Criticality and scaling in evolutionary ecology

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Fluctuations in ecological systems are known to involve a wide range of spatial and temporal scales, often displaying self-similar (fractal) properties. Recent theoretical approaches are trying to shed light on the nature of these complex dynamics. The results suggest that complexity in ecology and evolution comes from the network-like structure of multispecies communities that are close to instability. If true, these ideas might change our understanding of how complexity emerges in the biosphere and how macroevolutionary events could be decoupled from microevolutionary ones.

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Fractals are widespread in nature[1,2] and have features that look the same when there is a change in scale: they are called 'self-similar'. In biology, self-similar patterns are known to occur at many levels[1–4] (Box 1). But fractals are also present in time: the fluctuations of a given quantity can appear the same when observed at different temporal resolutions (Fig. 1a). This is the case for heartbeat intervals[5], epidemics in small islands[6], breeding bird populations[7] or the fossil record[8].

Because fractals involve long-range correlations, they also reflect some key features of how living systems are organized and how they evolve in time. The implications for evolution are very important, because cooperative effects emerging from the interactions can lead to new, sometimes counterintuitive, results. A consequence of this is that order could be generated through evolution by a synergy between natural selection and self-organizing processes.

Scaling and power laws

The common feature of self-similar behavior is the presence of scaling laws[4] (also known as power laws). Given the frequency distribution $N(s)$ of some quantity s (number of species, size, lifetime, etc.) it is said that it follows a power law if $N(s) = Cs^{-\tau}$ (Fig. 1a). Let us assume that s stands for size. Here C is a constant and

$\tau > 0$ is a given exponent, often called the critical exponent. The reason why these laws are characteristic of fractal objects is that they are the only functions displaying invariance under scale change. If we look at a larger or smaller scale – that is, if we take $s' = \gamma s$ – it is not difficult to see that $N(s') = C'N(s)$ or, in other words, a change of scale does not modify the basic statistical behavior.

The same argument can be employed for a time series (Fig. 1b). If self-similar behavior is present, then the time correlations should decay in a power-law fashion[9]. This is something that has been widely observed and is known as '1/f-noise'[6,8,9]. A 1/f-like signal looks like a mountain landscape in time, rather than space. The self-similarity is described by the power spectrum $P(f)$, which measures the contribution of each frequency to the overall time series[6]. The 1/f noise is defined as $P(f) \approx f^{\beta}$ being the exponent $0 < \beta < 2$.

Is there any particular situation where such complex structures emerge? The answer is yes. In physics, fractal structures in space and time were known to emerge in the proximity of some types of phase transition[10,11]. The classic example is a magnetic material. A small piece of iron can tug on a paper clip at room temperature, but if we heat it to a high temperature T, no magnetic power is observed. We say the magnetization M is zero. The atoms that form the iron are themselves like small magnets. Each atom only interacts with its nearest neighbors and their natural tendency is to align spontaneously into small domains with the same orientation. At high T the coupling between nearest atoms breaks down because of thermal perturbations and, therefore, the atoms can have any polarity (up or down) and $M = 0$. But suddenly, when the material is cooled down, order spontaneously shows up. There is a critical temperature at which global magnetization appears ($M > 0$) and both fractal-spatial and fractal-temporal features arise. These transitions are described by an 'order parameter' (here M), which is zero at the disordered phase and positive otherwise.

Self-similarity is a defining characteristic of the critical state. The surprise came when physicists realized that very different systems behaved exactly the same when close to critical transition points[6,10,11]. Surprisingly, extremely simple models of these systems provided an exact description. This is a consequence of the so-called 'universality'. Universality means that systems sharing a small number of basic features behave identically at the critical point. Are there also universal principles behind apparently different biological phenomena?

From RNA viruses to epidemics

Starting at the molecular level, an example of a critical point in biological systems can be exemplified by the dynamics of RNA viruses[12]. The understanding of how these entities evolve and adapt must take into account their extreme variability, caused by the error-prone RNA polymerase activity and the lack of proofreading mechanisms[13]. Instead of a given single sequence, we have


Box 1. Fractals everywhere

The patterns displayed by many natural systems do not allow for a simple description using Euclidean geometry: they present scale-invariance; that is, no characteristic length measure can be obtained from them. Therefore, when observed at different resolutions, they display the same pattern. This is the case of river networks and mountains[1], tree branching and blood vessels[3] or forest spatial structures[2,4]. Even at the molecular level, fractals can be observed: if we analyse the linear distribution of nucleotides in a DNA chain, a self-similar pattern can also be detected[5]. These structures – the so-called fractals – share the presence of long-range correlations.

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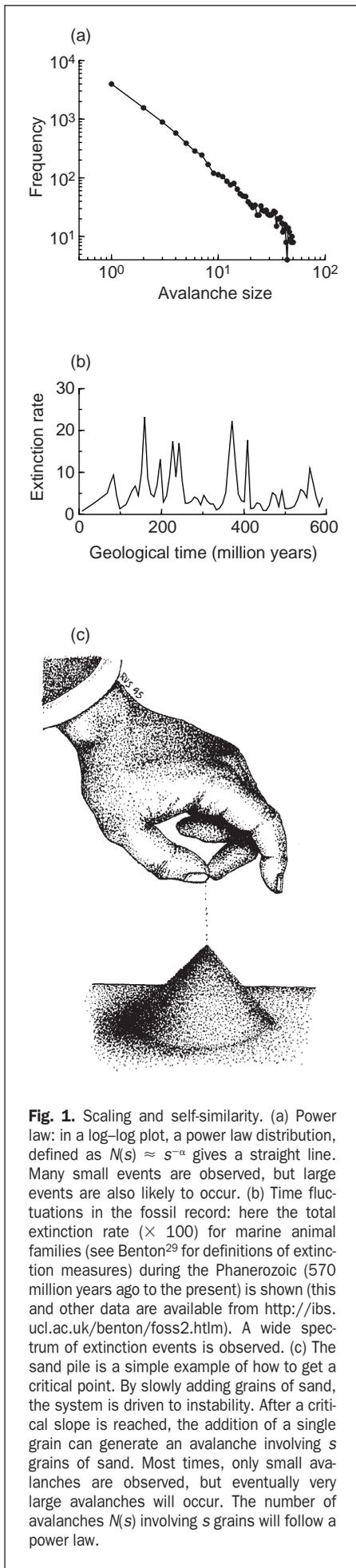
Fig. 1. Scaling and self-similarity. (a) Power law: in a log–log plot, a power law distribution, defined as $N(s) \approx s^{-\alpha}$ gives a straight line. Many small events are observed, but large events are also likely to occur. (b) Time fluctuations in the fossil record: here the total extinction rate ($\times$ 100) for marine animal families (see Benton[29] for definitions of extinction measures) during the Phanerozoic (570 million years ago to the present) is shown (this and other data are available from http://ibs.ucl.ac.uk/benton/foss2.htlm). A wide spectrum of extinction events is observed. (c) The sand pile is a simple example of how to get a critical point. By slowly adding grains of sand, the system is driven to instability. After a critical slope is reached, the addition of a single grain can generate an avalanche involving s grains of sand. Most times, only small avalanches are observed, but eventually very large avalanches will occur. The number of avalanches $N(s)$ involving s grains will follow a power law.

Box 2. Recipe for a catastrophe: the error catastrophe

A population of strings is simulated to explore how the 'master' sequence population behaves when the mutation rate is changed (a). Here, $N = 100$ strings of size $\nu = 15$. Each string is defined by a sequence $S_1 S_2 ... S_\nu$ where $S_i \in \{0,1\}$. At each time step, we choose a string and make a copy of it after removing another randomly chosen string. This replication takes place with probability $P = 1$ if $S_i = 1$ for all units (this is the master sequence) and with probability $P = 0.05$ for any other string[16]. The copy process involves a mutation rate μ, which means that the probability of error per unit and per replication cycle is μ for each string. Starting from a random population, we repeat the same rules over 1×10^4 steps and at the end we look into the system to see if there is any copy of the master sequence. Here the master sequence is the string 1111…11; that is, the one with the highest replication rate. This is averaged over 1×10^2 trials and for each mutation rate we compute how many of these replicas (P_m) have at least one master sequence. Although our intuition would expect a smooth, continuous decay of this probability, there is actually a sharp decay close to a given critical mutation rate (i.e. P_m acts as an order parameter for this transition). This phenomenon is known as the 'error catastrophe'. It describes the breakdown of heredity and the transition from a localized set of mutant sequences (localized around the master sequence in sequence space) towards a random set of strings[17]. The inset graphs show the evolution of relative population sizes of strings when (b) $\mu = 0.05$ and (c) $\mu = 0.12$. The master sequence is indicated by the unbroken line in these two graphs.
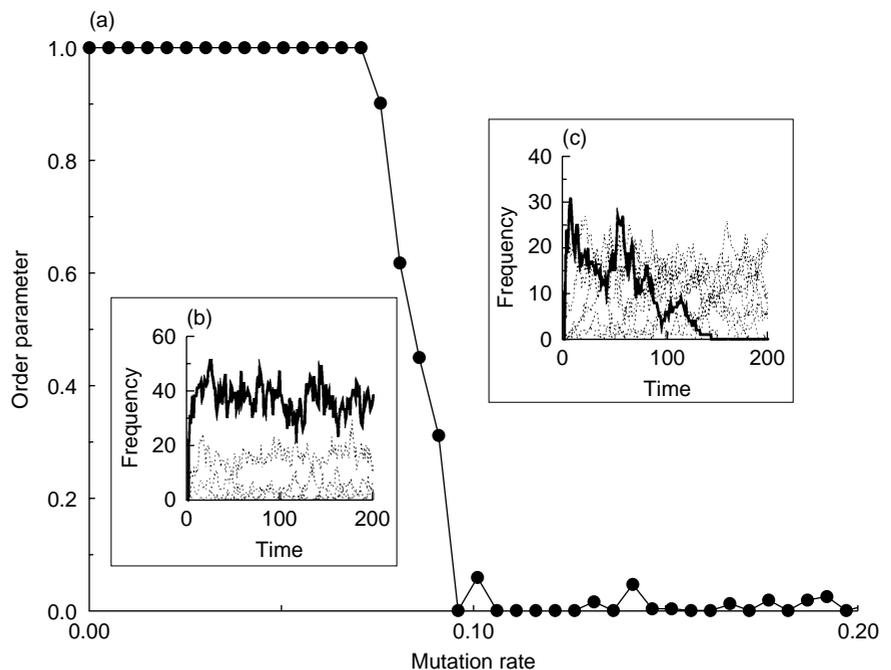

(Online: Fig. I)

a cloud of mutants around the so-called 'master' sequence. This cloud is known as a quasispecies, a term first coined by Manfred Eigen in 1971 (Refs 14,15).

RNA viruses adapt to a changing environment by making use of their variability. Selection pressures by the immune system force the virus quasispecies to evolve. The quasispecies model is consistent with this observation, but something defeats our intuition: there is a critical mutation rate beyond which heredity breaks down. This is referred to as the error catastrophe, and it is nothing but a phase transition point, which poses serious limitations to the virus complexity (Box 2). (In fact, the quasispecies model behaves as a magnetic system[15].) Available molecular data confirmed the theory: RNA viruses do replicate close to the error catastrophe[16,17]. This property can only be understood under the framework of critical transitions. Recent experimental[18] and

theoretical[19] work show that critical points could play a very important role in the evolution of quasispecies.

These transitions are well known in the dynamics of infectious diseases[20] and in some habitat fragmentation models[21]. A simple, but important, illustration of a critical phenomenon in epidemics is provided by contact processes[22,23] (CPs). The rules in the simplest model are defined as follows (Fig. 2): (1) active (infected) particles (A) die (becoming inactive or susceptible) with probability γ; (2) if a given active particle survives, each susceptible or inactive neighbor can become infected or active, respectively, with probability β. For a given γ, propagation occurs only if a given threshold β_c is reached.

Another instance of threshold phenomena in ecology has been recently reported in relation to the avifauna of Hawaiian Islands[24]. After a gradual accumulation of species, numerous extinction
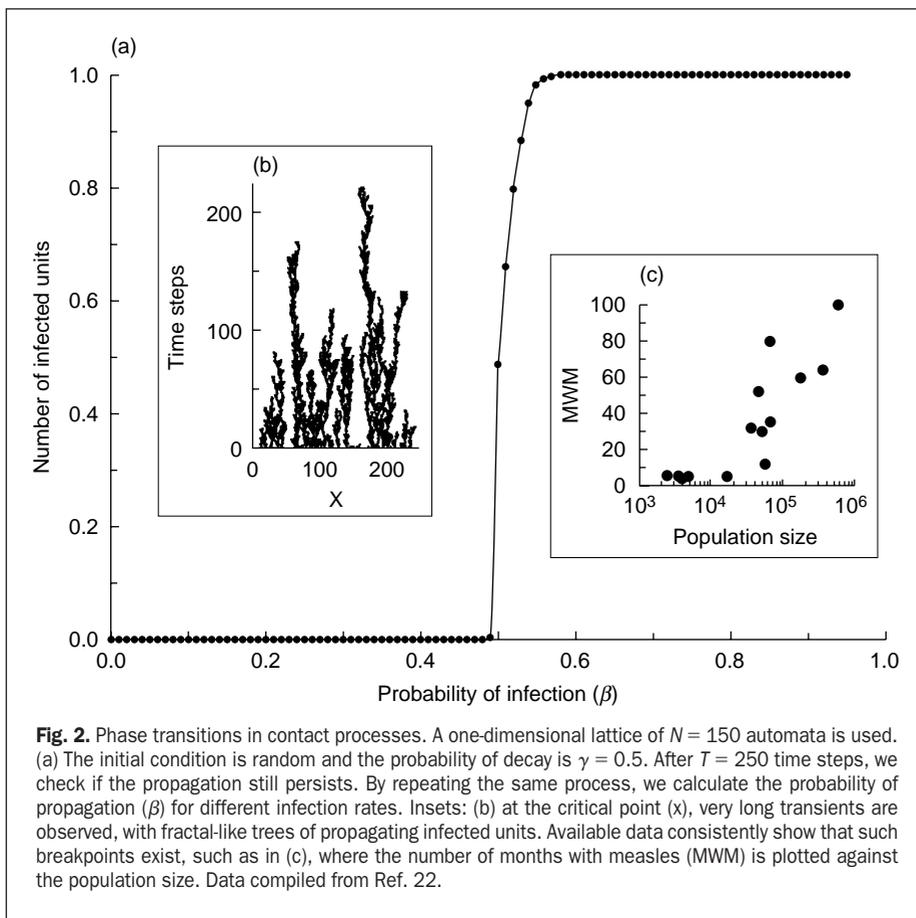
Fig. 2. Phase transitions in contact processes. A one-dimensional lattice of $N = 150$ automata is used. (a) The initial condition is random and the probability of decay is $\gamma = 0.5$. After $T = 250$ time steps, we check if the propagation still persists. By repeating the same process, we calculate the probability of propagation (β) for different infection rates. Insets: (b) at the critical point (x), very long transients are observed, with fractal-like trees of propagating infected units. Available data consistently show that such breakpoints exist, such as in (c), where the number of months with measles (MWM) is plotted against the population size. Data compiled from Ref. 22.

events occurred once a critical number of introduced species was reached. The statistical features where shown to be power-law distributed, which suggests that the accumulation of new species drive ecosystems to criticality. However, this is different from the previous scenarios. Now, there is no parameter tuning the dynamics: as species number increases the system becomes spontaneously unstable.

Criticality and self-organized criticality

If fractal structures and self-similar fluctuations are so common, perhaps some universal dynamical processes are at work. A possible scenario was proposed in 1987 (Refs 25–27) and is known as self-organized criticality (SOC). Self-organized criticality is easily stated as follows: large, far from equilibrium, complex systems, formed by many interacting parts, spontaneously evolve towards the critical point.

A simple metaphor of an SOC process is provided by a sandpile[25,26] (Fig. 1c). We add sand slowly, one grain at a time. At the beginning, we have a flat pile, and the grains stay where they land. The grains are basically independent and their behavior described by gravity and friction forces. But, as the slope increases, we reach a regime where avalanches involving grains in interaction are occurring

all the time. At the SOC state, there is one complex system, with its own emergent dynamics. This new state cannot be anticipated from the properties of individual units. In an ecological context, the addition of new species would place ecosystems close to a critical state, where the collective and not the individual species would be the relevant object in the long run.

Models of SOC systems are very simple and typically parameter-independent. In spite of their simplicity (and because of their universality), they can be used to model complex systems. In this respect, it has been shown that the dynamics of measles in small islands show power law behavior[6]. In this study, the basic rules are precisely the ones involved in the 'forest fire' model, one of the simplest and best-known models displaying SOC (Box 3)[26,27].

Evolution and extinction

The fossil record is almost entirely formed of extinct groups[28,29]. If extinction is the fate of most lineages, one should ask whether an external or internal process is the relevant aspect of extinction dynamics. Many recent theories claim that external stresses are the cause of extinction events[28]. However, we should ask if these events are the causal agents of extinction or the trigger points for a complex biotic response.
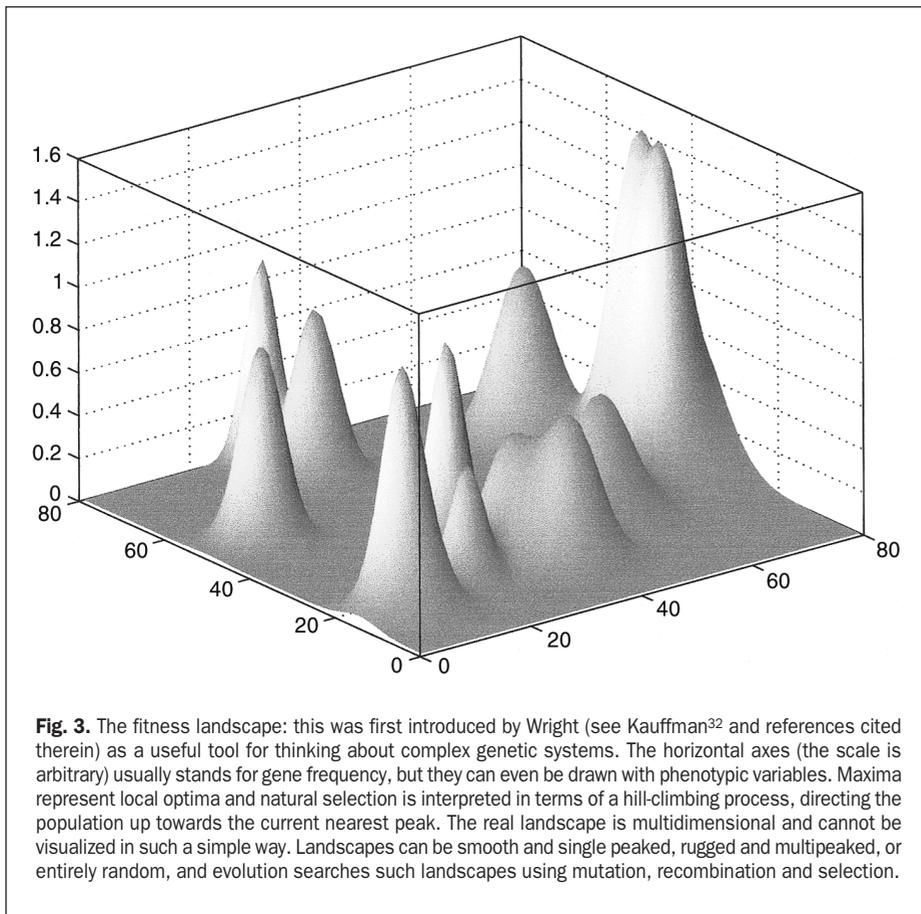
Power laws are observed not only in the distribution of extinction events and lifetimes[30], but also in the tree-like organization of taxonomy[31]. The presence of these power laws soon led to the proposal that large-scale evolution would be the result of an SOC-like phenomenon. This idea generated a number of models exhibiting criticality. Among them, the following can be cited.

• Models based on tunable rugged fitness landscapes (Fig. 3): in these models, species are evolving on landscapes that deform because of the adaptive moves[32] of other species. Genetic changes in different species alter the ruggedness of their landscapes. If useful in the future evolution of the progeny, the ruggedness itself evolves. Species can also invade one another's niches. The losing species goes extinct, whereas the invaders comprise a new sibling species created in the niche. Species whose landscapes have a ruggedness that is useful tend to succeed at invasion. The result is that landscape ruggedness evolves without group selection to reduce the probability of extinction events and increase mean fitness. The result also yields a power law distribution of extinction events (also called coevolutionary avalanches).

• Models with external dynamics: in the Bak–Sneppen (BS) model[26,30,33], species are first assigned random fitness values. At each time step, the species with the lowest fitness goes extinct, and is replaced by, or mutates to, another species with a random fitness. This affects the livelihood of interacting species, which are also assigned new random fitnesses. As this darwinian evolution continues, extinction eventually takes place in the form of coevolutionary avalanches

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Box 3. The forest fire cellular automaton

This is a cellular-automata model, which has been shown to display complex spatial and temporal fractal behavior[26]. Because of its simplicity and its relation with infectious dynamics, it has been used as a model of epidemics on small islands[6]. The system is described by a two-dimensional lattice of $L \times L$ nodes where 'trees' are scattered. Each site can take three allowed states: empty (E, no tree), green (G, tree) or burning (B, burning tree). The rules are defined by a set of transitions between states. Specifically, E→G with probability p and G→B with probability f. An additional rule is required for the propagation of the fire front: if one of the eight nearest trees of a green tree is burning, the tree starts to burn. Burning trees only burn for a single step (becoming empty afterwards). Fractal clusters of burning trees are

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Prospects

Scaling behavior and critical points are commonplace in different biological systems. In some cases, such as in epidemiology or the effects of habitat fragmentation, the available information is rather detailed. But many open problems remain to be solved, and new theoretical and field studies are needed, in particular:

• The analysis of scaling in multispecies communities. New models involving ecological timescales that can incorporate individual-based interactions should be explored[38].

• Analysis of long-term field studies of species removal and development of new theoretical models able to test the presence of criticality and avalanches in response to perturbations, as well as the relevance of higher-order interactions[35].

• Studies on the spatiotemporal behavior of rainforest plots[4], both in terms of species diversity and canopy structure. Calculation of fractal properties and temporal dynamics would greatly help, as a quantitative way to understand how diversity and nonequilibrium dynamics are related[38].

• Fine-scale analysis of fossil record time series, with comparisons between fluctuations in physical variables (such as in Newman[39]) and biotic fluctuations. Analysis of fractal patterns of diversification and taxonomy and their possible dynamical origin are also required.

There is a need for new theoretical frameworks that allow us to understand how self-organization, selection and historical accident find their natural places with one another.

The great success of theoretical physics gives us confidence that simple models can account for the macroscopic behavior of complex systems. This statement is apparently unlikely to be extended to biology, where details often matter. But population and evolutionary biologists have been successfully using oversimplified models of ecology and evolution – and certainly, at some scale, many details do not matter. We should not forget that physics and biology have often come to a common language where challenging ideas have been born. We believe that the potential results of such a dialogue are well worth the effort.

Fig. 3. The fitness landscape: this was first introduced by Wright (see Kauffman[32] and references cited therein) as a useful tool for thinking about complex genetic systems. The horizontal axes (the scale is arbitrary) usually stands for gene frequency, but they can even be drawn with phenotypic variables. Maxima represent local optima and natural selection is interpreted in terms of a hill-climbing process, directing the population up towards the current nearest peak. The real landscape is multidimensional and cannot be visualized in such a simple way. Landscapes can be smooth and single peaked, rugged and multipeaked, or entirely random, and evolution searches such landscapes using mutation, recombination and selection.

of all sizes. The largest ones can represent mass extinction events, which thus might take place without an external stress. This model leads to SOC and power laws for any macroscopic quantity.

• Network-ecosystem models: here, the system is assumed to be defined at the ecological timescale by a network of connections[34]. Ecological responses are the relevant component of the dynamics, instead of coevolutionary avalanches. At each step, random changes in the connectivity are allowed to occur. The response of the system to such changes is highly nonlinear and might generate large extinction events. Diversification is introduced and the correct statistical distribution of extinction events, lifetimes and even a fractal taxonomy[34] are obtained.

A particularly important consequence of these models is the decoupling between micro- and macroevolutionary processes[34]. Across some short timescale, adaptation of species to a given abiotic and biotic environment takes place. We can clearly identify coevolution between directly related species, but little attention has been paid to the indirect effects (i.e. higher-order interactions[34,35]). Because such interactions reflect network properties, which are not reducible to the two-species pairs, we might ask how relevant are such indirect effects in the long run. If network properties are important, a change in one species could propagate through the system in a highly nonlinear, unpredictable way. The consequences of such propagation are unlikely to be explained through the adaptation or selection processes that can be applied to single species or simple two-species systems. The highly unpredictable network dynamics could provide the natural source of decoupling between micro- and macroevolutionary dynamics[34].

It is worth mentioning that field data support the view of a patterned, network-dependent response of ecosystems to perturbations. In this context, the collective features of network interactions become clear when the energy flow between species is analysed. Links representing a relatively small strength can have a large impact on stability, whereas interactions involving an important flow of energy can have a small impact[36]. In addition, at a different scale, an extensive analysis of available ecological time series revealed that in most cases the observed fluctuations were characterized by a very small Largest Lyapunov Exponent[37] (LLE). Roughly, the LE is negative for equilibrium points and positive for chaotic dynamics, respectively. The SOC theory typically predicts an LE close to zero, precisely at the point separating stable from unstable dynamics.

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Poles apart

The Biology of Polar Habitats

by G.E. Fogg

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*T*he Biology of Polar Habitats is one of a series of texts giving overviews of different habitats. The series' remit is to give an overview of design, physiology, ecology and behaviour of organisms in the specific habitats, pitched at a level appropriate for the biological or environmental student, new field worker or knowledgeable naturalist.

Within this remit, it is plainly simplistic to attempt to recognize a 'polar' habitat. This volume aims to demonstrate the range of habitats that exist towards both poles, the various important ways in which these two regions differ, and how the regions influence or are used as models or sensitive barometers for processes that take place at lower latitudes much closer to home. In taking an holistic approach across marine, freshwater, terrestrial and ice-driven biomes, Fogg has created a volume that fills an important and vacant niche.

It quickly becomes apparent that despite the many similarities to be found in comparisons of the two polar regions they are by no means two simple alternatives. Many of the differences that exist are driven by geography. The Arctic consists of northern continental regions fringing a largely enclosed, relatively shallow and cool ocean, whereas the Antarctic is a large continent (greater in area than Europe or Australia) surrounded by a very cold ocean and isolated from the rest of the world by oceanic and atmospheric currents. The book highlights the scale of the polar regions' role as an energy sink, by which they exert an important controlling influence on global climates and circulation patterns.

Fogg introduces the reader to the major types of polar habitat: glacial (ice and snow), periglacial terrestrial, inland water, marine benthos, sea ice and open seas. The text is peppered with references to the importance of polar habitats in the global system but does not overlook some of the remarkable features that allow polar organisms to survive and even flourish *in situ*. On the one hand, we learn that rivers draining 14% of the Earth's land area drain into the Arctic Ocean, yet the longest river in Antarctica is only 40 km and spends most of the year completely frozen. On the other hand, approximately 15×10^6 km^2 of sea-ice form and melt over the Southern Ocean each year, influencing the biota of seas, which are thought to be an important carbon sink, possibly buffering increasing atmospheric CO_2 levels, while also accounting for *c.* 25% of biogenic silica deposition worldwide.

Productive areas of research are likely to benefit from synergies of disciplines across major biomes. Thus, fundamental differences in patterns of environmental variability acting on different timescales in marine and terrestrial habitats are probably behind the differences in physiology,