

# Dynamics of competing species in a model of adaptive radiation and macroevolution

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We present a simple model of adaptive radiation in evolution based on species competition. Competition is found to promote species divergence and branching, and to dampen the net species production. In the model simulations, high taxonomic diversification and branching take place during the beginning of the radiation. The results show striking similarities with empirical data and highlight the mechanism of competition as an important driving factor for accelerated evolutionary transformation.

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## INTRODUCTION

The process of adaptive radiation (AR) is believed to play a major role in the evolution of diverse life forms on Earth. In the fossil record, large-scale AR's are seen as "explosions" of new taxonomical groups during particularly active periods in time. The greatest AR of all times was the Cambrian explosion that gave rise to most of all the known animal phyla. Small-scale AR's usually occur in limited and isolated environments. A prime example is Darwin's finches on the Galapagos Island that have adapted from a single immigrating species to occupy different ecological niches [1].

Despite great variability in size, AR's share common characteristics. (1) They are initiated when new resources become available to a founder species, e.g., because it develops a key character, or in the wake of a mass extinction. (2) The availability of resources triggers rapid evolution of morphologically distinct groups to fill ecological niches not yet occupied. (3) The creative phase is followed by a longer phase of species multiplication with limited creation of novelty [2].

A characteristic pattern of AR's is that high taxonomic groups are established early and anticipate the creation of low-level groups (Fig. 1). Why does the branching of major groups take place at the origin of the radiation and becomes rare afterward? The question is part of a fundamental controversy that spans the last century of evolutionary thinking, namely, whether the origin and proliferation of novelties has been gradual or whether the history of life has moved in leaps. In other words, are the forces that shape long-term evolution (macroevolution) identical to the ones that operate at the level of individuals (microevolution)?

According to the widely accepted neo-Darwinian theory [2,3], adaptive evolution is a gradual process that is well explained by the conjunction of mutation, natural selection, and genetic drift. Still, other evolutionists argue that macroevolutionary patterns are more than simply the accumulation of microevolutionary processes over long periods of time. For instance, in the macromutation hypothesis [4] it is

claimed that major taxonomic groups have formed as a result of infrequent, but large "jumps" in genotypic appearance. More recently, it is stated in the theory of punctuated equilibrium [5] that evolution proceeds through long periods of stasis "punctuated" by rapid bursts of speciation. The fast proliferation, in turn, leads to selection on higher taxonomic levels and introduces a hierarchical and directed structure to macroevolution [6].

Neither theory is able to account for the uneven appearance of high-level taxa in the fossil record. For example, if large morphological jumps may occur at any time, why is the creation of high taxonomical categories only present in the beginning of a radiation? And which forces prevent the radiation from progressing forever?

It has been argued that genetic stability has increased during evolution, thereby favoring early development of higher taxa [7]; the hypothesis of genetic robustness has also been studied theoretically [8]. An alternative hypothesis that has

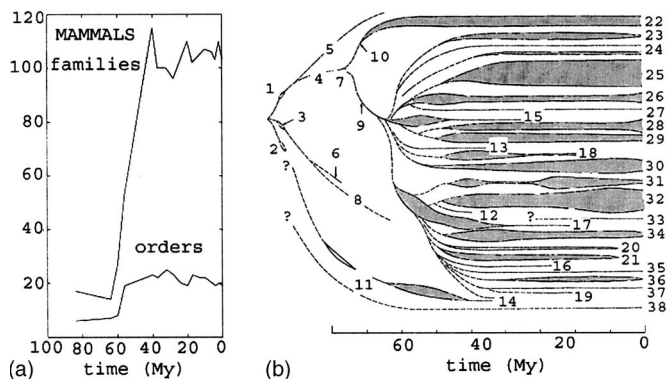


FIG. 1. Adaptive radiation of mammals in the tertiary. (a) Total number of mammalian families and orders as function of time; redrawn from Ref. [25]. (b) Animals and plants are classified in a hierarchical taxonomic system according to kingdom, phyla, class, order, family, genera, and species. The figure is redrawn from Ref. [26] and shows a graphical representation of the evolutionary relationships among orders of mammals (a so-called *phylogenetic tree*). The thickness of each group is proportional to the number of genera in that group. Notice the rapid establishment of basic lineages (here orders); taxa of lower systematic levels (e.g., families, genera) generally peak at later times compared to higher levels [27].

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gained increasing acceptance is that major morphological innovation decreases during the radiation as a consequence of ecological saturation following niche occupation [9]. Valentine *et al.* [10,11] have used computer models to study the influence of ecospace colonization on AR's. In the models, an ecological niche capable of supporting a species is represented by a tessera in a two-dimensional "adaptive space." Thus, each tessera can be occupied by at most one species, and species may colonize new tesserae by sending a daughter species. Local colonization of a neighboring cell (microevolution) is assumed to be more frequent than large jumps spanning the distance of more tessera (macroevolution). Large jumps are mostly successful in the beginning of the radiation when space is relatively free, and hence, the model rightfully explains the uneven appearance of major groups. However, the concept of macromutation is controversial, and the use of tessera makes the model stiff.

Competitive interactions play a key role in ecological dynamics, and competition also appears to be essential for species proliferation. Noticeably, an AR often produces morphologically different species where seemingly no adaptive reason for the diversification exists; e.g., the finches on the Galapagos Islands are similar in key characteristics when occurring on different islands, while they differ markedly when present on the same island. The nonadaptive diversification shows that competition between species exploiting the same resources is important for creation of diversity [1]. Recent laboratory bacterial experiments have significantly increased our understanding of evolutionary processes and suggest that species branching is promoted by competition [12,13]. The test-tube bacterial experiments show spatial patterns, which resemble grand-scale AR's observed in fossil lineages. This apparent scale independence may reflect that small- and large-scale AR's are driven by the same forces of mutation and natural selection [14]. Competition between high taxonomical groups may also play a major role in macroevolution [15].

We present a simple model for the dynamics of AR's based on interspecies competition. In the model we use a morphospace representation of species, which measures the disparity of organisms in shape, form and structure. Each axis quantifies a single phenotypic character, and each species is represented by a single point in the space when measured for the various characters. Phenotypic similarity between species implies that they are likely to exploit the same resources [16]. The observation is used to "translate" competition among species for ecological niches and resources into strong competition among neighboring species in morphospace. However, even species that are far morphologically may compete for common resources, like the competition for light among plants. Long-range competition is accounted for by allowing a finite tail in the competitive interaction for morphologically distant species. The morphometric framework allows a direct comparison with the rate of change and variability in forms in the fossil record.

Methods borrowed from complex system analysis and statistical physics have been applied to study the extinction and origination statistics in the fossil record [17–19]. Instead, only few models have addressed the creative phase of evolution. In the present work we study the dynamics of adap-

tive radiation by seeking for significant morphospace occupation patterns based on a set of simple rules. The model demonstrates that during periods of plentiful ecological opportunities, it is possible to produce rapid and extreme diversification through gradual changes in morphology.

## THE MODEL

Let each species  $S$  be characterized by a fixed number  $D$  of phenotypes  $P = \{p_1, p_2, \dots, p_D\}$ , and let the different phenotypic traits be independent. Then we can symbolize each species in a  $D$ -dimensional morphospace  $M_D$  by a single point. We will use  $D=2$  as a reasonable compromise between unrestricted freedom in the dynamics and fast computation and possibility of visualization. The model dynamics is as follows.

(1) *Initialization.* At the beginning of each simulation, one single species is dumped at a central position in  $M_D$ .

(2) *Speciation.* New species are formed at each time step  $\Delta t$  with a speciation rate  $s$ , which is constant for all species. A new species originates as a propagule from the parent species in a random direction; the distance between parent and offspring is taken to be Gaussian distributed with variance  $\sigma$ .

(3) *Competition.* Species compete for resources and may become extinct if these resources are shared among too many competitors. The extinction probability per time unit  $p_{ext}$  of species  $S_i$  depends on density and relative position on the other species, whilst it is independent on absolute position in  $M_D$ . It is calculated as a sum over all species of the competition function  $f$ :

$$p_{ext}(S_i) = \varepsilon \sum_{j \neq i} f(d_{i,j}), \quad d_{i,j} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}, \quad (1)$$

where  $d_{i,j}$  is the distance between species  $S_i$  and species  $S_j$ , and  $\varepsilon$  is a constant. Lacking a sound biological argument for the functional form of  $f$ , different functions I and II were studied and the robustness of the results was tested against these forms.

*Model I: The smoothed sphere*

$$f_I(d_{i,j}) = \frac{f_0 - f_\infty}{1 + \exp\left(\frac{d_{i,j} - R}{a}\right)} + f_\infty \quad (2)$$

where the radius of short-range competition is controlled by an effective radius  $R$ , and the smoothness of influence is quantified by the diffusivity  $a$ . The competitive interaction between two species is  $f \approx f_0$  (short range) when their distance  $d_{i,j} < R$  and becomes  $f \approx f_\infty$  when  $d_{i,j} > R + 2a$ . In particular, for  $a \rightarrow 0$  the function becomes step sized (hard sphere).

*Model II: A step function with power-law tail*

$$f_{II}(d_{i,j}) = \begin{cases} f_0 & \text{for } d_{i,j} < R, \\ f_0 \left(\frac{d_{i,j}}{R_L}\right)^{-\beta} & \text{for } d_{i,j} \geq R, \end{cases} \quad (3)$$

where again  $R$  is the radius of short-range competition,  $R_L$  is the long-range competition range and  $\beta$  is the scaling constant of the power-law tail.

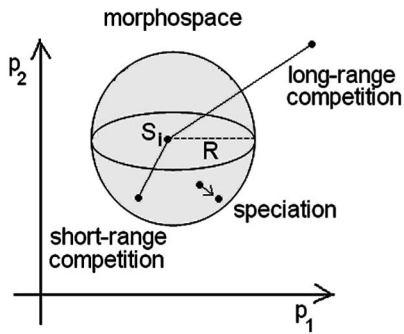


FIG. 2. Model schematics. Species are described by their coordinates in a two-dimensional morphospace defined with reference to two quantifiable phenotypic forms. Species compete with close-by species within a radius of  $r < R$  through a short-range competition function and with species further away through a long-range competition function. New species originate as propagules of the parent species within the short-range competition radius.

The fitness concept is here based on the morphological disparity of a species in comparison with other species, rather than being defined on intrinsic morphological advantages, which is equivalent to stating that the fitness landscape is flat. Since no species is favored, the model dynamics does not contain any real “adaptation” and thus in this work the term adaptive radiation is intended in a broad sense. Introducing a space-dependent fitness would complicate the model without providing new insight into the main study of competitive interactions on morphospace. Finally, population abundance is not explicitly accounted for, as species are identified as points in morphospace. The simulations are run up to 300 000 time steps. The basic ingredients of the model are summarized in Fig. 2.

**RESULTS**

Numerical calculations were performed with different forms of the short-and long-range competition function. In

all simulations the short-range radius  $R$  was chosen larger than the speciation range  $\sigma$  so that speciation takes place within the range of the short-range competition.

**Morphological diversification**

Figure 3 shows the results of a simulation with a power-law decaying tail of the competition function (model II). The number of species follows a growth curve reminiscent of a logistic growth, with rapid diversification in the beginning that slowly decelerated to reach a constant level [Fig. 3(a)]. A closer look at the early phase [inset of Fig. 3(a)] reveals that the increase in species number is stepwise interrupted by static periods that prolong with time. The nonuniform growth in the beginning of the radiation is further illustrated by plotting the mean square morphological distance of the entire species distribution [Fig. 3(b)]. It is seen that the separation in phenotypic traits after a sufficiently long time increases roughly with  $\sqrt{t}$ , indicating a diffusion-controlled divergence in morphological appearance of the species. The effect is independent of the form of competition function, provided it does not drop abruptly as a function of the distance in morphospace.

The general features of the model can be understood analytically by studying the species density distribution  $\Lambda(x, t)$ . When  $R > \sigma$ , the species development can be treated as a pointlike process, and  $\Lambda(x, t)$  evolves approximately as

$$\frac{\partial \Lambda(x, t)}{\partial t} \approx s \Lambda(x, t) - \hat{E} \Lambda(x, t) + K \sigma^2 s \nabla^2 \Lambda(x, t) \quad (4)$$

where  $s$  is the speciation rate and  $K$  is a geometrical constant. The first term defines local proliferation of species, the second term is the extinction caused by competition, and the last term is a diffusion term accounting for the fact that speciation is nonlocal with a range  $\sigma$ . The extinction kernel is given by

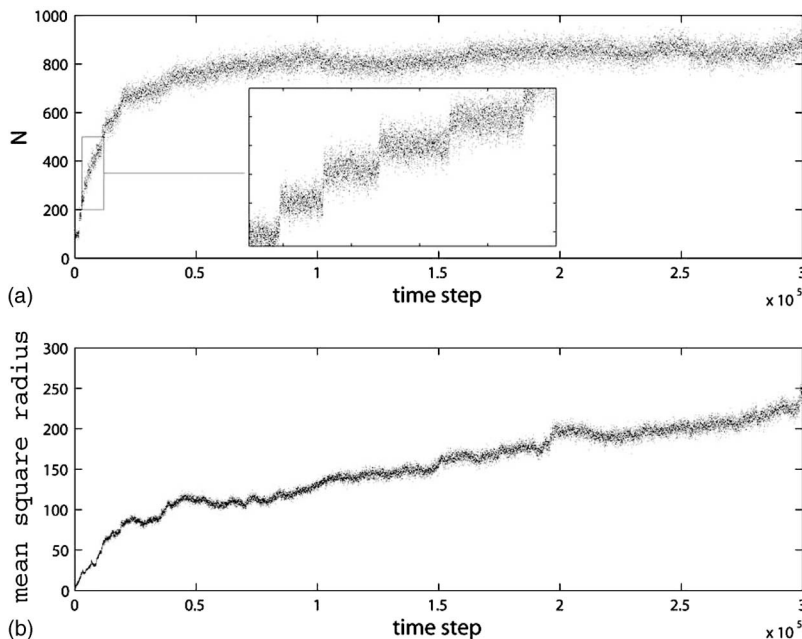


FIG. 3. Species number and morphological disparity. (a) Number of species plotted as function of time; the inset shows the initial phase displaying steplike growth. The simulation is made using a constant short-range competition function with a power-law tail for long-ranges (model II). The constants are  $\sigma=1$ ,  $R=20\sigma$ ,  $\beta=0.1$ ,  $\epsilon=0.8$ ,  $f_0=1$ ,  $s=100$ ,  $dt=0.005$ , and  $R_L=30\sigma$ . (b) The mean square radius of the species density distribution  $\langle r^2 \rangle = \sqrt{(x_j^2 + y_j^2)}$  plotted as a function of time. The competition function and parameters are identical to the case described above.

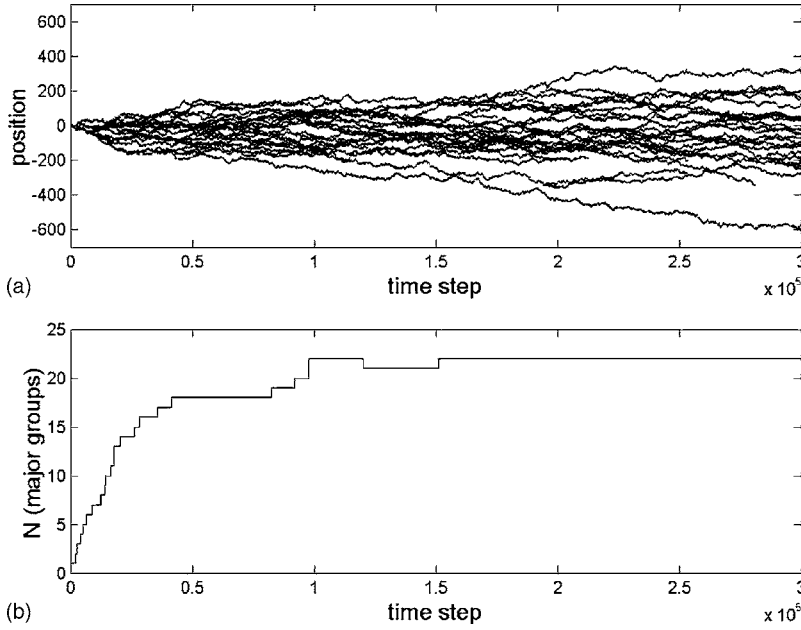


FIG. 4. Phylogenetic tree and lineage dynamics. (a) A phylogenetic tree constructed by plotting the  $y$  coordinate of all living species as function of time. (b) The number of lineages plotted as function of time. Note that the morphospace is bidimensional, and therefore the occupation patterns are partly masked by the superposition of lineages on the same line of sight.

$$\hat{E} = \varepsilon \int_{M_2} d^2x f(x-x') \Lambda(x', t) \quad (5)$$

where we have explicitly set  $D=2$  for the morphospace  $M_D$  and the integration is carried out over the entire morphospace. First, we consider the long-distance behavior ( $d > R$ ); substituting the competition function  $f$  with its average value  $\bar{f}$ , the extinction kernel can be written as  $\hat{E} \approx \varepsilon \bar{f} N(t)$ , where  $N(t)$  is the total number of species,

$$N(t) = \int_{M_2} d^2x \Lambda(x, t). \quad (6)$$

By integrating Eq. (6) and using Eq. (4), we find upon application of Gauss's theorem the time-differentiated species number to be

$$\frac{dN(t)}{dt} \approx sN(t) - \varepsilon \bar{f} N^2(t), \quad (7)$$

which shows that the growth is sigmoidal, i.e., the species number initially increases exponentially to reach an asymptotic value  $N(t \rightarrow \infty) \equiv \bar{N} = s/(\varepsilon \bar{f})$ . The limit corresponds to the plateau in Fig. 3(a).

We now turn to the large-scale behavior of the model. For simplicity we may neglect short-range competition and the evolution of the species density distribution becomes

$$\frac{\partial \Lambda(x, t)}{\partial t} = s\Lambda(x, t) + K\sigma^2 s \nabla^2 \Lambda(x, t) - \varepsilon \bar{f} N(t) \Lambda(x, t). \quad (8)$$

The diffusion-controlled species divergence from the center of radiation can be understood by defining the Fourier transformation of the species density distribution

$$\Lambda(k; t) = \int_{M_2} d^2x \exp(ikx) \Lambda(x). \quad (9)$$

Substituting Eq. (8) in Eq. (9), the decay of each mode is found to be

$$\Lambda(k; t) \propto \exp[(-k^2 K \sigma^2 s - \varepsilon \bar{f} N(t) + s)t]. \quad (10)$$

By using Eq. (4) to calculate  $\Lambda(k; t)$  [20], the mean square radius of the distribution becomes

$$\langle r^2 \rangle = \int_{M_2} d^2x x^2 \Lambda(x) \approx 4\sigma^2 s K t \exp\{[s - \varepsilon \bar{f} N(t)]t\}. \quad (11)$$

Here it is assumed that the species density distribution is symmetrical around the radiation center. For sufficiently long times, the total species number  $N(t) \approx s/(\varepsilon \bar{f})$  and thus  $\langle r^2 \rangle \approx 4\sigma^2 s K t$ , hence the process is diffusive with a diffusion constant  $D_{diff} = \sqrt{4\sigma^2 s K}$ . However, at the beginning of the radiation, before the species number saturates, the mean square radius of species distribution grows exponentially. One can speculate that the transition between exponential and diffusive growth may parallel the rapid morphological expansion typical of the initial phase of an adaptive radiation followed by slow accretion in the late stages. Because there are physical constraints on the morphology, it is possible that a nonflat fitness landscape at the edges of morphospace may contribute to slow down the adaptive radiation, although this is not required by the model.

### The branching process

Figure 4(a) shows an artificial phylogenetic tree obtained by plotting the  $y$  coordinate in  $M_D$  of all species present at a given time. The figure shows that species are not uniformly distributed, rather they appear to form clearly separated lineages. Although species from different lineages compete



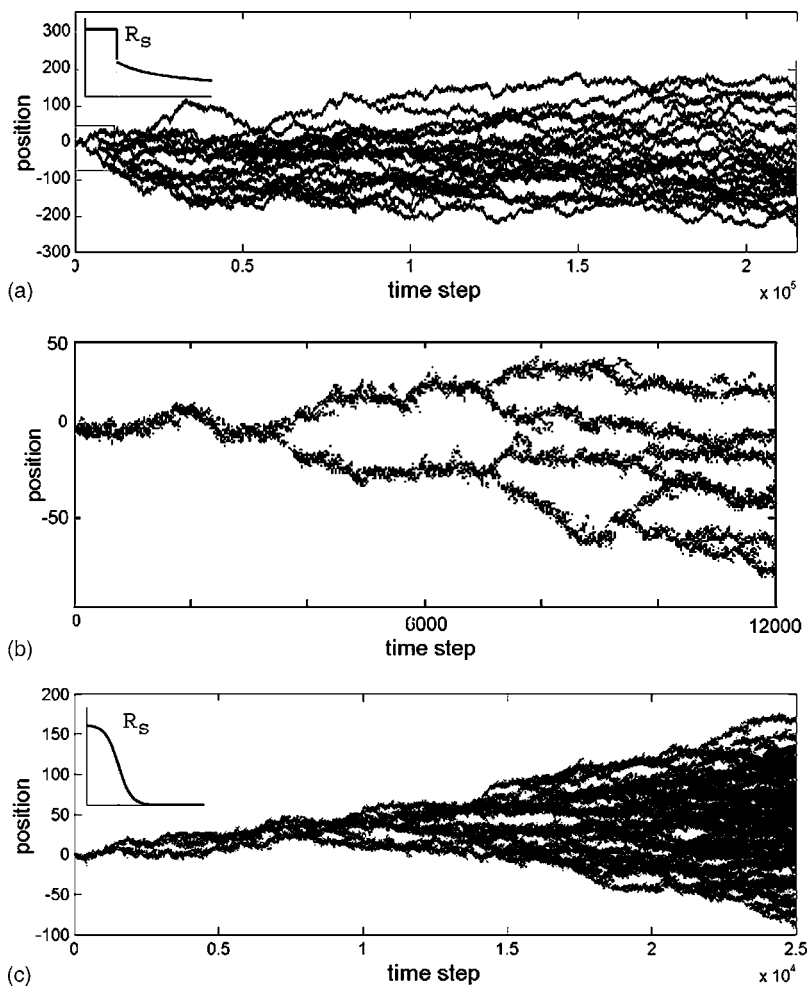


FIG. 5. Lineage dynamics with different competition functions: The number of lineages plotted as a function of time. (a) Smoothed sphere competition with finite long-range competition (model I). Parameter values are  $\sigma=1$ ,  $R=20\sigma$ ,  $\varepsilon=0.8$ ,  $s=100$ ,  $dt=0.005$ ,  $f_0=1$ ,  $f_\infty=0.2$ , and  $a=2$ . (b) Magnification of the first 12 000 time steps of same simulation. (c) Smoothed sphere competition with long-range competition dropping to zero (model I). Parameter values as in (a) except that  $f_\infty=0$ .

with each other, lineages do not intersect [the apparent crossing of lineages in Fig. 4(a) is due to the one-dimensional projection of the plane]. By comparison with Fig. 3(a), it is clear that the observed stepwise growth corresponds to the creation of new lineages.

Branching is controlled by short-range competition. Consider a radiation stemming from one single species, and let us for simplicity assume a stepwise competition function (model I). In the beginning, species are few and their number grows exponentially. At some point the cluster reaches a local equilibrium density  $\Lambda_{eq}=s/(\varepsilon\bar{f})$ , where the number of species going extinct per unit time equals the number of speciation events. From this point in time, the cluster will grow in size while maintaining an almost constant number of species. After a time  $\tau \approx R^2/(2s\sigma^2)$ , when the diameter of the cluster reaches the size of the short-range competition ( $D_{cluster} \approx R$ ), the competition felt by species at the periphery diminishes because species residing opposite on the cluster becomes sufficiently far. Consequently, peripheral species tend to survive longer and have the potential to originate a new branch. In morphospace one observes that the cluster splits in a characteristic “fission effect.”

#### Lineage dynamics

Figure 4(b) reports the total number of lineages as a function of time. The graph is made by counting the number of

separate clusters at fixed times; despite some uncertainty with the identity of cluster in few cases, the cluster number could be identified with high precision. It is seen that the generation of new lineages is concentrated at the early phase of the radiation.

The hindrance to further branching is an effect of the long-range competition (see the Appendix). With time, when species become numerous and occupy larger portions of morphospace, the survival advantage of peripheral species is greatly lost because they begin to experience long-range competition from species belonging to other clusters. Thus, the splitting rate of new lineages drops. Another interesting property of the spatial occupation pattern is the spontaneous appearance of empty zones or voids in morphospace. This effect is a result of increased extinction rate for species occupying the region between approaching lineages.

#### Dependence of competition function and of dimensionality

The influence of the interspecies competition on the temporal occupation pattern in morphospace is studied by simulations using different forms of competition functions (Fig. 5). Provided that the long-range competition remains finite, all cluster separations are found early in the radiation process [Fig. 5(a); cf. Fig. 4(a)]. Hence, the results are insensitive to the fine details of the competition function. Figure

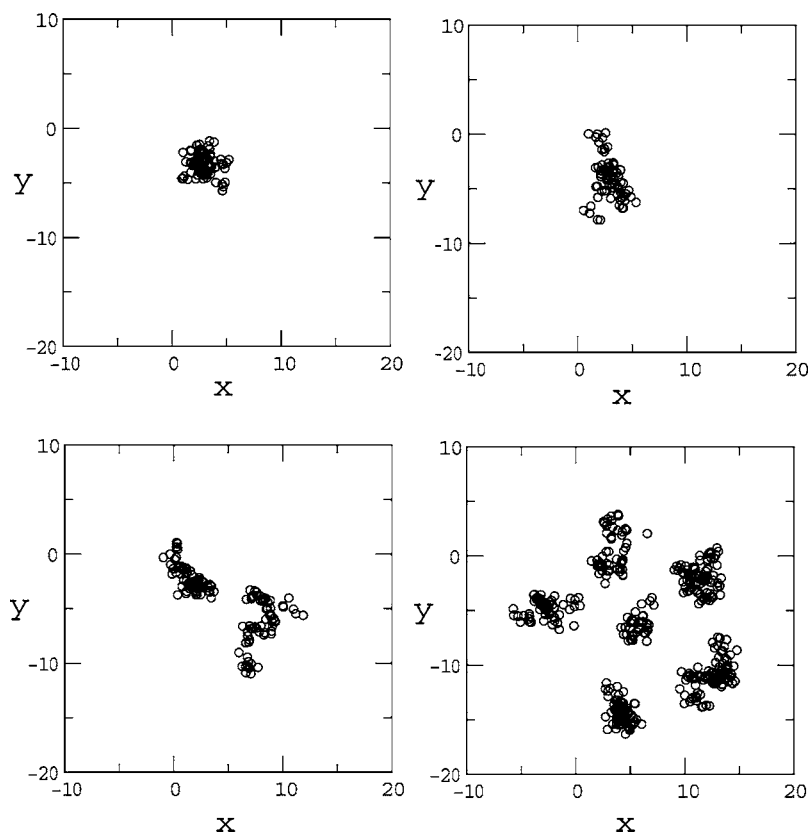


FIG. 6. Branching: Species distribution in morphospace at four different times. Top left, after 1000 time steps from the beginning of the simulation; top right, after 2000 time steps; bottom left, after 3000 time steps; bottom right, after 8000 time steps. The figure shows the dynamics of cluster fission during branching and the regular cluster distribution in morphospace. Model II with  $\sigma=1$ ,  $R=18\sigma$ ,  $\beta=0.1$ ,  $\varepsilon=0.8$ ,  $f_0=1$ ,  $s=80$ ,  $dt=0.005$ , and  $R_L=30\sigma$ .

5(b) is a blowup of the early phase of the same simulation and shows in more details the branching pattern. Notice the numerous aborted branches, which commonly arise from central species. If the long-range competition goes to zero, the creation of new lineages is found to continue in time [Fig. 5(c)]. This demonstrates the role of long-range competition in dampening the branching at later stages. The morphological clusters tend to occupy regular positions with nearly constant average distance from nearest neighbors (Fig. 6) and branching is visible as “fissioned” clusters.

## DISCUSSION

Most of present biodiversity has evolved through explosive diversifications of coexisting species during adaptive radiations [21]. With use of a simple stochastic model we have studied the ecological hypothesis that the ultimate cause of AR's is species competition due to resource depletion, which leads to divergent selection for different habitats and ecological niches.

The present model is aimed at describing the morphological divergence of species in a statistical sense, and the results (Figs. 3–6) bear interesting qualitative resemblances to real AR's. First, the morphological diversification of species is faster at the beginning of the radiation and decreases with time, as shown by the temporal mean square radius of the species distribution, which initially growth exponentially and then as a diffusive process. Second, lineages are created spontaneously through branching processes; during further evolution these groups remain isolated from species belonging to other lineages and interact only through long-range

competition. Thus, the model suggests that competition is the driving force for creation of voids and patches in morphospace. Third, the creation of new lineages is concentrated in the early stages of the radiation, thereafter their number remains approximately constant with time. Finally, the occupation in morphospace remains limited after the initial phase (although the occupied volume continues to expand slowly) without the need to impose boundaries. In short, the model suggests a scenario for establishment of higher taxonomic groups, which accounts for biological data, without the use of extraordinary evolutionary jumps or phenotypic restrictions. From the numerous simulations performed, we can state that the significant patterns of the model are qualitatively robust, and independent of the exact form of the competition function.

The model described here is closely related to the Turing mechanism in chemical and biological systems [22]. Turing considered an ensemble of building blocks (e.g., molecules) that are activated by an autocatalytic activator, a substance produced by the molecules themselves. At the same time, molecules also produce a fast-diffusing inhibitor, which deactivates them. This combination of activation, inhibition, and diffusion is widely used to explain pattern formation in chemical and biological systems [22]. The similarity with our model follows by identifying speciation and short-range competition with the activation and the inhibition processes, respectively. It is possible that the model presented here may provide a particle analogue to Turing's mechanism with applications to other fields beyond adaptive radiations.

Competition between (haploid) organisms is studied, for example, in the model of Bagnoli and Bezzi [23] where,

similar to the present work, competition substitutes the chemical inhibitor originally introduced by Turing.

The dimensionality of morphospace affects the maximum number of neighbouring clusters that can exist. In the two-dimensional model explored here, mutually repulsive clusters tend to occupy the plane in a regular lattice at a distance of the order  $R$  (neglecting the long-range competition). The maximum number of clusters surrounding a central one is 6, equal to the number of vertices in a regular hexagon. Extrapolating this reasoning to three dimensions, one would expect the formation of 12 clusters at a distance of  $0.95R$ , approximated by the number of vertices in an icosahedron. Hence, increasing the dimensionality of morphospace entails greater potential for high-level taxa to be founded. However, the effect is quantitative and does not change the qualitative properties of the model.

It is difficult to analyze the results beyond the two-dimensional case  $D=2$ . The one-dimensional case  $D=1$  is easier, since the shape of lineages can be more directly traced. Results from the simulations were found comparable to the two-dimensional case. The case  $D=1$  could be useful for a more strict comparison to biological data. For example, one can calculate the number of branches leading to a stable progeny (these branches correspond to the ones with long-lasting progeny in the mammal data of Fig. 1). The one-dimensional simulations indicate that dead branches are very rare at the beginning of the simulated adaptive radiation, and become more common at a later stage. The one-dimensional case could also be useful to investigate the prediction of the model on the observed fractal character of taxonomical distribution of organisms.

Some generalizations of the model have been carried out. (1) Simulations have been performed where each species  $S_i$  is assigned with randomly chosen short-range competition ranges  $R=R_i$ . This modification did not change the general trend of the results. (2) To simulate phyletic evolution, i.e., phenotypic changes in time without real speciation events, a diffusion term was added to the Gaussian distribution of species coordinates in time. The effect of this change was also not noticeable.

The model could be implemented in many ways. First, it does not account for population dynamics but represents each species as a single point in morphospace. It would be possible to introduce species abundance based on Lotka-Volterra coupled equations with a competition term depending explicitly on the distance in morphospace. This would complicate tremendously the numerical solution, and we speculate that the results would not appear as radically different. Population-based models are currently investigated in connection with sympatric speciation [24]. Another possible implementation is the introduction of spatial extension of populations. Because populations can migrate to avoid competing with strong neighbors, spatial extension will relieve competition between species at the beginning of the radiation, when space is still free. The effect probably diminishes of importance at later times, when the whole space becomes more densely populated and species distributions become frozen in space.

Finally, in a more detailed model one could introduce predation and trophic levels, although this is not conceptually

straightforward in a morphospace representation, since predation does not necessarily depend on morphological disparity between species.

#### APPENDIX: ANALYTICAL ESTIMATE OF TEMPORAL BRANCHING RATE

The decreasing branching rate during the progression of an AR is derived analytically. Consider a step-sized competition function given by

$$f(d_{i,j}) = \begin{cases} \varepsilon f_0, & d_{i,j} < R, \\ \varepsilon f_\infty, & d_{i,j} \geq R, \end{cases} \quad (\text{A1})$$

where  $f_0 < f_\infty$ . With time species become arranged in clusters that develop into separate lineages. Let there be  $C$  clusters at a given point in time that each contains  $m$  species, where  $m \geq 1$ . The number of species in a cluster evolves according to

$$\frac{dm}{dt} \approx sm - \varepsilon[f_0(m-1)^2 + f_\infty m^2 C] \approx sm - \varepsilon m^2(f_0 + f_\infty C). \quad (\text{A2})$$

Here the first term describes the proliferation of species, the second term is the short-range competition from the  $(m-1)$  other species belonging to the same cluster, and the third term is the long-range competition from  $mC$  species inside external clusters. The equilibrium number of species in a cluster is found from Eq. (A2) to be

$$\bar{m} = \frac{s}{\varepsilon f_0 + f_\infty C}. \quad (\text{A3})$$

The species number in a cluster changes slowly during the splitting of a new lineage, and in this case we may use that  $m \approx \bar{m}$ .

The generation of new lineages occurs at the edge of clusters where the short-range competition is reduced. The lowered short-range interaction can be quantified by the factor  $\chi \leq 1$ . Thus, for a central species  $\chi \approx 1$ , while a species at the cluster border has  $\chi < 1$ . The probability per unit time that a species will form a new lineage is given by

$$\frac{dp}{dt} = s - \varepsilon \bar{m}(f_0 \chi + f_\infty C) = s \left( 1 - \frac{f_0 \chi + f_\infty C}{f_0 + f_\infty C} \right) \quad (\text{A4})$$

where the right hand side expression is found by insertion of Eq. (A3). The probability has the limiting behavior

$$\lim_{t \rightarrow \infty} \left( \frac{dp}{dt} \right) = s(1 - \chi), \quad \lim_{t \rightarrow \infty} \left( \frac{dp}{dt} \right) = 0, \quad (\text{A5})$$

showing the potential for new lineages to form at early stages when few clusters are present ( $C \approx 0$ ), while in later stages when clusters are numerous, the survival probability of the colonizer drops to zero.

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- [27] The numbers between 1 and 21 refer to extinct orders and scattered genera usually poorly represented in the fossil record. 22, Marsupialia; 23, Edentata; 24, Lagomorpha; 25, Rodentia; 26, Primates; 27, Dermoptera; 28, Chiroptera; 29, Insectivora; 30, Carnivora; 31, Cetacea; 32, Artiodactyla; 33, Tubulidentata; 34, Perissodactyla; 35, Hyracoidea; 36, Proboscidea; 37, Sirenia; 38, Monotremata.