that took place near the boundary of the Middle Ordovician and the Upper Ordovician. A decrease in the rate of morphological evolution was also advocated on the basis of the shape of the disparity curve (Foote 1992) and on estimates of morphological separation between closely related taxa (Wagner 1995a). The reduction in μ , however, is not responsible for the apparent deceleration of morphological diversification observed during the first third of the clade's history when μ was apparently constant.

The estimates of μ reported above are very close (proportionally) to estimates reported by Wagner (1995b, 1999), with one major difference (P. J. Wagner, personal communication). His analysis suggests that the rate of morphological evolution of blastozoans during the Lower Cambrian, which could not be estimated from the regression, was much greater than during subsequent intervals. The apparent constancy of μ from the Lower Cambrian to the Upper Ordovician corroborates Smith's (1988) arguments but contradicts those of Campbell & Marshall (1987).

The fossil record shows that there has been significant decline in rates of origination within major taxa through their histories (e.g. Van Valen 1985; Sepkoski 1998). The moderate size of the decrease in μ observed for blastozoans, together with a significant decrease in speciation rates, would suggest that for this clade morphological evolution is driven mainly by anagenetic rather than cladogenetic changes. Although the fact that blastozoan taxonomic diversity increased initially and declined later on (see figure 2a) is compatible with the decline in speciation rates, this is not a definite conclusion. The decline in taxonomic diversity can be caused by an increase in extinction rates rather than by a decrease in origination rates. Additional data are needed for reaching more precise conclusions.

5. DISCUSSION

It is important to realize that apparent secular changes in the rates of morphological evolution for a clade as a whole do not necessarily mean secular changes in the processes acting at the level of individual lineages. In particular, the observed deceleration of morphological disparity does not necessarily imply a decline in the size or probability of morphological changes for individual lineages. The model presented here has demonstrated that

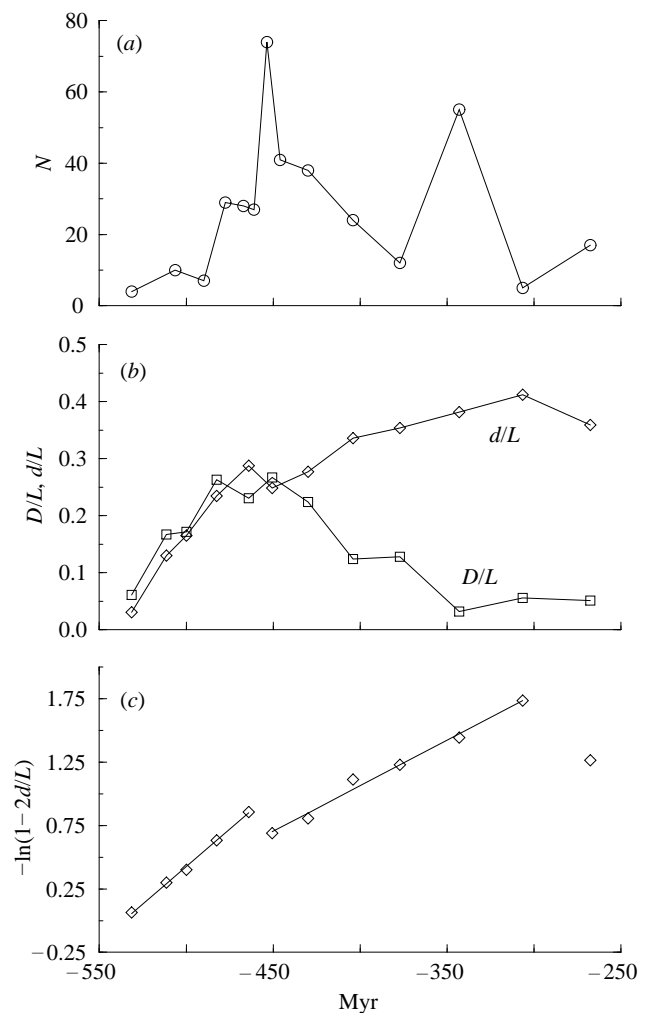


Figure 2. Reanalysis of the data (Foote 1992, 1996a) on the morphological and taxonomic diversification of Blastozoans. (a) The number of genera (which is considered to be a good proxy of the number of species N). (b) Morphological disparity and the average distance from the founder measured as the total number of differences divided by the number of characters compared (corresponding to d/L and D/L in the notation of our model). For each stratigraphic level except the first one, the average distance from the species-founder d was approximated by the average distance between the current level and the first level. For the first stratigraphic level, d was approximated as half of D . (c) Transformed values of d and the corresponding linear regression (see text for more details). The last datum point was not included in computing the regression lines. In (a) the 14 data points correspond to the following stratigraphic levels: Cambrian (Lower, Middle/Upper), Ordovician (Tremadoc, Arenig, Llanvim, Llandeilo, Caradoc, Ashgill), Silurian, Devonian (Lower, Middle/Upper), Carboniferous (Lower, Upper) and Permian. (b, c) A coarser resolution is used with only three Ordovician intervals (Lower, Middle and Upper).

such a deceleration is expected from the geometric structure of the morphospace and the effects of extinction and speciation on morphological disparity, even when all relevant processes are time-homogeneous. These theoretical predictions appear to be very robust. In particular, the differences between exponential and logistic growth in the taxonomic diversity do not translate into significant changes in the corresponding dynamics of morphological diversification. Our basic conclusions will definitely be

valid if the traits have more than two discrete states, and should be valid if the morphological space is continuous rather than discrete, as long as it is finite. In the continuous case, the effects of speciation of the first type and subclade extinction on disparity will be similar to that in the discrete model considered here. Although demonstrating the existence, nature and importance of morphological boundaries can be difficult (McShea 1994; Foote 1996a), it is intuitively obvious that, given they exist, the process of divergence will slow down even if these two factors are absent. The potential importance of the model I present is not only that it quantifies and trains our intuitions, but also that it allows one to test whether, in the case of discrete characters, the observed deceleration in morphological diversification is likely to be a simple consequence of the nature of evolution on a binary hypercube, and thus whether it is necessary to invoke temporal heterogeneities in evolutionary rates and mechanisms to explain an observed pattern. The model makes falsifiable predictions about the dynamics of morphological disparity and the average distance of the clade from its ancestral state, provides a simple method to evaluate the rate of morphological evolution, and suggests an approach for comparing the importance of anagenetic and cladogenetic changes in morphological diversification. In the case of blastozoans, I find no evidence that major changes in evolutionary rates and mechanisms are responsible for the deceleration of morphological diversification seen during the period of this clade's expansion. At the same time, there is evidence for a moderate decline in overall rates of morphological diversification concordant with a major change (from positive to negative values) in the clade's growth rate.

The model has its limitations. The most significant is probably that it describes only average behaviour and says nothing about variation, which will always be present in the fossil record (and numerical simulations). In particular, this makes it difficult to evaluate the statistical power of the test of time-homogeneity proposed above. The model developed above makes no restrictions on morphology in the sense that all character combinations are assumed to be potentially realizable. In terms of the metaphor of 'adaptive landscapes' (Wright 1932), the model assumes a 'flat' landscape similar to those in models of neutral molecular evolution (e.g. Derrida & Peliti 1991). In general, because of genetic, developmental or ecological constraints, some of the possible character combinations can be prohibited. In this case, the morphospace will be mathematically equivalent to a hypercube with 'holes' (with 'holes' representing prohibited character combinations) and the corresponding adaptive landscape will be 'holey' (Gavrillets 1997, 1999; Gavrillets & Gravner 1997; Gavrillets *et al.* 1998) rather than 'flat'. If the proportion of holes is not extremely high, 'viable' character combinations will form a 'giant' cluster extending through the whole morphospace. A characteristic signature of a random walk on the giant cluster appears to be a stretched exponential dependence of overlap q on time (e.g. Lemke & Campbell 1996): $q(t) \approx \exp(-(t/\tau)^\beta)$, where τ and $\beta \leq 1$ are parameters (with no holes $\beta = 1$). The fitting of the stretched exponential curve to blastozoan data has led to inconclusive results: although the fit is good, it is not better

than the fit of a simple exponential curve described above. More detailed data sets are needed for more precise conclusions.

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APPENDIX A

Here I outline the derivation of equations (2) and their solutions.

(a) *Dynamics of N*

The clade's growth rate is equal to the difference between speciation and extinction rates as reflected in equation (2a).

(b) *Dynamics of d*

Extinction of lineages is not expected to change d . Consider a lineage that is different from the founder in d traits. Each new trait in a lineage increases or decreases its distance from the founder by one with probability $1 - d/L$ and d/L , respectively. With L traits, the expected number of new traits is μL . Thus, the overall expected change in d is $\mu L[1 \times (1 - d/L) - 1 \times d/L]$, which reduces to equation (2c).

(c) *Dynamics of D*

Because each lineage in a randomly chosen pair can evolve morphologically, the rate of change in D induced by phyletic evolution and by cladogenesis is twice as big as in the case of d and is $-4\mu(D - L/2)$. Speciation events of the first type will decrease D because the distance between the immediate descendants of a species that has split will be zero. To quantify this effect we will need some notations. Let P be the probability that two randomly chosen lineages originated from a split of a species in the previous time-interval. Probability P can be represented as $P \approx (\text{var}(k)/\bar{k} + \bar{k} - 1)/N$ where \bar{k} and $\text{var}(k)$ are the average and the variance of the number of 'offspring' species that a species leaves (counting itself) in the next time-interval (Crow & Kimura 1970). Assuming that a proportion δ of species goes extinct, whereas the remaining species survive and speciate, the average number of new species per a surviving species is $A = \alpha/(1 - \delta)$. Thus, a species leaves 0 or $i > 0$ 'offspring' with probabilities δ and $(1 - \delta)\exp(-A)A^{i-1}/(i - 1)!$, respectively. This results in $\bar{k} = 1 + \sigma - \delta$ and $\text{var}(k) = \sigma + \delta$ where the last equality assumes that both extinction and speciation rates are small. Substituting into the expression for P given above, one finds that $P \approx 2\sigma/N$ (cf. Derrida & Peliti 1991). Distance D after the speciation events of the first type can be represented as $P\sigma_1/\sigma \times 0 + (1 - P\sigma_1/\sigma) \times D$, where the first term represents the contribution of the pairs of new sister species and the second term represents the contribution of all other species pairs. Thus, the expected reduction in D due to the speciation events of the first type is $-(2\sigma_1/N) \times D$. Finally, consider the effects of extinction. Extinction of individual lineages is not expected to change D . To quantify the effects of subclade extinction, let

us assume that there are f T -subclades ($f \gg 1$) and let D_b be the average morphological distance between two T -subclades. The average distance within the whole clade can be approximated as $D \approx (N/f)^2 D_b f(f-1)/N^2$. Here N/f is the average number of lineages in a subclade, $(N/f)^2 D_b$ is the contribution of a given pair of T -subclades into the total sum of distances, $f(f-1)$ is the number of pairs of T -subclades, and N^2 is the number of terms in the total sum of distances. After extinction of a T -subclade, the number of pairs of T -subclades is $(f-1)(f-2)$, whereas the number of terms in the total sum of distances is $[(1-1/f)N]^2$. Accordingly, the average distance after extinction of a T -subclade is approximately $D_e \approx (N/f)^2 D_b (f-1)(f-2)/[(1-1/f)N]^2$. Calculating the difference of D and D_e one finds that extinction of a T -subclade reduces D by D/f^2 . Let η be the probability of extinction of a T -subclade per unit time-interval. The rate of reduction in D due to T -subclade extinction becomes $D\eta/f^2$, which is equivalent to $D\delta_2\phi$, where $\phi = 1/f$ is the proportion of the clade that goes extinct, and $\delta_2 = \eta\phi$ is the probability that a lineage goes extinct as a member of a T -subclade. Thus, the overall change in D is given by equation (2b).

(d) Some solutions of equations (2)

In the main text, a case with all parameters constant was considered. Here I list several other cases that can be treated analytically. Let the growth rate decrease linearly with the clade's size: $R \equiv \sigma - \delta = r(1 - N/K)$. Then the clade's size approaches the 'carrying capacity' K according to the logistic curve $N(t) = Ke^{\tau t}/(e^{\tau t} + K - 1)$ where $\tau = rt$. The difference between exponential and logistic growth in N should be most important after a transient time when the exponential model predicts very large values of N , whereas in the logistic model N approaches the carrying capacity K . However, if N is large, the second term in the right-hand side of equation (2b) is negligible. Thus, the difference between exponential and logistic models for N is not expected to translate into significant changes in the dynamics of morphological evolution if K is not too small. Below I make this argument more precise. The decrease in the growth rate R with the clade's size can result from decrease in the origination rates and/or increase in the extinction rates. I assume that other parameters do not change. If $\sigma_2 = \text{const.}$, then the dynamics of d are still described by equation (4c). If σ_2 decreases linearly with the clade's size N from $\sigma_2(1)$ to $\sigma_2(K)$, then the dynamics of d are approximated by the equation

$$d(t) = \frac{L}{2} \left[1 - e^{-C\tau} \left(1 + \frac{e^{\tau}}{K} \right)^{2\mu_2 \Delta\sigma_2/\tau} \right]. \tag{A1}$$

Here $C = 2\mu^*/r$, $\mu^* = \mu_1 + \mu_2\sigma_2(1)$, $\Delta\sigma_2 = \sigma_2(1) - \sigma_2(K)$ is the overall change in σ_2 , and it is assumed that $K \gg 1$. To solve equation (2b) analytically when extinction and/or origination rates change with N one needs additional simplifying assumptions. If δ_1 changes with N , whereas all other rates are constant, the dynamics of D are described by (4b) with $a = (4\mu + 2\sigma_1/K + \delta_2\phi)/r$, $b = 2(1 - 1/K)\sigma_1/r$, $c = 2\mu/r$. Note that if the 'carrying capacity' K is large, coefficients a , b and c are close to the values corresponding to the exponential growth case and

the dynamics of D under exponential and logistic growth are similar. If σ_1 decreases linearly with the clade's size N , whereas other rates are constant, D evolves according to equation (4b) with $a = (4\mu + 2(\sigma_1(1) - r)/K)/r$, $b = 2(1 - 1/K)\sigma_1(1)/r$, $c = 2\mu/r$. If the growth rate r is small relative to the origination rate $\sigma_1(1)$, the dynamics of D will be similar to those under exponential growth. If all speciation events are of the second type ($\sigma_1 = 0$) and there is no family extinction ($\delta_2 = 0$), then the dynamics of D are described by the right-hand side of equation (A1) with $C = 4\mu^*/r$. Let the clade's size decrease linearly in time: $N(t) = N(0) - rt$. Then the average pairwise distance D changes according to the equation

$$D(t) = D(0)e^{-a\tau} \left(\frac{N(t)}{N(0)} \right)^b + ca^{b-1} e^{aN(t)} N(t)^b \times [\Gamma(1 - b, aN(t)) - \Gamma(1 - b, aN(0))], \tag{A2}$$

where $\tau = rt$, parameters a , b and c are defined below equation (4b), and $D(0)$ is the initial value of D .

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