Competition between cryptic species explains variations in rates of lineage evolution

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Gradual evolution is a common phenomenon in the fossil record of marine microplankton, yet no theoretical model has so far been presented to explain the observed pattern of unidirectionality in trait evolution lasting over tens of millions of generations. Recent molecular genetic data show that the majority of microfossil-producing plankton groups harbors substantial cryptic diversity. Here, we examine the effect of cryptic diversity on apparent rates of lineage evolution. By using a theoretical approach, we show that under resource competition, an increasing number of sibling species within a hypothetical lineage leads to an exponential slowdown of the apparent rate of evolution. This mechanism explains both the remarkable variation in apparent rates of evolution observed in marine plankton, as well as the presence of long gradual evolutionary trends.

evolutionary rate | foraminifera | fossils | diversity | ecological dynamics

The fossil record of marine microplankton has been instrumental in providing quantitative data on the rates and patterns of morphological evolution. Contrary to terrestrial and shallow-marine settings, deep-sea sediments routinely provide long, well dated, continuous sequences documenting changes in the morphology of the fossilized remains of marine plankton at the resolution of a few thousand years (1). The data on evolutionary rates of marine microplankton (mostly planktonic foraminifera) derived from the fossil record indicate a striking range of rates of lineage evolution: whereas some transitions are completed in $<10^5$ to 10^6 generations [assuming a monthly reproductive cycle in planktonic foraminifera (2)] (3–5), long unidirectional trends in morphological traits have been documented to last $>10^7$ or even 10^8 generations (6–10) (Fig. 1).

The remarkably slow rate of morphological evolution in some marine microplankton lineages has attracted considerable attention, particularly because long-lasting gradual trends are not easy to accommodate within neo-Darwinian evolutionary mechanisms (11). However, no appropriate explanation has ever been put forward. The apparent rate of morphological evolution in these lineages appears much slower than predicted by classical evolutionary theory (12). Lande (13) postulated that the gradual patterns could represent random genetic drift, but increasingly sophisticated statistical analyses of the *Contusotrucana* lineage (10) (Fig. 1), for example, indicated a significantly directional component deviating from random null models (14, 15). An explanation involving the tracking of a gradually shifting optimum by the evolving lineages is equally illusory: on geological time scales, the variance in surface ocean properties is dominated by orbitally driven insolation changes with periods between 20 and 400 kyr, as was the case for the late Cretaceous habitat of the *Contusotrucana* lineage (16).

All earlier interpretations of gradual trends in fossil microplankton relied on the assumption that each of the evolving lineages represented a single (chrono-) species. The discovery of a prevalent cryptic genetic diversity within species of planktonic foraminifera (17) and other fossil-producing plankton (e.g., ref. 18) implies that evolutionary patterns extracted from fossil microplankton may represent the development of a cohort of cryptic sibling species. Available data indicate that, in many cases, these sibling species can be genetically and ecologically distinct, but the morphologies of their fossilized remains cannot be distinguished (19–22). Importantly, the cryptic genetic diversity within morphologically defined species appears finite; for example, so far only two to seven genetic types have been described per morphospecies of planktonic foraminifera, with as many as four co-occurring at the same location (17). The existence of such cryptic diversity implies that the observed morphological evolution in marine microplankton lineages may need to be subdivided among the contributions of several coevolving species, whose interactions may have an impact on how, and how fast the consortium evolves.

Although the discussion of mechanisms explaining the pattern of continuous evolutionary change and stasis in fossil lineages has recently received renewed attention (e.g., 23, 24), none of the models presented to date explicitly accounts for the ecological interaction between coevolving (sibling) species. Therefore, they overlook frequency dependence processes, that is, how population dynamics are affected by the frequency of each morph in the population. Here, we investigate explicitly the consequences of cryptic diversity for the apparent rate of evolution. To do so, we formulate a theoretical model for a number of interacting morphologically cryptic species and analyze the model to determine quantitatively how cryptic diversity can affect the rate of evolution within the system. In this model, instead of an absolute fitness measure that depends only on the trait of an individual, we use a relative fitness measure that depends on the value of all of the other traits and the frequency at which they occur.

Results

Little is known about the ecological interaction between contemporary foraminifera, and even less information is available about the interactions between fossil species. Not knowing any details, we will describe the interactions with the Lotka–Volterra interaction model, which provides a general template to describe the interactions between species (25). In the absence of any details, we postulate that the interaction between foraminifera is dominated by competition for resources and formulate a model that captures the essence of competition for resources among morphologically cryptic sibling species. This chosen model is considered representative inasmuch as we expect that the general findings derived from it would be qualitatively similar to those derived from other or more complex models. We then proceed to extract the selection pressure on the different

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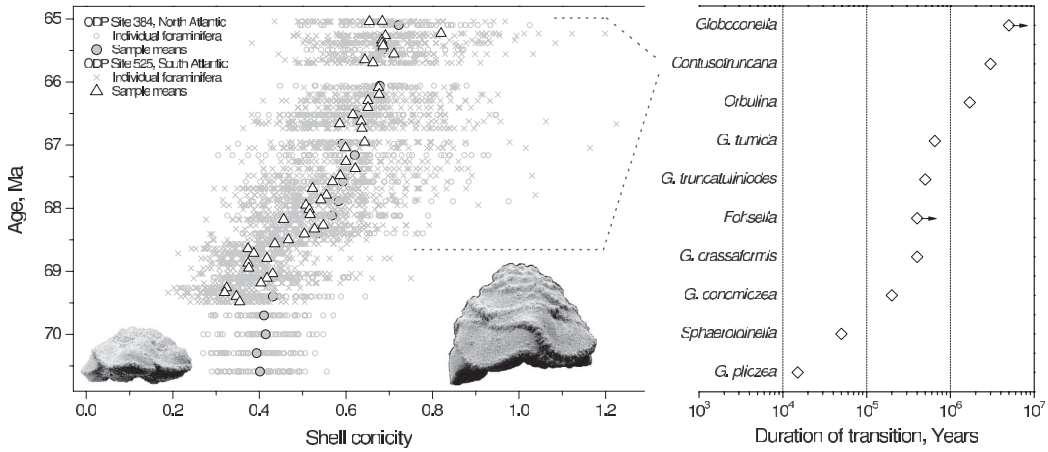

Fig. 1. Gradual increase through time in shell conicity of the planktonic foraminifer *Contusotruncana* at two distant locations in the Late Cretaceous Atlantic Ocean (data from ref. 10) compared with the estimated duration of morphological transitions in a range of Cenozoic planktonic foraminifer lineages (*Right*). Arrows indicate minimum durations due to incomplete coverage of the lineage by the study (*Fohsella*) and the extent of the transition to the present day (*Globoconella*). The transitions represent: a shell coiling parameter in *Globoconella* (8, 39), development of engulfing last chamber in *Orbulina* (5), transition in shell outline and size between *G. plesiotumida* and *G. tumida* (3), the divergence in shell form of *G. truncatulinoides* (40), change in shell outline in *Fohsella* (41), *G. crassaformis* (9), *G. conomiozea* and *G. pliozea* (39), and the development and size of supplementary apertures in *Sphaeroidinella* (3).

species from this model and use this to make inferences about the effect of diversity on the rate of evolution. Our model consists of a number of cryptic foraminifer species that can coexist and compete for food particles of different size, and therefore energetic value. The species differ in the spectrum of particles they ingest and we assume that the mean size of food particles they ingest (μ_i) can evolve. This formalism assumes frequency-dependent selection, where the variation in the population is partitioned among the different cryptic species and that new forms are generated that differ marginally from existing cryptic species. First, we will present the results obtained from a deterministic, analytical approach, which we will then supplement by numerical simulations.

One could study other traits involved in resource competition in a similar fashion. The rate of evolution depends on the ecological dynamics of the species in the ecosystem that are affected by one another, which is insensitive to the exact details of the interaction; therefore, different models that account for several interacting species can be expected to give similar results. The one exception is if different species in an ecosystem all perform different tasks, each of which is essential for the survival of all of the species. If that is the case the rate of evolution for all species will decrease with diversity.

For our model, it is possible to calculate analytically the rate of evolution of all species (see *The Model* and *SI Text Appendix A*). This allows us to compare the evolutionary dynamics of the trait in a system with a one species to the evolutionary dynamics of a system with three species. In both cases, we change the environment by gradually increasing $s_{\max}$, the maximum size of the food particles in the system (Fig. 2). We find that in a system with a single species, the evolution is fast and the single species can track the change in the environment in real time. However, if three species are competing for food in the system, only the most competitive species evolves rapidly, whereas the subdominant competitors change much more slowly. There is thus an asymmetry in the evolutionary responses of the species. This is because more diverse communities of competing species have a larger proportion of the population that is competitively inferior. These populations tend to have smaller population sizes and smaller selection differentials (Fig. S1), indicating that the observed slowdown of the evolutionary response in the subdominant species is not simply a function of their population size. The same phenomenon can also be demonstrated by considering the dominant eigenvalue of the Jacobian of the evolutionary rates vector (see *The Model* and *SI Text Appendix A*, *Calculating the selection differential and the evolutionary rate*), which reflects the mean evolutionary speed of the system. We find that there is an exponential decay in the evolutionary rate with the increase in the number of cryptic species (Fig. 3). As discussed above, subdominant competitors can only evolve if the dominant competitors have vacated empty niche space through adapting to larger food particles. Note that we obtain qualitatively similar results by decreasing $s_{\max}$. This result concerning the evolutionary slowdown is fundamentally different from models that use a single species where an increase in the variation of the trait would lead to an increase in the evolutionary rate. The deterministic approach allows us to derive analytical results on the rate of

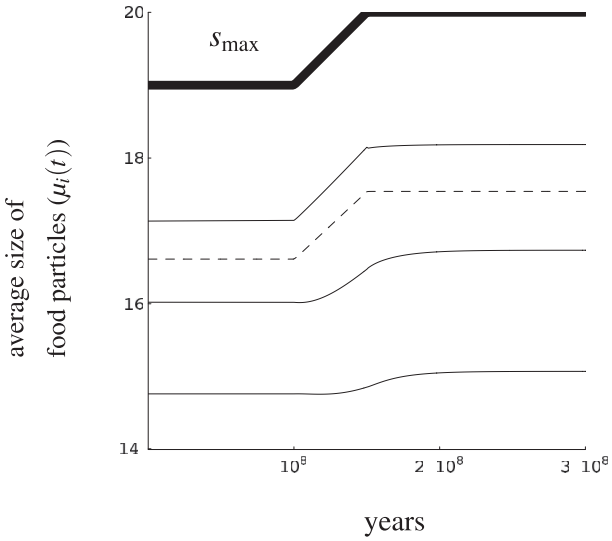

Fig. 2. Variation of the average food particle size of species i [$\mu_i(t)$] in a system with three species (plain curves) or with one species (dashed curve). At $t_{var} = 10^7$ years, the system is at equilibrium and we progressively change the value of s_{max} (the thick curve) from 19 to 20 (in 5×10^6 years). This modifies the equilibrium values of the traits and mimics a slight environmental change (here the arrival of larger prey). Parameter values are $\gamma = 25$ and the mutation rate $\tau = 10^{-5}$ (see *The Model*).

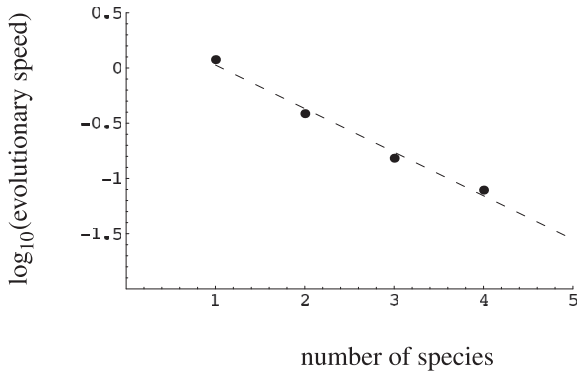

Fig. 3. Influence of the number of species on the evolutionary speed of the system. The log-linear relationship is $y = 0.42 - 0.40x$ ($R^2 = 0.987$). Parameter values are $s_{max} = 20$ and $\gamma = 20$ (we choose this value instead of 25 to allow the coexistence of >3 species in the system).

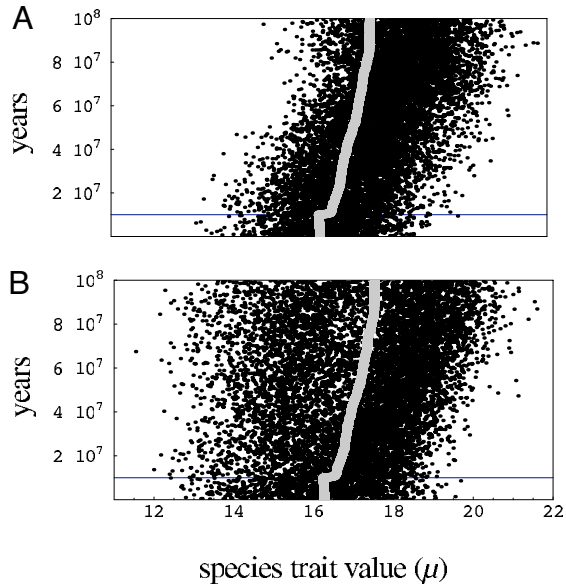

Fig. 4. Stochastic simulation of the evolution of trait μ_i in a system with one (*A*) or with three species (*B*). At $t = 10^7$ years (horizontal line), we gradually change s_{max} from 19 to 22 (in 10^6 years). The average value of the trait (bold gray line) evolves more slowly when there are more species in the system. In both *A* and *B*, $\gamma = 25$ and $\tau = 10^{-5}$. For further details, see *SI Text Appendix B*.

evolutionary change. To arrive at such results we assumed that populations are at their equilibrium and that the trait variance within a species is proportional to their population size. To demonstrate that our results are robust against relaxing these assumptions, we simulated an equivalent system for which these assumptions were not made. We assumed that there is an underlying trait that is under selection (exactly as in the deterministic model) and that small mutations in this trait occasionally occur by chance. To reflect the fact that this trait is correlated, but not identical, to a morphological variable (such as the conicity of the shells) we assumed that morphological variables are normally distributed, with a constant variance and a mean that equals the value of the underlying trait. Fig. 4 shows two simulations with such a model, which we set up to accommodate either a single species or three cryptic species. The underlying evolutionary dynamics of the trait are very similar to the dynamics shown in Fig. 2 (for details, see *SI Text Appendix B*, and Fig. S2).

Discussion

In this study, we show how taking into account hidden diversity in an evolving lineage may help to understand patterns of evolutionary change in marine microplankton. An increase in cryptic diversity leads to an evolutionary slowdown of the evolving system through resource competition. The exact mechanism can easily be understood by considering the competition between the cryptic species (Fig. S3). By changing the environmental parameters, the most dominant competitor will respond first by adjusting its trait. Once this has happened, the next species in the competitive hierarchy feels the selection pressure and, consequently, the trait of this species changes. Only then can the next species in the hierarchy respond and move toward its new ecological niche. The key point to use in interpreting our results is the time factor: subdominant species can only evolve once the dominant species have evolved. For a species that has i species above it in the competitive hierarchy to evolve, i times the number of mutations are needed, and the rate of evolution of the ith species will depend on the product of the phenotypic variation of the i best competitors. This creates the observed exponential decay. This mechanism is not restricted to cryptic sibling species. However, because sibling species can be expected to compete for resources much more intensely than nonsibling species of foraminifera, the evolutionary slowdown will be more pronounced for sibling species, than similar effects resulting from competition with other organisms.

A secondary effect that explains the relatively slow evolution of assemblages of cryptic species is that these species are likely to have less phenotypic variation per species, simply because the cryptic species will differ from one another. Lumping several cryptic species together into a single morphospecies will drastically overestimate the amount of variation within that morphospecies. Arguments about the rate of evolution based on the evolution of a single species thus overestimate the rate of evolution when applied to an assemblage of cryptic species.

Our model shows how and why the presence of cryptic species in an evolving lineage leads to a slowdown of apparent morphological evolution. Despite the lack of parameterization, we observe remarkable consistency between the predictions of our model and fossil data. First, analytical solutions of our theoretical model indicate that a two-orders-of-magnitude slowdown in a system with four cryptic species and a three-orders-of-magnitude slowdown could be achieved in a system with only seven cryptic species; both the implied variation in rates of evolution (Fig. 1) and number of cryptic species (17) agree with observations. Second, the model predicts an asymmetrical pattern in the evolution of the lineage with a more rapid change at one end of the morphospace. This feature has been observed in the *Contusotrunacana* lineage (Fig. 1).

The phenomenon of cryptic (or sibling) species is well documented in the plankton (26), but it is by no means restricted to this ecological group, nor is there any evidence that it is more common among protists (most literature on cryptic species actually derives from insects; see, e.g., ref. 27). Therefore, in theory, our model could be applied to any group of organisms. There is, however, one major limitation: to engage in competition, the cryptic sibling species in our model must occur in sympatry and share the same resources. This often holds in the pelagic environment, which is relatively unstructured spatially. In a large compilation of fossil data, Hunt (28) shows that gradual unidirectional evolution is rare, in general, but appears more frequent among planktonic organisms. This could indicate that the mechanism described by us may be more pertinent for this environment.

It is increasingly recognized that ecological feedback can have profound effects on the evolution of traits. These insights

have been supported by both theoretical and experimental studies (29–35). Here, the application of the competition concept to a consortium of cryptic sibling species offers the first theoretical explanation for the existence of long unidirectional patterns of trait evolution observed in the fossil record of marine microplankton.

The Model

Our model has N species, where individuals of each species i are characterized by the mean size of the food particles they ingest (μ_i). This leads to N ordinary differential equations that describe the dynamics of the population density of species i denoted $x_i(t)$ and one partial differential equation to describe the change in the amount of food particles of size s denoted $n(s,t)$. The equations read:

$$\frac{\partial n(s,t)}{\partial t} = n(s,t)(1-n(s,t)) - \sum_{j=1}^{N} x_j(t)k(\mu_j,s)n(s,t) \qquad [1]$$

$$\frac{dx_i(t)}{dt} = x_i(t)\int_0^{s_{\max}} k(\mu_i,s)n(s,t)c(s)ds - \gamma x_i(t), \qquad [2]$$

where γ is the mortality rate of all species, $c(s)$ is the energetic value of food particles of size s, and $s_{\max}$ is the size of the largest particles. The kernel function $k(\mu_i,s)$ describes the proportion of food particles of size s eaten by a species that ingests, on average, food particles of size μ_i.

To analyze the above system, we assume a homogeneous carrying capacity for the food particles population such that, without consumption, at equilibrium, Eq. **1** becomes $\tilde{n}_0(s) = 1$. (Here, as in the following, tildes indicate equilibrium values.) Next, as in previous studies (36), we choose a kernel function that has a double-exponential shape centered around μ_i (*SI Text Appendix A*, *Choice of a kernel function*). Finally, we choose an energetic-value function that depends linearly on the food particle's size, that is, $c(s) = s$ (taking the energetic value proportional to volume would not modify the results qualitatively and would complicate the calculations).

If the resource population reaches its equilibrium much faster than the plankton populations [i.e., that $n(s,t) \approx \tilde{n}(s)$], we can easily reformulate our equations to a classical Lotka–Volterra competition model (*SI Text Appendix A*, *Derivation of the Lotka–Volterra model*):

$$\frac{dx_i}{dt} = x_i\left(R(\mu_i) - \sum_{j=1}^{N} x_j(t)\alpha(\mu_i,\mu_j)\right), \qquad [3]$$

where $R(\mu_i) = \int_0^{s_{\max}} k(\mu_i,s)c(s)ds - \gamma$ and $\alpha(\mu_i,\mu_j) = \int_0^{s_{\max}} k(\mu_i,s)k(\mu_j,s)c(s)ds$. As we show in *SI Text Appendix A*, *Finding the equilibrium densities of the populations*, obtaining the species equilibrium densities ($\tilde{x}_c$) from Eq. **3** is straightforward. Theses equilibrium densities depend on $R(\mu_i)$ and $\alpha(\mu_i,\mu_j)$.

We then use Eq. **3** to derive the invasion fitness function of a rare mutant. The mean particle food size of a mutant (μ_i^*) differs slightly from that of the resident (μ_i). After some simplification (*SI Text Appendix A*, *Introducing a mutant*), the equation describing a mutant's density can be written as

$$\frac{dx_i^*}{dt} \approx \left(R(\mu_i^*) - \sum_{j=1}^{N} x_j\alpha(\mu_i^*,\mu_j)\right)x_i^*. \qquad [4]$$

The invasion fitness W_N of a mutant of resident species i in a system with N species is given by

$$W_N(\mu_1,\ldots,\mu_i,\ldots,\mu_N,\mu_i^*) = \frac{1}{x_i^*}\frac{dx_i^*}{dt}. \qquad [5]$$

From Eq. **4**, we get

$$W_N(\mu_1,\ldots,\mu_i,\ldots,\mu_N,\mu_i^*) = R(\mu_i^*) - \sum_{j=1}^{N} \tilde{x}_j\alpha(\mu_i^*,\mu_j). \qquad [6]$$

The fact that the mutant is rare (compared with the resident) allows us to assume that resident species do not "feel" the presence of a mutant population. If the resident populations are also at equilibrium, the density values x_j can be replaced by their equilibrium values $\tilde{x}_j$.

From Eq. **6**, we derive the effect on the invasion fitness of a mutation causing a small change in a resident trait μ_i. This marginal fitness gives us the value of the selection differential (sd) of a mutant of resident species i, which indicates in which direction the trait evolves and at which speed. The selection differential value is obtained by deriving $W_{i,N}$ with respect to μ_i^*,

$$sd_{i,N} = \left.\frac{dW_N(\mu_1,\ldots,\mu_i,\ldots,\mu_N,\mu_i^*)}{d\mu_i^*}\right|^*_{\mu_i=\mu_i}. \qquad [7]$$

See *SI Text Appendix A*, *Calculating the selection differential and the evolutionary rate*, and Figs. S4 and S5, for further details. If $sd_{i,N} = 0$, species i is at an evolutionary equilibrium. If $sd_{i,N} > 0$, mutants with $\mu_i^* > \mu_i$ will be selected for and if $sd_{i,N} < 0$ mutants with $\mu_i^* < \mu_i$ will be selected for. Because we have a community of N species, which may all create mutants, we get N values for the selection differential of the system.

Knowing the selection differentials allows us to quantify the rate of the evolutionary process and follow variations in trait value (μ_i). Generally, the rate of evolution is the product of the selection differential and the amount of heritable variation (13, 37, 38). The amount of variation generally will scale with number of mutations, which is proportional to the size of the population and the mutation rate (38). Therefore, we can write the rate of evolution in the mean food particle size of any species i in the system as

$$\frac{d\mu_i(t)}{dt} = \tau\tilde{x}_i\, sd_{i,N}, \qquad [8]$$

where τ is a constant proportional to the mutation rate, which is the same for all species in the community.

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