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Large Species Shifts Triggered by Small Forces

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ABSTRACT: Changes in species composition of communities seem to proceed gradually at first sight, but remarkably rapid shifts are known to occur. Although disrupting disturbances seem an obvious explanation for such shifts, evidence for large disturbances is not always apparent. Here we show that complex communities tend to move through occasional catastrophic shifts in response to gradual environmental change or evolution. This tendency is caused by multiple attractors that may exist in such systems. We show that alternative attractors arise robustly in randomly generated multispecies models, especially if competition is symmetrical and if interspecific competition is allowed to exceed intraspecific competition. Inclusion of predators as a second trophic level did not alter the results greatly, although it reduced the probability of alternative attractors somewhat. These results suggest that alternative attractors may commonly arise from interactions between large numbers of species. Consequently, the response of complex communities to environmental change is expected to be characterized by hysteresis and sudden shifts. Some unexplained regime shifts observed in ecosystems could be related to alternative attractors arising from complex species interactions. Additionally, our results support the idea that ancient mass extinctions may partly be due to an intrinsic loss of stability of species configurations.

Keywords: community shifts, assembly rules, alternative stable states, resilience, regime shift, competition models.

Studies in lakes, coral reefs, dry lands, and other ecosystems show that remarkably sudden switches to contrasting community states may occasionally occur (Carpenter 2001; Scheffer et al. 2001). Although such discontinuities in the

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otherwise smooth change in species composition are usually ascribed to disrupting stochastic events, evidence for strong disturbances is not always convincing. An alternative explanation is that the system might shift between alternative attractors (Scheffer et al. 2001). If a system has alternative attractors, this has three important implications, which can be understood intuitively from graphs of stability landscapes (fig. 1.; Scheffer et al. 2001). First, dramatic shifts in species composition may occur in response to a small change in an external condition (e.g., temperature or exploitation pressure) exceeding a critical limit (catastrophic transitions). Second, the phenomenon that catastrophic shifts are not reversible by an equally small reverse change in the external condition (hysteresis). Finally, the size of the basin of attraction (resilience sensu Holling 1973) changes with external conditions, implying that the brittleness of the system changes; that is, the likelihood of a stochastic event triggering a regime shift changes (changing resilience).

Alternative attractors are hard to prove empirically (Scheffer and Carpenter 2003), and in the opinion of Bertness et al. (2002, p. 3434) even "an interesting theoretical idea without a definitive empirical example." However, recent experimental studies have provided strong evidence of alternative stable states in floating aquatic vegetation (Scheffer et al. 2003b), in freshwater or marine sediments (Van de Koppel et al. 2001; Scheffer et al. 2003a), and in benthic pond food webs (Chase 2003).

The existence of alternative attractors has often been explained from particular feedback mechanisms between organisms and the environment. Examples include the effect of vegetation on precipitation in dry regions (Brovkin et al. 1998), of aquatic plants on water clarity in shallow eutrophic lakes (Scheffer et al. 1993), and the effect of the salt cedar on the water conditions and flood regime of rivers in the southwestern United States (Busch and Smith 1995; Dent et al. 2002). However, there are other cases in which ecosystems show symptoms of alternative attractors (sensu Scheffer and Carpenter 2003), but simple feedbacks that might explain this phenomenon have not yet been clearly identified. Examples include the sudden shifts in coral reef communities (Done 1991; Knowlton 1992; Nystrom et al. 2000), kelp forest dynamics (Steneck et al.
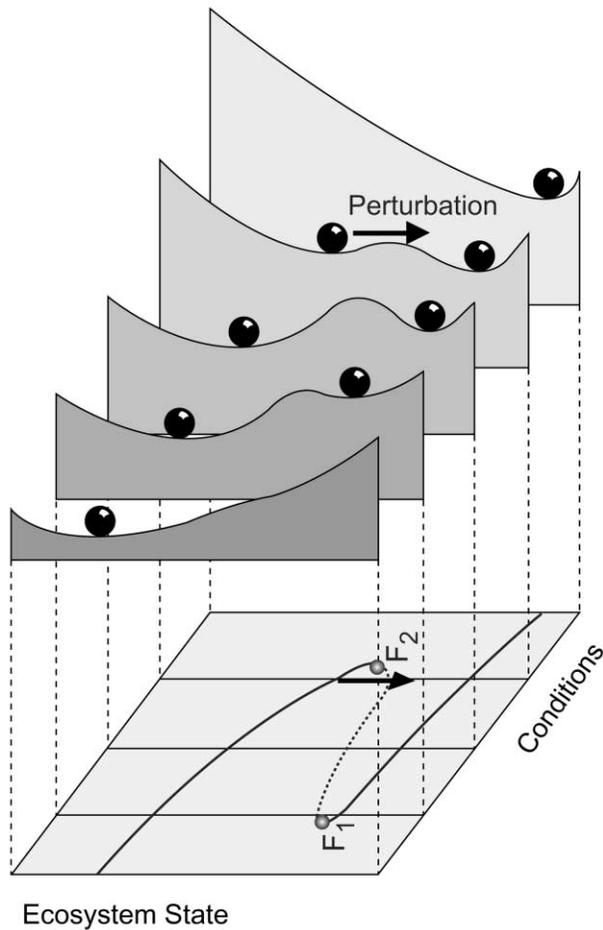
Figure 1: Implications of alternative stable states in ecosystems visualized by means of stability landscapes in which valleys represent the basins of attraction, that is, the system states that are drawn to the equilibrium state at the bottom of the valley. The bottom plane shows the equilibrium states of the system as a function of environmental conditions. When the system is in a state on the left branch of this folded curve and conditions change sufficiently to pass the threshold ("saddle-node" or "fold" bifurcation F_2), a catastrophic transition to the right branch occurs. In order to induce a switch back to the upper branch, it is not sufficient to restore the environmental conditions before the collapse (F_2). Instead, one needs to go back beyond the other bifurcation point (F_1), where the system recovers by shifting back to the upper branch. The difference between forward and backward switches is known as hysteresis. For conditions at which there are alternative stable states, a sufficiently severe perturbation may also bring the system into the basin of attraction of another state. This happens more easily if the basin of attraction (the resilience) is small. (Figure adapted from Scheffer et al. 2001.)

2002), regime shifts in pelagical marine ecosystems (Steele 1996; Hare and Mantua 2000), alternative vegetation compositions in a wet calcareous dune slack on the island Texel, the Netherlands (Adema et al. 2002), and periodical species shifts in boreal forests, where fir and birch dominance alternate with spruce and fir dominance (Ludwig et al. 1997; Augustine et al. 1998). Here, we explore the possibility that the complex web of interactions in multispecies communities may lead to alternative attractors, implying a potential catastrophic species shift, which is difficult to reverse because of hysteresis.

Multiple alternative attractors in certain multispecies competition models have already been demonstrated in the 1960s and 1970s (Levins 1966; Gilpin and Case 1976), and it has also been shown experimentally that several alternative endpoint communities can arise under similar environmental circumstances (Drake 1991). These results are usually discussed in relation to invasion resistance (Case 1990; Law and Morton 1996) and the theory of assembly rules (Drake 1990). Surprisingly, the existence of alternative attractors in community composition has never been linked to the potential consequences for the response to environmental change. The only study we are aware of that touches the topic is an analysis of effects of different types of noise on catastrophic transitions in a mean field model of an infinite number of interacting species by Mankin et al. (2002).

Here, we first check the robustness of earlier findings by exploring the factors that might affect the occurrence of alternative attractors in multispecies models. Subsequently, we analyze the effect of trends and fluctuations in environmental conditions on such models. We argue that the mere occurrence of interactions between the many species in biological communities may cause their response to environmental change to be characterized by periods of hysteresis punctuated by sudden shifts. We also discuss potential consequences of these insights for the history of earth biota on a geological timescale.

The Models

A Multispecies Competition Model

As a basis for our analyses, we use a slightly modified version of the classical Lotka-Volterra model, which has been used in many analyses of biodiversity questions before (Levins 1968; Case 1990, 1991; Law and Morton 1993, 1996; Morton et al. 1996):

$$\frac{dN_i}{dt} = \frac{rN_i\left(K_i^* - \sum_j \alpha_{i,j} N_j\right)}{K_i^*} + u, \qquad (1)$$

where $i = 1, 2, \ldots, n$; $\alpha_{i,i} = 1$; and $K_i^* = K_i(1 + M\eta_i)$. Unlike traditional multispecies Lotka-Volterra models, this formulation allows us to explore the effect of external forcing, as the carrying capacity of each species is made subject to a hypothetical environmental factor (M) through a randomly assigned sensitivity coefficient (η_i). A

small immigration factor (u) was used to prevent unrealistically low species biomasses. As an alternative, we also investigated the effect of species truncation if a species falls below some threshold (Gilpin and Case 1976).

For some analyses, noise was added to the environmental factor M. This was done using a simple recurrence equation for red noise by Hasselmann (1976):

$$M_t = \left(1 - \frac{1}{\lambda}\right)(M_{t-1} - M_o) + M_o + \beta\varepsilon, \qquad (2)$$

where λ is a parameter that expresses the approximate period of the noise in days (or other time units; $\lambda > 1 =$ red noise), M_o is the approximate mean of the red noise, β is parameter that expresses the daily deviation, and ε is drawn daily from a standard normal distribution.

Parameterization

To estimate the probability of alternative attractors in randomly generated ecosystems, we created 150 sets of 20 random species. The carrying capacity (K) of each species was drawn from a uniform distribution between 80 and 120 arbitrary units. All species had the same arbitrary growth rate (r) of 0.5. The immigration rate (u) was set to a small value of 0.01 for all species. The sensitivity coefficients (η) of each species were uniformly distributed numbers between 0 and 1. Intraspecific competition terms ($\alpha_{i,i}$) were set to 1, as the single species equilibrium equals K_i by definition. In our default approach, interspecific competition coefficients ($\alpha_{i,j}$) were uniformly distributed random numbers between 0 and 1. Furthermore, we have studied sets in which we had drawn numbers for $\alpha_{i,j}$ between 0 and 1.5 to allow interspecific competition to exceed intraspecific competition. In addition, we explored the effect of symmetrical competition by mirroring the community matrix.

A Two Trophic Level Model

To investigate the effect of predation (or grazing), we created an extension of this model with n competing prey species (P) and m predators (or grazers; C). This model extension is based on a standard Lotka-Volterra predator-prey model (May 1971) but with a Type II functional response and food preference (cf. Pelletier 2000; Van Nes et al. 2002). The available food (F_k) for each predator (C_k) is defined as follows:

$$F_k = \sum_i (S_{i,k}P_i), \qquad (3)$$

where $k = 1 \ldots m$, and $S_{i,k}$ is the preference of the prey

species P_i for predator C_k. This food preference is a parameter between 0 and 1 indicating the availability of the prey i for predator k. The realized consumption of the predator C_k is modeled as a Type II functional response with a maximum consumption of g and a half saturation constant of H:

$$\text{cons}_k = g_k C_k \frac{F_k}{F_k + H_k}. \qquad (4)$$

The growth of the predators is proportional to their consumption:

$$\frac{dC_k}{dt} = e_k \text{cons}_k - m_k C_k, \qquad (5)$$

where e_k is the assimilation efficiency of predator k and m_k is a loss factor for each predator.

Each predator consumes a fraction cons_k/F_k of its total available food (F_k). The total consumption of each predator is divided proportionally with the selectivity $S_{i,k}$ over all available food species. Consequently, the sum of the consumptions of all predators is subtracted from the prey biomass:

$$\frac{dP_i}{dt} = rP_i\frac{K_i^* - \sum_j(\alpha_{i,j}P_j)}{K_i^*} + u - \sum_k\left(S_{i,k}P_i\frac{\text{cons}_k}{F_k}\right), \qquad (6)$$
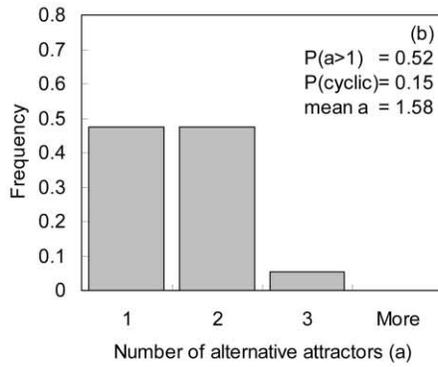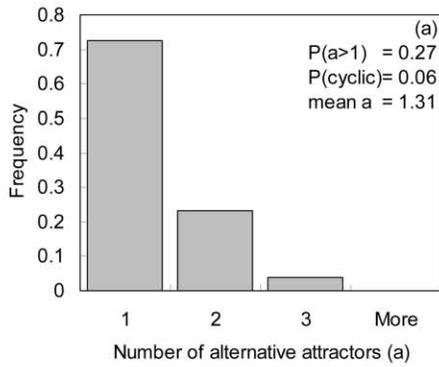
where $i = 1 \ldots n$, and $K_i^* = K_i(1 + M\eta_i)$. The matrix with the food preferences S was drawn from a uniform distribution between 0 and 1. We also checked the effect of these food preferences by setting S and the number of predator species m to 1. All other parameters of the predators were equal for all predators and were arbitrarily set to similar values as used in algae-zooplankton models (Scheffer and Rinaldi 2000; $r = 0.5$, $e_k = 0.7$, $g_k = 0.4$, $m_k = 0.2$), but the predators have been made less efficient ($H_K = 40$) because the modeled zooplankton species (*Daphnia* spp.) are exceptionally efficient grazers. Both models were implemented using our software package GRIND for MATLAB (freely available at http://www.dow.wau.nl/aew/grind/), which uses a Runga-Kutta method to solve the differential equations.

The Occurrence of Alternative Attractors

To scan for alternative attractors in each of the 150 randomly drawn species pools, we did 100 simulation runs with randomly drawn initial conditions of all species (between 0 and the maximum K). After 4,000 days, we checked automatically whether the system had reached a point attractor and whether the same equilibrium had oc-
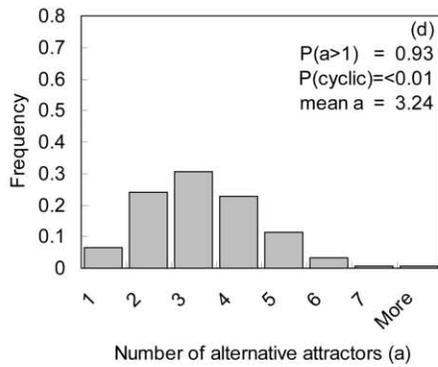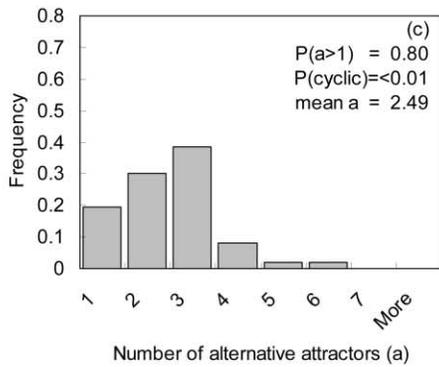
Interspecific ≤ intraspecific competition
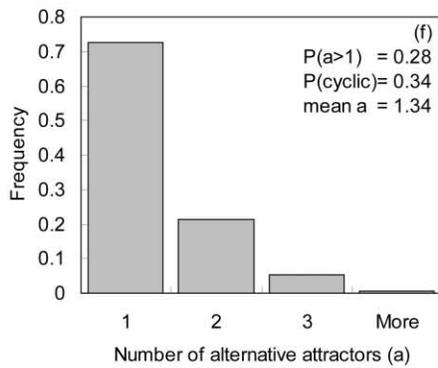
Interspecific can be larger than intraspecific competition

Competition only

(a)
P(a>1) = 0.27
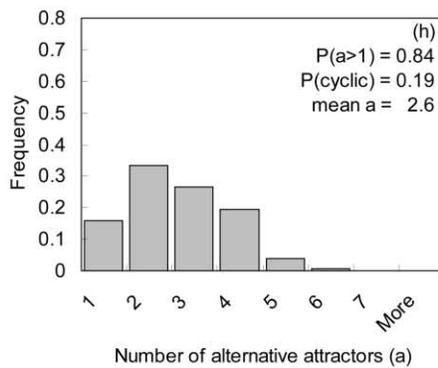P(cyclic)= 0.06
mean a = 1.31

Frequency

Number of alternative attractors (a)

Asymmetrical competition

(b)
P(a>1) = 0.52
P(cyclic)= 0.15
mean a = 1.58

Frequency

Number of alternative attractors (a)

(c)
P(a>1) = 0.80
P(cyclic)=<0.01
mean a = 2.49

Frequency

Number of alternative attractors (a)

Symmetrical competition

(d)
P(a>1) = 0.93
P(cyclic)=<0.01
mean a = 3.24

Frequency
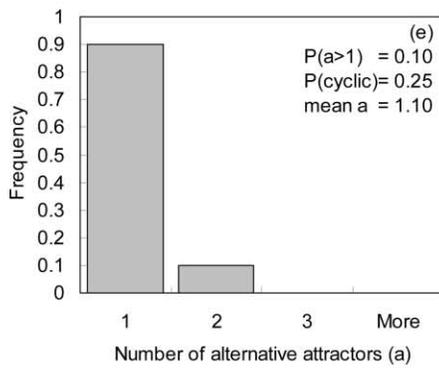
Number of alternative attractors (a)

Predation and competition

(e)
P(a>1) = 0.10
P(cyclic)= 0.25
mean a = 1.10

Frequency

Number of alternative attractors (a)

Asymmetrical competition

(f)
P(a>1) = 0.28
P(cyclic)= 0.34
mean a = 1.34

Frequency

Number of alternative attractors (a)

(g)
P(a>1) = 0.56
P(cyclic) = 0.31
mean a = 1.73

Frequency

Number of alternative attractors (a)

Symmetrical competition

(h)
P(a>1) = 0.84
P(cyclic) = 0.19
mean a = 2.6

Frequency
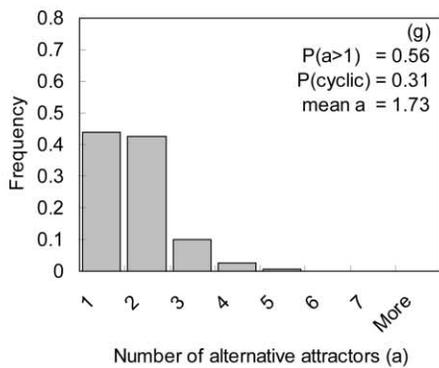
Number of alternative attractors (a)

curred with other initial states too. If there were some runs that had not yet reached a point attractor or if the system had become cyclic, the number of alternative attractors was counted by visual inspection of the runs. The results show that from a given species pool several alternative communities can usually be assembled (fig. 2). These alternative communities are stable in the sense that they are resistant to small immigration (in our model the inflow u) by other species from the pool. Although most communities are stationary equilibria, others take the form of complex cyclic attractors or chaos.

The probability of alternative attractors was strongly dependent on the way interspecific competition terms ($\alpha_{i,j}$) were selected. In our default approach, interspecific competition coefficients were uniformly distributed random numbers between 0 and 1 (fig. 2, *left panels*). However, this choice implies that interspecific competition is always smaller than intraspecific competition, which is not necessarily true in nature (Begon et al. 1996). To study the effect of including cases in which intraspecific competition is lower than interspecific competition, we have drawn numbers for $\alpha_{i,j}$ between 0 and 1.5 (fig. 2, *right panels*). We also analyzed the effect of symmetry in competition by simply mirroring the community matrix (fig. 2c, 2d). Finally, we studied the effect of adding a second trophic level on the occurrence of alternative attractors (fig. 2e–2h). In the following sections, we discuss the effects of these different choices on the attractors of the models.

Effect of the Balance between Intraspecific and Interspecific Competition

Comparison of the left panels and the right panels of figure 2 reveals that alternative attractors are more common if interspecific competition coefficients are allowed to exceed intraspecific competition. However, unlike in the classical two-species Lotka-Volterra competition model, this is not a necessary condition. One can usually understand alternative attractors are the result of a positive feedback (Scheffer et al. 2001; Scheffer and Carpenter 2003). For a two-species competition model, this is intuitively straightforward. If intraspecific competition is smaller than interspecific competition, it is better to have conspecifics around, which leads to a positive feedback in the abundance of either species as it starts displacing its competitor. It makes intuitive sense that this mechanism also promotes
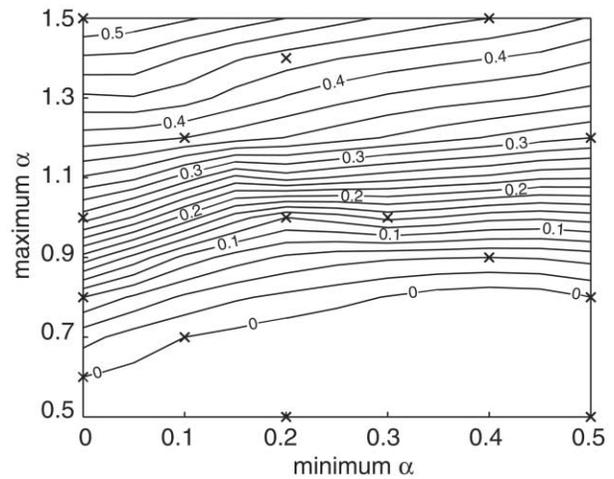

Figure 3: Dependence of probability of alternative attractors on the range of α's (all drawn from uniform distributions). Crosses denote the ranges of α's that were examined. The probability of alternative equilibria was estimated using 150 different generated communities.

alternative equilibria in the higher dimensional systems. But why are alternative attractors still quite common if all interspecific competition coefficients are smaller than the intraspecific competition (fig. 2a, 2c)? Although it is hard to grasp what is happening in a 20 × 20 species matrix, we found a possible mechanism in a four-species competition model (see fig. A1 in the online edition of the *American Naturalist*). The essence is that clusters of species may form an "alliance" in the sense that the competition within each cluster is lower than the competition between clusters. Each alliance thus can be self-reinforcing. This is possible if the average of the intraspecific and interspecific competition coefficients within each cluster is lower than the average of the interspecific competition coefficients between the two clusters. Obviously, more complex alliance structures are possible if the number of species increases, but the probability of alternative equilibria will be strongly dependent on the maximum interspecific competition coefficient (fig. 3). For a four-species system, alternative states are not possible if competition coefficients are drawn from a uniform distribution in the range of (0, 0.5) or smaller because the maximum average interspecific competition (0.5) cannot exceed the minimum average competition within a cluster (average of 0 and 1). This

Figure 2: Relative frequency of the number of attractors. The legends for a species pool of 20 competing species give the following: $P(a > 1)$, the probability to have more than one attractor; $P(cyclic)$, the probability of limit cycles or chaos; *mean a*, the mean number of alternative attractors found. The panels represent different models: *a*, random competition matrix, mean $\alpha = 0.5$; *b*, random competition matrix, mean $\alpha = 0.75$; *c*, half-symmetrical competition matrix, mean $\alpha = 0.5$; *d*, half-symmetrical competition matrix, mean $\alpha = 0.75$; *e, f*, competition like *a* and *b*, but with 10 predators added.
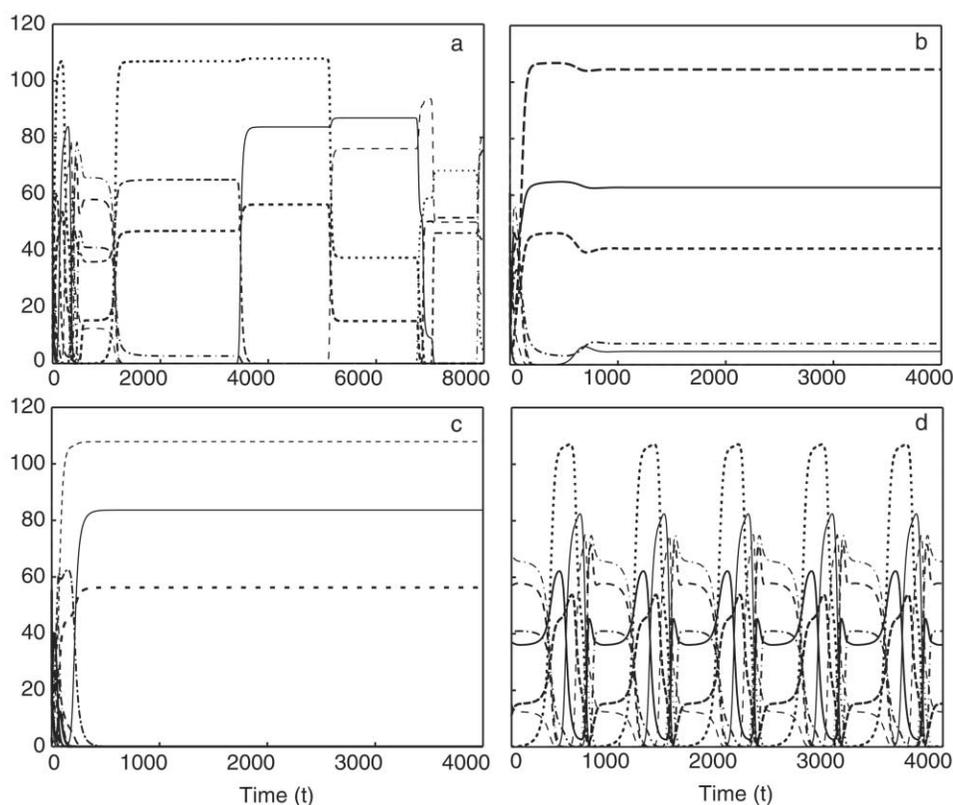
Figure 4: The classical Lotka-Volterra model can produce chaotic dynamics with near extinctions at which species biomass reaches unrealistically low values (*a*). Such cycles have long, seemingly stable periods in which a species is recovering from such extremely low biomass. Truncation of all species with a biomass of <0.001 to 0 causes the cycle to be replaced by multiple alternative equilibria (e.g., *b*, *c*). By contrast, a continuous small immigration (0.001 day^{-1}) of all species leads to a regular cycle without the quasi-stable episodes. For parameters, see the ASCII data file in the online edition of the *American Naturalist*.

might also explain why Case (1990) found no alternative attractors if competition coefficients were constructed using resource utilization overlap matrices (for details, see Levins 1966; Case 1990). The resulting α values then have a skewed bell-shaped distribution with a mean of around 0.45 (Case 1990).

The Effect of Symmetry in Competition

In earlier work, it has been a common approach to draw all competition terms in the interaction matrix at random (May 1971; Gilpin and Case 1976; Case 1990). However, this implies the assumption that the effect of species A on species B is not related to the effect of species B on species A. Such a lack of correlation between mutual effects will be unrealistic for many communities, as competition will often be more or less symmetrical among species sharing a common resource (Gilpin and Case 1976). To explore the potential implication of symmetry, we analyzed the effect of perfect symmetry using a mirrored competition matrix. The results show that symmetry in competition strongly promotes multiplicity of attractors (fig. 2*c*, 2*d*). By contrast, we did not find any limit cycles or chaos in these communities with symmetric competition.

The Effect of Adding a Second Trophic Level

Inclusion of a second trophic level in the model reduced the probability of alternative attractors. In most cases, the alternative attractors seemed to be caused by the dynamics of the competing prey species. We rarely found a community of alternate predators on similar communities of prey. It should be noted that the results of adding predators are quite sensitive to the parameter settings of the predators. While there are fascinating patterns to be explored here, we do not pursue this further in the scope of the current article. However, one important observation is that complex cycles and chaotic attractors become much more common if the second trophic level is added. This is quite relevant in the current context, as cycles may disintegrate
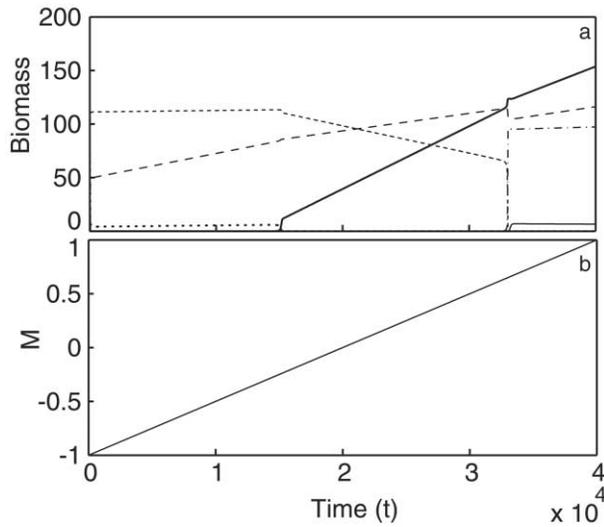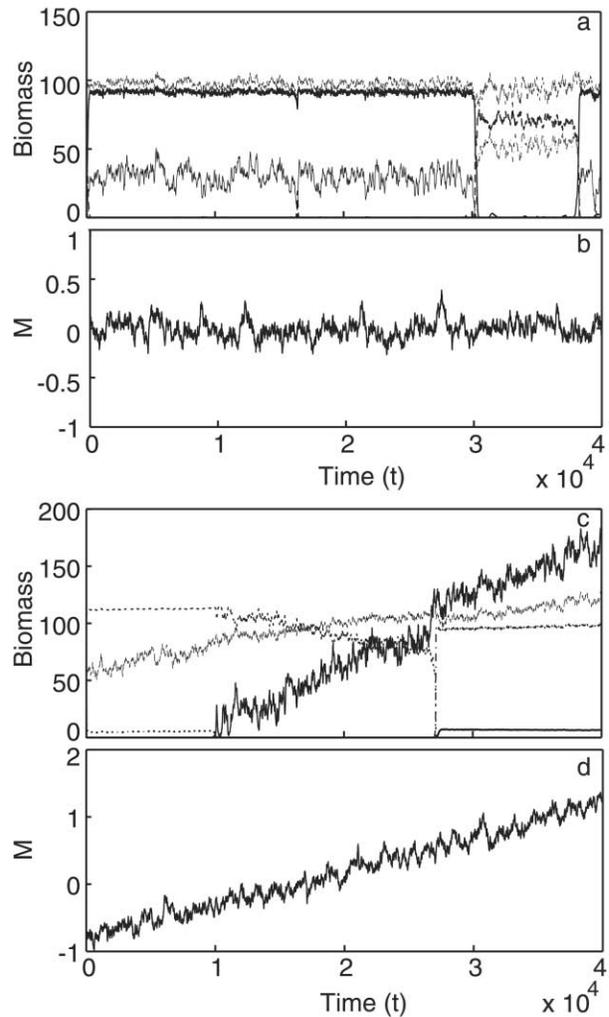
Figure 5: Gradual change in the environment (*b*, *M* moves linearly from −1 to 1) results in gradual change in species abundances until at a critical threshold a shift to another community composition occurs (*a*). For parameters, see the ASCII data file in the online edition of the *American Naturalist*.

into multiple stable states depending on assumptions about immigration and extinction.

Implications of Cycles for Alternative Attractors

The existence of cycles may reduce the scope for alternative attractors. This is because intrinsic oscillations, just as external disturbances, can bring the system across the boundaries of a basin of attraction, implying that the attractor no longer exists, a phenomenon known as nonlocal bifurcation (Rinaldi and Scheffer 2000) or basin boundary collision (Vandermeer and Yodzis 1999). A particular situation arises if the biomass of a population approaches 0. In simulations with the model (1) without the immigration term *u*, extinction of species appears as an asymptotic approach of their biomass to 0. At some point, one may argue that for all practical purposes, a species with extremely low biomass (e.g., 10^{-200}) has gone extinct. However, there can also be cycles in which biomass of a species becomes (unrealistically) low but subsequently recovers. This typically leads to extremely long and irregular cycles (fig. 4*a*). During seemingly stable periods, species are recovering exponentially from very low values to invade and change the system. Such cycles easily become chaotic because the recovery from these near extinctions implies a large sensitivity to the initial conditions (Rinaldi and Scheffer 2000). One may argue that in a heterogeneous world there will always be a small immigration from an

area in which the species is thriving (Scheffer and De Boer 1995). Mimicking this by a tiny immigration term (such as our *u*) prevents such long-stretched cycles with near extinctions (fig. 4*d*). However, another approach is to truncate species below an arbitrary threshold to 0 (Gilpin and Case 1976). The idea is that species with very low numbers are at high risk of true extinction (Rosenzweig 1971). Indeed, truncation of species can be regarded as a simple implementation of an Allee effect. Significantly, truncation of species at low numbers can boost the num-

Figure 6: A shift to an alternative community composition (*a*) may be triggered by random fluctuations (red noise; λ = 200 days, β = 0.009) in the environment (*b*). Exposed to gradual environmental change combined with some fluctuation in conditions (red noise; λ = 200 days, β = 0.01), the model predicts that pronounced shifts triggered by stochastic events are bound to punctuate periods of gradual change and small fluctuations in biological communities (*d*). For parameters, see the ASCII data file in the online edition of the *American Naturalist*.
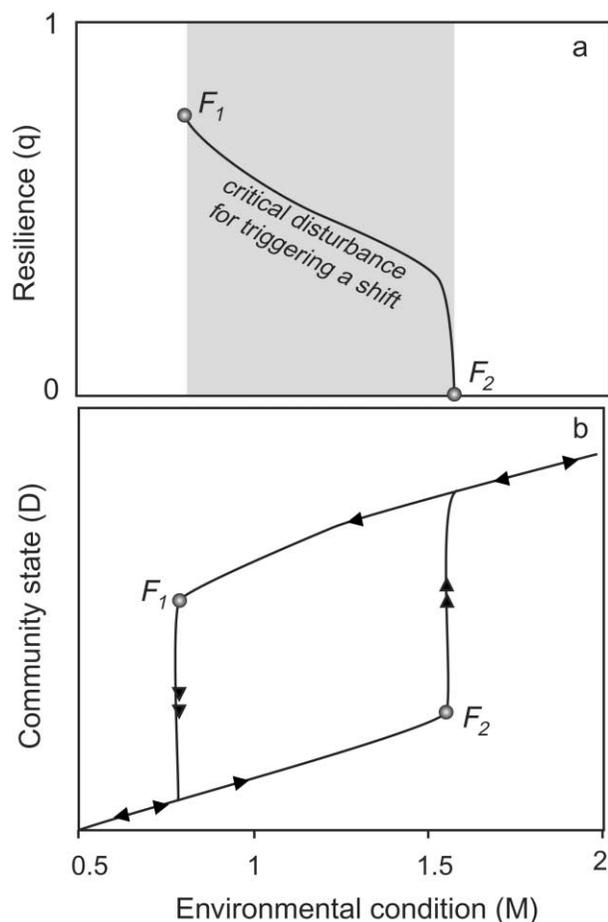
Figure 7: *a*, Over a range of environmental conditions (*shaded area*) a disturbance beyond a critical size can cause a shift to an alternative community. The disturbance needed (resilience) shrinks to 0 as change in the environmental condition (*M*) moves the system to a critical bifurcation point (F_2). *b*, Gradual increase of the environmental parameter *M* causes the community to shift at a critical condition (F_2). If the change in *M* is subsequently reversed, the system shows hysteresis, and a shift back occurs only when *M* has decreased enough to reach the other bifurcation point (F_1). The community state is represented in a relative way by plotting dissimilarity (*D* = Euclidean distance) from the initial state (*M* = 5).

ber of attractors. This is because complex cycles that pass through low numbers of some species tend to be trapped into one of several alternative attractors in which those species go extinct. For example, in the case illustrated in figure 4, six alternative attractors replace the cycle. Perhaps this explains why Gilpin and Case (1976), using truncation, found no cycles in hundreds of systems they explored. In any case, the fact that we used a small immigration term in all simulations implies that estimated numbers of alternative attractors are conservative compared to what one would expect if species were truncated if their biomass

falls below a certain critical limit. This is especially true for situations in which complex cycles are common, such as in the models with two trophic levels.

Conclusion

In conclusion, alternative attractors are a robust phenomenon in the multispecies models we explored, especially if one allows interspecific competition to exceed intraspecific competition, and if one assumes some symmetry in competition, multiplicity of attractors is the rule rather than the exception. Alternative attractors also occur if two trophic levels are included. The complex oscillations common in this case can lead to a further multiplicity of attractors if Allee effects truncate populations to 0 if their density falls below a critical level.

Response to Environmental Change

Unlike numerous similar models studied previously, our model communities can be exposed to environmental change. The typical response to slow linear change in the environmental parameter is one of periods of gradual change in species abundances interrupted by sharp shifts to alternative community states (e.g., fig. 5). Exposed to random fluctuations rather than gradual change in conditions, the response of the model communities depends on the amplitude of the noise. Very small or large fluctuations in the environmental factor simply result in small or large fluctuations in community composition. However, at intermediate environmental forcing, communities fluctuate around certain conditions for long episodes of time until an incidental forcing condition triggers a shift to a distinctly different dynamic regime (fig. 6, *upper panels*). In nature, most communities are obviously exposed to gradual trends in conditions combined with erratic environmental fluctuations. Not surprisingly, the model communities under these conditions fluctuate in gradually changing regimes, which at times shift sharply to alternative regimes (fig. 6, *lower panels*). Note that no dramatic extremes in the environmental conditions are needed to invoke such switches.

Loss of Resilience and Hysteresis

These patterns are a consequence of the multiplicity of attractors that characterize the model. As in any dynamical system with more than one attractor, change in conditions is bound to alter not only the position of attractors but also their basin of attraction (fig. 1). At certain critical conditions, attractors disappear through catastrophic bifurcations, inducing a shift to an alternative state from which the model only recovers after conditions have re-

turned beyond another critical point. However, approaching the bifurcation, the attraction basin typically shrinks. This loss of resilience (sensu Holling 1973) implies that the system becomes increasingly likely to be pushed into an alternative basin of attraction by erratic events. Although the complexity of our model prevents a simple mapping of the equilibria and their attraction basins, the loss of resilience can be shown through an analysis of the strength of a disturbance needed to invoke a shift to an alternative community state. Since we have a multidimensional system, one needs to be explicit not only about the size of the disturbance but also about the direction. Our approach has been to measure disturbance as the relative displacement q in the direction of an alternative attractor. To determine this value, we first determined the equilibrium biomass vectors N_{eq} for two alternative equilibria and subsequently ran the model from different initial states computed as weighted averages between both equilibria: $N = N_{eq}(1 - q) + N_{eq2}q$. The minimum q at which the system switches to the alternative state is the critical disturbance, which we take as a measure of resilience. Systematic numerical experiments illustrate that, indeed, resilience shrinks to nil as one approaches the catastrophic bifurcation (fig. 7a). In addition, numerical experiments in which one gradually increases the environmental factor M until a shift occurs, which subsequently slowly reverses the change in M, illustrate that, as expected, the model shows hysteresis in response to changing conditions (fig. 7b).

Conclusions

In conclusion, our numerical experiments illustrate that the existence of multiple attractors in complex communities has essentially the same implications for the response to environmental change as predicted by simple tractable models. Gradual environmental change results in a gradual response in species abundances, but as a catastrophic bifurcation point is approached, resilience of the current state shrinks. Consequently, the system becomes increasingly brittle to the point that even a moderate stochastic event triggers a shift to an alternative attractor, which is difficult to reverse.

Discussion

Our results suggest that multiplicity of attractors is a common and robust phenomenon in the multispecies models we explored, where it leads to occasional catastrophic transitions in community state if environmental conditions change. We propose that multispecies competition can potentially explain catastrophic shifts in cases where there seems no other explanation (e.g., Hare and Mantua 2000).

The big question is, of course, whether these insights really are relevant to our understanding of patterns in the real world, which has so many features which are not captured by our toy models. Here, we discuss possible empirical evidence for alternative attractors in community states and ponder the relevance of our theory for understanding effects of global change and the causes of ancient mass extinctions.

Empirical Evidence of Alternative Attractors in Communities

Whether the proposed mechanisms can indeed be responsible for catastrophic shifts in species composition depends essentially on the question of whether the underlying phenomenon of alternative stable community states is a realistic feature of natural communities. There is some evidence that suggests this is indeed the case. Authors working on community assembly rules have extensively explored this point in laboratory experiments showing that the history of colonization leads to various alternative communities (Drake 1990; Samuels and Drake 1997). While these experiments are all on relatively small scales, real food webs are usually much more complex (Dunne et al. 2002). Our models barely scratch the surface of the complexity of multispecies interactions in nature, and yet they reveal a high frequency of multiple attractors. It seems unlikely that systems with yet more complex webs of interaction would be less likely to have multiple attractors.

Implications for Global Change

If multiplicity of stable states does indeed commonly arise from biotic interactions in multispecies communities, the potential implications are profound. It has been shown earlier that removing one species from a community may result in a cascade of secondary extinctions (Paine 1966; Bender et al. 1984; Borrvall et al. 2000; Dunne et al. 2002). Our results suggest that the omnipresent gradual environmental change can also lead to such cascades. Virtually all biological communities are exposed to slow change in climate, nutrient concentrations, groundwater levels, harvest rates, and other factors (Vitousek et al. 1997; Tilman et al. 2001), and effects on biodiversity over the coming century will probably be enormous. A recent analysis suggests that midrange projected effects of climate change alone might lead to extinction of about a quarter of terrestrial species by 2050 (Thomas et al. 2004). The existence of alternative attractors in community composition implies that although the resulting change in biodiversity will usually be smooth, it might incidentally show sharp shifts, which are difficult to foresee and to reverse.

As discussed in the introduction, this point has been made earlier for particular ecosystems in which well-defined dominant feedbacks lead to alternative attractors. However, if interactions among many species imply a tendency to multiplicity of attractors, catastrophic shifts might be more common than previously thought. Why then does change in nature seem to be gradual rather then catastrophic in general? Obviously, as our simulations illustrate, one should expect gradual change to be the rule, even if alternative attractors are present. Catastrophic shifts are predicted only in narrow windows of critical conditions. Thus, absence of catastrophic shifts is no evidence for the absence of alternative attractors. However, it could also be that our models systematically ignore aspects of the real world that prevent catastrophic transitions. One obvious candidate is spatial heterogeneity. Although only a few studies have explicitly addressed the effect spatial complexity has on stability shifts in ecosystems (Sternberg 2001; Rietkerk et al. 2002; Foley et al. 2003; Scheffer and Carpenter 2003), an overall smoothing effect of spatial heterogeneity seems obvious (Loreau et al. 2003). Nonetheless, model analyses indicate that spatial exchange of organisms and substances tends to make even extensive spatially complex systems respond in synchrony with occasional catastrophic transitions. Perhaps this explains why some of the more dramatic regime shifts have been documented in marine systems where hydrodynamic exchange is common (Done 1991; Knowlton 1992; Steele 1998; Hare and Mantua 2000; Nystrom et al. 2000).

A Mechanism for Ancient Mass Extinctions?

Our results also hint at an empirical ecological foundation for the idea that stability shifts in complex biotic interactions may be a crucial ingredient of mass extinction events. The change of biodiversity over evolutionary history has been notoriously irregular. The fossil record suggests that periods of relatively little change have been interrupted by five large and many smaller shifts in species composition (Hubbard and Gilinsky 1992; Benton 1995). Huge disturbances such as bolide impacts (Olsen et al. 2002) or supernova explosions (Ellis and Schramm 1995) have been thought to explain some of the largest species shifts. However, signs of exceptionally large external impacts are not evident for all mass extinction events. Alternatively, it has been suggested from random process models that evolution may also lead to occasional cascades of extinctions of species without an external forcing (Bak and Sneppen 1993). Evidence for this line of reasoning is claimed to be present in statistical patterns in the fossil record (Sole et al. 1997), although these patterns may be interpreted in alternative ways (Newman 1997).

We did not explicitly model evolution. However, the struggle for life in our changing environment (M) is in fact analogous to random evolution. This is because the differential response (η) of species to gradual environmental change leads to shifting fitnesses in a way that is analogous to differential evolution of species. Our results may thus be seen as an independent support for the idea that evolution in complex communities might lead to periods of gradual change punctuated by rapid and widespread extinction events. Clearly, unlike the change in our environmental parameter M, evolution cannot be reversed. Thus, a complete hysteresis loop cannot be expected in evolution. Nonetheless, the intrinsic tendency to multiplicity of attractors in complex communities implies that any gradual change (in species or environment) is likely to hit incidentally on a catastrophic bifurcation.

Significantly, our interpretation of an underlying multiplicity of attractors unifies the idea of intrinsically driven extinction events with the ruling paradigm that external disturbances such as bolide impacts (Olsen et al. 2002) or supernova explosions (Ellis and Schramm 1995) are responsible for mass extinctions. The clue is that in a world with multiple attractors, gradual change in species traits or the environment inevitably leads to reduction of the basin of attraction around the current state at times (figs. 1, 7). Random events become increasingly likely to trigger a shift to another attractor in such situations. This suggests a multiple causality of mass extinction events. Slow decrease of resilience due to evolutionary change and/or environmental change makes the system increasingly brittle, allowing a stochastic disturbance event to finish the job.

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