Possible Origin of Stagnation and Variability of Earth's Biodiversity

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The magnitude and variability of Earth's biodiversity have puzzled scientists ever since paleontologic fossil databases became available. We identify and study a model of interdependent species where both endogenous and exogenous impacts determine the nonstationary extinction dynamics. The framework provides an explanation for the qualitative difference of marine and continental biodiversity growth. In particular, the stagnation of marine biodiversity may result from a global transition from an imbalanced to a balanced state of the species dependency network. The predictions of our framework are in agreement with paleontologic databases.

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Biodiversity has expanded from few species at the beginning of the Phanerozoic (541 Ma ago) to some million species today. Large collections of fossils have enormously increased our understanding of the history of Earth's biodiversity. The underlying processes governing this diversification are, however, poorly understood, and a compelling interpretation of the fossil data remains challenging [1]. Whereas it is commonly accepted that continental biodiversity exhibited exponential growth [2–6], the growth dynamics of marine life, albeit documented in substantially larger detail, has been controversially debated.

Pioneering work on both the Fossil Record 2 [15] and Sepkoski's compendium [7] suggested that after a first increase the total diversity remained fluctuating around a constant level for roughly 200×10^6 years and suddenly began to increase [8,9]. The constant level has traditionally been associated with the equilibrium of a logistic growth. In particular, Sepkoski identified three evolutionary faunas and modeled their diversity by three coupled logistic equations with model parameters fitted to the fossil data [10,11]. This model explains the emergence of a biodiversity equilibrium together with a subsequent increase. A model combining exogenous impacts and logistic growth has been suggested by Courtillot and Gaudemer [12]. Their model is based on four time segments separated by three mass extinctions, where each segment is described by a logistic growth process with an individual equilibrium level. More recently, an analysis that identifies and overcomes the sampling bias in previous fossil data analyses suggests that the increase in biodiversity after the 200×10^6 year period of stagnation may be a mere artifact [13], consequently simple logistic growth with fluctuations around a single equilibrium level would be a sufficient model (see Fig. S1 in the Supplemental Material [14]).

These models are based on the assumption that new species establish and remain present only if they successfully compete for space or resources. Therefore, the diversity at large scales approaches an equilibrium as a result of a global logistic growth process. Empirical evidence for this hypothesis has been found in the fossil data [1,18], in particular, the observation that the extinction and origination rates are dependent on the relative number of species [19].

The causes for equilibria in the diversity of marine life have been discussed controversially. The equilibria might be the result of an expanding diversity punctuated by extinction events [20] or an artifact of the subsumption of species in higher taxonomic groups [21]. Exponential growth may display an equilibrium due to an overcompensating correction of sampling bias [5]. In contrast, recent studies strongly support the exponential hypothesis for continental biodiversity [3–6], suggesting either that the growth dynamics of continental diversity may crucially differ from marine diversity [3,5] or that both grow exponentially [2].

This demonstrates that arguments and empirical evidence in this debate on equilibrium and expansion are contradictory. While there is a large body of work on logistic growth models, frameworks based on the assumption of an expanding diversity are, to our knowledge, absent.

We present a model supporting the expansion hypothesis with few simple reasonable assumptions. The dynamics of this model results in exponential growth that, however, transiently slows down or is even interrupted for some time. Specifically, while the average diversity grows exponentially, the species dependency network may develop into an unstable imbalanced state where many species depend on few. In our model a transiently increased extinction rate compensates the speciation rate and causes a reorganization of the network to the balanced state as being the attractor of the system. The impact of this mechanism, which results in periods of a stagnating diversity, is determined by the ratio of the extinction to speciation probability. A comparison with the fossil data suggests that marine and continental taxa indeed have different ratios of the extinction to the origination probability, which may explain the qualitative difference of marine and continental biodiversity growth.

Model.—In our model, species can become extinct due to abiotic causes (random exogenous extinctions) like a changing environment, or are threatened by biotic causes from extinction cascades in the dependency network (endogenous extinctions). As a result, the size of extinction events ranges from one to all species, which is in agreement with the fossil data [19]. In contrast to ecological networks, such as food webs, mutualistic networks, and host-parasitoid networks [22–25], the dependency network does not represent the interactions between individuals of different species but whether the existence of one species necessarily requires the presence of another species.

Two types of species are organized at certain dependency levels $l \geq 1$. Species at level $l = 1$ are independent. In each iteration, they become extinct, with probability ε, or speciate to a new species, with probability μ. Hence, the relative extinction probability

$$\lambda = \varepsilon/\mu \tag{1}$$

is the main parameter of the model.

In marine genera evidence has been reported for an age selectivity implying an extinction risk that "drops off rapidly among the youngest age cohorts and thereafter shows little relationship to age" [26]. Here we model speciation-extinction processes on long time scales.

Thus, firstly, we ignore the increased risk for the youngest cohorts and consider a constant extinction probability, known as Van Valen's law [27]. Secondly, species at level $l \geq 2$ are directly dependent on only one other species [28].

In each step, these species give rise to a new species with probability μ, or become extinct if the species they depend on becomes extinct (Fig. 1). Thirdly, we ignore interspecies competition, which may be a dominant force on short but not on long time scales [29,30].

The dependencies are determined by the following rules. Initially there are $n_1(0) = k$ independent species at the lowest level $l = 1$. If a species at level $l = 1$ gives rise to a new species, then the new species is placed with a probability $\gamma \leq 0.5$ at level $l = 2$, thus being dependent, and with the probability $1 - \gamma$ at level $l = 1$, in this case being independent of other species. If a species at a higher level $l \geq 2$ speciates, with the probability γ we place the new species at level $l - 1$, with probability γ at level $l + 1$, and with probability $1 - 2\gamma$ at level l, the level of its ancestor. When a species originates at level $l \geq 2$, it becomes dependent on a randomly chosen species located at level $l - 1$.

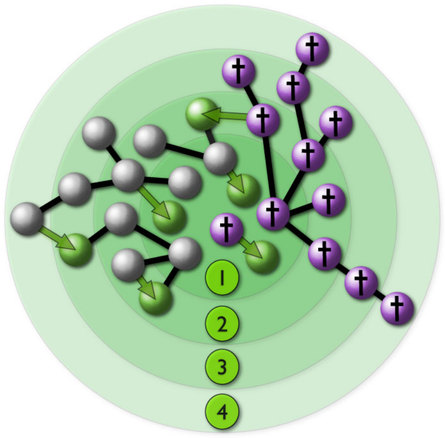

FIG. 1 (color online). Sketch of the model. The species in purple (crosses) become extinct at level 1 by exogenous causes and at higher levels due to their dependence on species at lower levels. The species in green (gray) originate from existing species (arrows).

Using a mean-field approximation for the dependency network and the continuum limit for time t, levels l, and occupation numbers n_l, we obtain the reaction-diffusion equation

$$\frac{dn_l}{dt} = \gamma\mu \frac{d^2 n_l}{dl^2} + (\mu - \varepsilon) n_l, \quad \text{with} \quad \left.\frac{dn_l}{dl}\right|_{l=1/2} = 0. \tag{2}$$

Since the model is defined only for $l \geq 1$, the Neumann boundary condition at $l = \frac{1}{2}$ ensures a zero net diffusion between $l = 0$ and $l = 1$.

Regardless of the initial conditions, the occupation numbers n_l, the solution of Eq. (2), equilibrate to a half-normal distribution

$$n_l(t) = \frac{2N(t)}{\sqrt{4\pi\gamma\mu t}} \exp\left(-\frac{(l - \frac{1}{2})^2}{4\gamma\mu t}\right); \tag{3}$$

see Fig. 2. The balanced state characterized by Eq. (3) is the attractor of the dynamics, where the expectation value of the extinction rate equals λN and the diversity grows exponentially, $N(t) := \sum_l n_l \sim e^{(\mu-\varepsilon)t}$.

The lifetime distribution for species within a given time window of size T follows an exponential decay

$$L_T(a) = \mu e^{-\mu a}, \tag{4}$$

where a is the species age. This result is in agreement with the majority of the literature on marine species [31–34].

Episodic stagnation.—All species that are dependent on a common species at level 1 constitute a dependency tree.

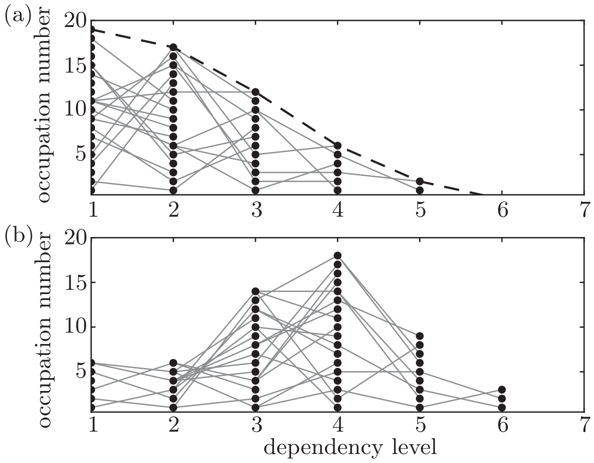

FIG. 2. Sketch of a dependency network in the balanced state (a) and the imbalanced state (b). Both networks consist of the same number of species. The dashed line is close to a half-normal distribution.

Given the survival of the root, the growth of tree i at level l is governed by the simple differential equation

$$\frac{ds_{il}}{dt} = \mu s_{i(l-1)}. \tag{5}$$

Given the root species of the tree appears at time $t = t_i$, we have $s_{i1}(t) = 1$ for $t \geq t_i$, which enables us to calculate the other occupation levels. Specifically, for a relative extinction probability $\lambda \lesssim 1$ close to unity, after a short transient period, dependency trees necessarily grow much faster than the (average) total diversity $N(t) \sim e^{(\mu-\varepsilon)t}$ as the solution of Eq. (5) reads

$$s_{il}(t) = \frac{1}{(l-1)!}[\mu(t-t_i)]^{l-1} \quad \text{for } t \geq t_i. \tag{6}$$

A sum over all levels yields the size of the complete dependency tree:

$$S_i(t) = \sum_{l=1}^{\infty} s_{il} = \sum_{l=0}^{\infty} \frac{[\mu(t-t_i)]^l}{l!} = e^{\mu(t-t_i)}. \tag{7}$$

This means that the longer an independent species is spared from extinction, the more species are dependent on it and that the number S of species of a dependency tree increases exponentially.

Since the growth of a dependency tree becomes substantially accelerated at higher levels [Eq. (6)], a single tree may lead to a sudden imbalance of the entire dependency network such that many species at high levels depend on few independent species at level $l = 1$ (Fig. 2). In particular, when the dependency network has not returned to the balanced state, large extinction cascades are more frequent. During such time periods the temporarily increased extinction rate results in the suppression of the diversity growth and the emergence of a plateau.

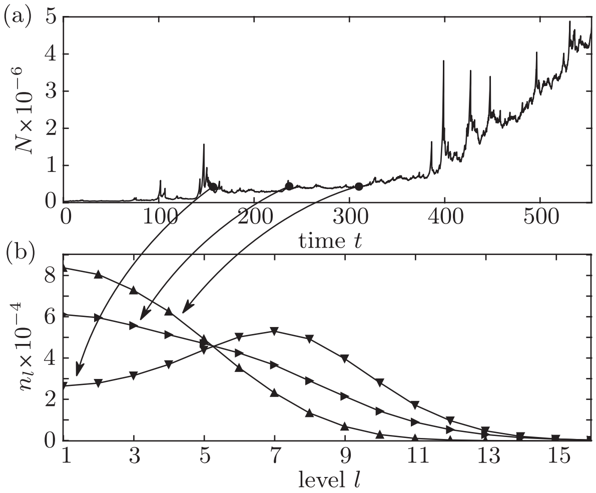

FIG. 3. Temporal development of a plateau. Single realization for extinction probability $\lambda = 0.985$ and $n_1(0) = 1000$ initial species. (a) The total diversity curve with three indicated points of effectively constant diversity. (b) The diversity distribution n_l at the three indicated times in (a). While the total diversity stagnates, the dependency network reorganizes from the imbalanced state (Filled downward triangle) to a half-Gaussian distribution (Filled upward triangle).

In Fig. 3 we have exemplified this behavior. An elevated value of the diversity drives the system to an imbalanced state, and peaks in the diversity are followed by relatively stable plateaus. Specifically, the system undergoes a transition back to a balanced state characterized by a half-normal distribution as depicted for three selected time points.

The probability of finding the system in an imbalanced state depends not only on λ but also on the total diversity N. To examine this by computer simulations, we characterize an imbalanced state by the criterion $\arg\max_l(n_l) \neq 1$. Thus, the system switches to an imbalanced state as soon as the level $l = 1$ ceases to be the most populated. Figure 4 (inset) shows how the probability P_{im} to find the dependency network in such an imbalanced state depends on λ and N. The reason for this emerging pattern is that imbalanced states are caused by large dependency trees. This, however, becomes unlikely for λ close to zero or a large total diversity.

Extinction rate distribution.—By employment of single event analysis [35–37], we calculate the size distribution of extinction events, the number of species S involved in single extinction cascades, which follows $P(S) = S^{-2}$ [14]. Many models have primarily aimed at reproducing this power-law behavior [38–40]. However, first, the distribution is not directly comparable to an extinction distribution obtained from the fossil data because the fossil data do not resolve distinct extinction cascades. Second, the type of the extinction distribution in the fossil data is controversial

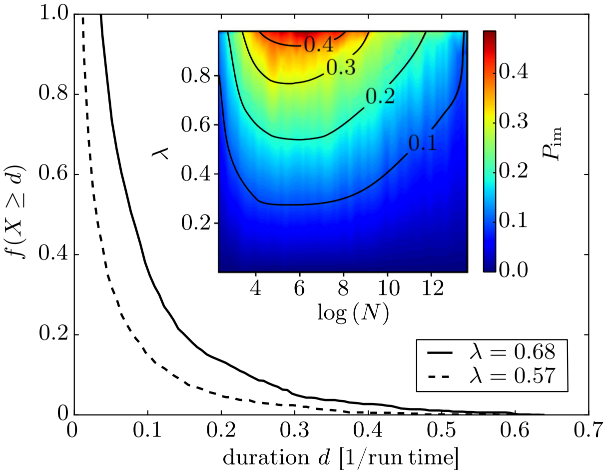

FIG. 4 (color online). Frequency of periods of imbalanced states lasting longer than a duration d. Each realization was stopped at the time step when the diversity reached 1000 species. The inset shows the probability P_{im} for an imbalanced state, based on 400 realizations.

[19,41,42]. Since the extinction rate depends on the size of the considered time interval [43,44] and the total number of species, its fluctuations are only properly characterized by conditional probability measures. This suggests that a discrimination be made between the extinction rate and the size of an extinction event. For this reason we calculated the extinction rate distribution in addition to the size distribution of extinction events. Irrespective of details of the extinction dynamics, we analytically demonstrate that an exponentially increasing extinction rate (caused by an exponentially growing biodiversity) necessarily leads to an extinction rate distribution following a double power law with an exponent of -1 for small rates and -2 for large rates, respectively (see Fig. S2 in the Supplemental Material [14]). Note that this prediction is exact.

Next we ask whether and how marine and continental diversity are determined by different values of λ. We test this (on the level of families [45]) by applying two different methods to the data of Fossil Record 2 [46]. Our model predicts the exponential growth of the diversity $N(t) \sim e^{\alpha t}$, $\alpha := \mu - \varepsilon$, together with the exponential decay of the lifetime distribution, Eq. (4). Fits of these functions to the fossil data yield the estimation of the parameters α and μ, and thus an estimation of the relative extinction probability $\lambda = [\mu - \alpha]/\mu$, Eq. (1). Applying this method to the fossil data (Fig. 5), we obtain $\lambda_{\mathrm{mar}} = 0.69(1)$ for the marine and $\lambda_{\mathrm{cont}} = 0.55(2)$ for the continental biodiversity. In a second approach, independent of predictions of our model, we study the relation between percent extinction and percent origination (Fig. 6). Bootstrapping suggests that the slope for the marine data λ_{mar} is higher than the slope for the continental data λ_{cont} (evidence ratio of 9:1), with the most likely values $\lambda_{\mathrm{mar}} = 0.68$ and $\lambda_{\mathrm{cont}} = 0.57$.

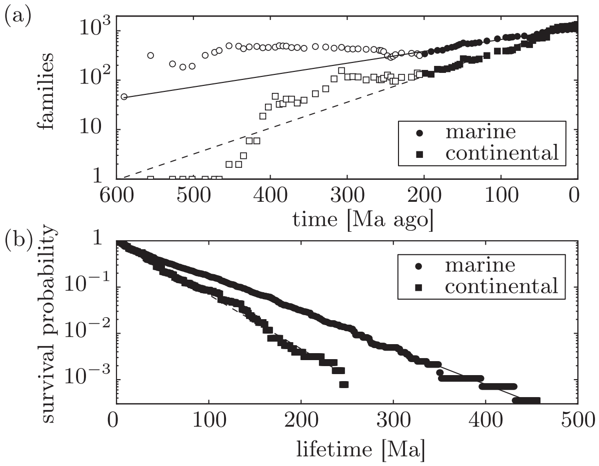

FIG. 5. (a) Marine and continental diversity. The lines are fitted to the data in the time range -200 to 0 Ma, yielding $\alpha = 0.0055(2)$ Ma^{-1} for marine diversity ($R = 0.987$, $P < 0.001$) and $\alpha = 0.0121(3)$ Ma^{-1} for continental diversity ($R = 0.990$, $P < 0.001$). (b) Survival probability (cumulative lifetime distribution) of marine and continental families. Best fits are $\mu = 0.017\,86(3)$ Ma^{-1} for marine data ($R = -0.998$, $P < 0.001$) and $\mu = 0.0269(1)$ Ma^{-1} for continental data ($R = -0.990$, $P < 0.001$).

Note that a conclusive comparison with the model is impossible because it would require multiple realizations of Earth's history. Instead, we ask how the behavior of the model qualitatively changes if λ jumps from λ_{cont} to λ_{mar}. As illustrated in Fig. 3, the duration of the imbalanced state correlates with the duration of the stagnation. Thus, we infer from Fig. 4 that stagnations lasting longer than a

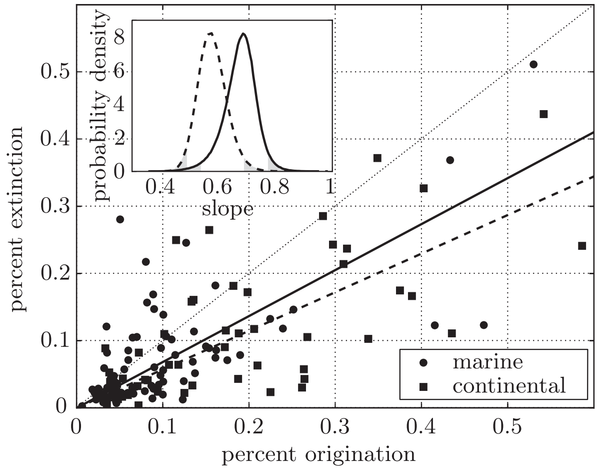

FIG. 6. Percent extinction of total diversity against percent origination for each stage. The solid line and the dashed line show the most frequent slope for marine and continental data found by the least-squares method in 10^6 bootstrap samples. The inset shows the bootstrap distribution of the data. The gray areas are the 2.5% quantiles. The maxima are at slopes 0.683 (marine) and 0.567 (continental).

certain duration d occur for $\lambda_{\mathrm{mar}} = 0.68$ more than 2 times as frequently as for $\lambda_{\mathrm{cont}} = 0.57$.

Discussion.—We have identified and studied a model where species speciate randomly and become extinct due to either endogenous or exogenous causes. Exogenous impacts occur with a constant probability whereas endogenous impacts are caused by extinction avalanches propagating through a system of interdependent species.

Assuming an expanding diversity, a long-term stagnation, such as in the marine diversity, seems unlikely to be the coincidental result of exponential growth superimposed by random extinction events. Using exact methods, we have demonstrated how a dependency network of species, which on very large scales grows exponentially, may evolve to an imbalanced state, which implies long-term stagnation. Imbalanced states, however, are unstable and thus the network necessarily reorganizes to a balanced state and continues growing. This means that by taking the dependencies of species into account, long stagnations turn out to be a typical behavior instead of a coincidental result; hence, the imbalanced states are a plausible origin for long-term stagnation of marine diversity.

The crucial parameter that determines this behavior is the ratio of the extinction to speciation probability. Two independent methods of analyzing the fossil data suggest that this ratio is substantially different for marine and continental diversity, which provides a potential explanation for the qualitatively different growth of marine and continental diversity.

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[1] M. Aberhan and W. Kiessling, *Earth and Life* (Springer, Amsterdam, 2012), pp. 3–22.

[2] D. Hewzulla, M. C. Boulter, M. J. Benton, and J. M. Halley, Phil. Trans. R. Soc. B **354**, 463 (1999).

[3] M. J. Benton, Geological Journal **36**, 211 (2001).

[4] H. Morlon, M. D. Potts, and J. B. Plotkin, PLoS Biol. **8**, e1000493 (2010).

[5] G. J. Vermeij and R. K. Grosberg, Integr. Comp. Biol. **50**, 675 (2010).

[6] A. Kalmar and D. J. Currie, Paleobiology **36**, 51 (2010).

[7] J. J. Sepkoski, Bull. Am. Paleontol. **363** (2002).

[8] D. M. Raup and J. J. Sepkoski, Science **215**, 1501 (1982).

[9] M. J. Benton, Science **268**, 52 (1995).

[10] J. J. Sepkoski, Paleobiology **10**, 246 (1984).

[11] J. Alroy, Evol. Ecol. Res. **6**, 1 (2004).

[12] V. Courtillot and Y. Gaudemer, Nature (London) **381**, 146 (1996).

[13] J. Alroy *et al.*, Science **321**, 97 (2008).

[14] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.112.228101 for a detailed presentation of the analytics and Refs. [15–17].

[15] M. J. Benton, *The Fossil Record 2* (Chapman and Hall, London, 1993).

[16] T. Lindeberg, IEEE Trans. Pattern Anal. Mach. Intell. **12**, 234 (1990).

[17] NIST digital library of mathematical functions, release 1.0.5 of 2012-10-01, http://dlmf.nist.gov.

[18] D. L. Rabosky, Ecol. Lett. **12**, 735 (2009).

[19] J. Alroy, Proc. Natl. Acad. Sci. U.S.A. **105**, 11 536 (2008).

[20] S. M. Stanley, Paleobiology **33**, 1 (2007).

[21] M. J. Benton and B. C. Emerson, Palaeontology **50**, 23 (2007).

[22] B. Drossel, P. G. Higgs, and A. J. McKane, J. Theor. Biol. **208**, 91 (2001).

[23] J. Bascompte and P. Jordano, Annu. Rev. Ecol. Evol. Syst. **38**, 567 (2007).

[24] T. C. Ings *et al.*, J. Anim. Ecol. **78**, 253 (2009).

[25] J. Bascompte, Science **325**, 416 (2009).

[26] S. Finnegan, J. L. Payne, and S. C. Wang, Paleobiology **34**, 318 (2008).

[27] L. V. Valen, Evolutionary theory **1**, 1 (1973).

[28] If a species were dependent on the simultaneous presence of m species and the extinction probability at level 1 is ε_1, species at higher levels would go extinct rapidly, because their extinction probability $\varepsilon_l = 1 - (1 - \varepsilon_{l-1})^m$ increases with l and m. If it were dependent on the presence of at least one of the other m species with extinction probabilities ε, it would show age selectivity because its extinction probability $\varepsilon_m(t) = \varepsilon^m$ increases while the species it depends on $E[m] = m_0 e^{-\varepsilon t}$ decrease with time.

[29] M. J. Benton, Science **323**, 728 (2009).

[30] T. B. Quental and C. R. Marshall, Science **341**, 290 (2013).

[31] K. Sneppen, P. Bak, H. Flyvbjerg, and M. H. Jensen, Proc. Natl. Acad. Sci. U.S.A. **92**, 5209 (1995).

[32] R. V. Solé and J. Bascompte, Proc. R. Soc. B **263**, 161 (1996).

[33] M. E. J. Newman and P. Sibani, Proc. R. Soc. B **266**, 1593 (1999).

[34] S. Pigolotti, A. Flammini, M. Marsili, and A. Maritan, Proc. Natl. Acad. Sci. U.S.A. **102**, 15 747 (2005).

[35] J. Nagler, A. Levina, and M. Timme, Nat. Phys. **7**, 265 (2011).

[36] J. Nagler, T. Tiessen, and H. W. Gutch, Phys. Rev. X **2**, 031009 (2012).

[37] M. Schröder, S. H. E. Rahbari, and J. Nagler, Nat. Commun. **4**, 2222 (2013).

[38] M. E. J. Newman and R. G. Palmer, arXiv:adap-org/9908002.

[39] L. A. Nunes Amaral and M. Meyer, Phys. Rev. Lett. **82**, 652 (1999).

[40] B. Drossel, Adv. Phys. **50**, 209 (2001).

[41] R. V. Solé, S. C. Manrubia, M. Benton, and P. Bak, Nature (London) **388**, 764 (1997).

[42] M. E. J. Newman and G. J. Eble, Proc. R. Soc. B **266**, 1267 (1999).

[43] J. Camacho and R. V. Solé, Phys. Rev. E **62**, 1119 (2000).

[44] R. V. Solé, *Biological Evolution and Statistical Physics*, Lecture Notes in Physics Vol. 585 (Springer, Berlin, 2002), pp. 312–337.

[45] We assume the large-scale dynamics on the level of families to be similar to a coarse-grained dynamics of the species level.

[46] Although the Paleobiology Database offers continental data, too, the Fossil Record 2 is the established database for comparisons between marine and continental data.