Research Focus

Understanding ecosystem robustness

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Understanding the properties of ecosystems that make them either vulnerable or resistant to species extinctions is vital in the context of rapidly increasing habitat modification and climatic warming. New research by Sinha *et al*. incorporating 'small-world' topologies and population dynamics into ecosystem network models provides new explanations for species link distributions, extinction events and the maintenance of biodiversity. Their work reveals that previously unconnected ecosystems that come into contact with each other by anthropogenic or natural means are vulnerable to large losses in species.

The historical context of complexity–stability relationships

Robert May's 1972 seminal paper, showing that randomly constructed ecological communities decreased in stability as they increased in complexity [1], created controversy among ecologists because it went against the empirical wisdom that diversity begets stability. The paper led to a flurry of activity among empiricists and theoreticians to ascertain the exact nature of the relationship between diversity and stability. The general approach of both empirical and theoretical studies since May 1972 has been to construct communities of increasing diversity and to measure the correlation between increasing ecological complexity and various measures of stability [2]. New theoretical work by Sinha and coauthors provides a fresh look at this problem [3–5]. Rather than build networks of increasing complexity and exploring changes in their stability, they assume that ecological complexity is a given. They then ask, what are the properties of these complex networks and what makes them robust to changes?

May [1] constructed random networks of N nodes (species), with a density of links between nodes C (species interactions) and an average interaction strength of σ. He showed that as you increase any one of these parameters, the probability of the network remaining stable under small perturbations decreases [1,6]. In their new work, Sinha and co-authors resurrect the network approach of May, but apply a suite of new analytical tools derived from statistical mechanics and graph theory [7]. From their work, a surprising number of new insights emerge regarding the maintenance and disappearance of biodiversity.

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'Small-world' effects on stability

A common criticism of May's 1972 paper is that species in food webs do not interact with each other at random. May himself recognized this and showed that if communities were compartmentalized into small blocks within which species interacted with each other but not with those outside the block, stability of the community was enhanced [8]. Recently, it has been suggested that species form clusters of interaction, whereby species within a cluster are more likely to interact with each other than with species outside the cluster [9]. These clusters are like May's compartments except that species within a cluster interact occasionally with species outside the cluster. Such 'small-world' networks are common in biological, social and man-made systems, and have been shown to affect disease spread, synchronizability and computational power, among other things [10]. Although the actual topology of real food webs seems to be varied [11], Sinha [5] explores the role of such clustering in conferring stability to ecological networks. He finds that the transition point between stability and instability for a given set of parameters (N, C and σ) does not differ between random and clustered food webs. However, the transition between stability and instability is sharper in the random than in the clustered case. This implies that unstable clustered communities will deteriorate more gradually than will their randomly connected counterparts. From a biogeographical perspective, where community size is dynamically controlled by colonization and extinction, clustered communities might seem more diverse than do randomly connected communities because instabilities leading to extinction will take longer to manifest.

Dynamical effects on persistence

A second common criticism of May 1972 has been that it ignores the population dynamics of the species in the network. May [8] and other ecologists have sought to address this issue by incorporating Lotka–Volterra-type dynamics between species (e.g. Ref. [12]), but these studies have been limited to considering networks of only a few species. Sinha and Sinha [3,4] use coupled maps, such as the Ricker equation (which determines the effects of density dependence on the time evolution of species population size) with interaction terms (which determine competitive affects between species), to explore the effects of species population dynamics on network stability. This enables them to explore a variety of dynamics, including periodic and chaotic behavior, and networks comprising large numbers of species. However, rather than examine local stability, which looks at whether the network returns to equilibrium after a small perturbation, Sinha and Sinha use persistence (i.e. the
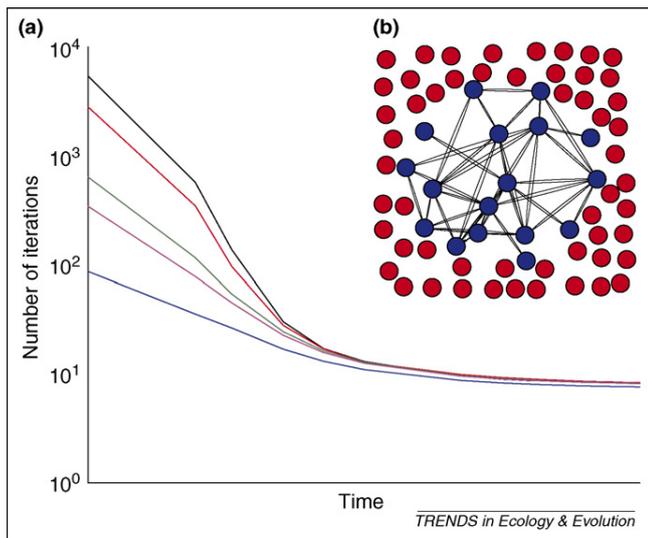
Figure 1. (a) The number of species (nodes) surviving to the asymptotic community size from an initial number of species (*N*). Convergence to similar community size results from the extinction of some species owing to intrinsic population dynamics and interactions with other species. The inset (b) shows a snapshot of the asymptotic interaction network. Each species is indicated by a node (o). The isolated nodes are the species that have gone extinct and therefore have dropped out of the network, whereas the connected nodes represent species with finite populations, which are still interacting with connected species. Although all nodes start out being connected to a few other nodes, a large number eventually drop out leaving the final network, which is qualitatively similar for different initial conditions and realizations. The number of species and mean number of links between them will be the same in each realization of the final network, although the actual nodes that survive will change from realization to realization. Figure reproduced from Ref. [3] with permission from S. Sinha.

probability that a species has non-zero abundance) as a measure of the stability of the system.

The authors begin with *N* species in their network with a density of links between species *C*, and average interaction strength σ. The community is then enabled to evolve over time. If the density of a species reaches zero, then that species is removed from the network. Over time, the number of species remaining in the network asymptotically approaches a final community size. The number of nodes remaining with persistent activity, N_{active}, is a measure of the global stability of the system. They find that their results quantitatively agree with May's, in that increasing either the size, connectivity and/or interaction strength of the network decreases stability, with a larger proportion of species liable to go extinct. What is notable about this result is the concordance with May given the different stability criteria used. Does this then imply, as May's original model did, that increased biodiversity is likely to lead to decreased stability? No, rather it strengthens previous results based on local stability analysis suggesting that nature builds robust networks slowly over time by eliminating species and links that are destabilizing [13].

Biodiversity implications

The ecosystem network model of Sinha and Sinha has some remarkable properties. For instance, the asymptotic size of the network, N_{active}, is independent of the initial size *N*. If two networks of size N_{active} are then joined together, the
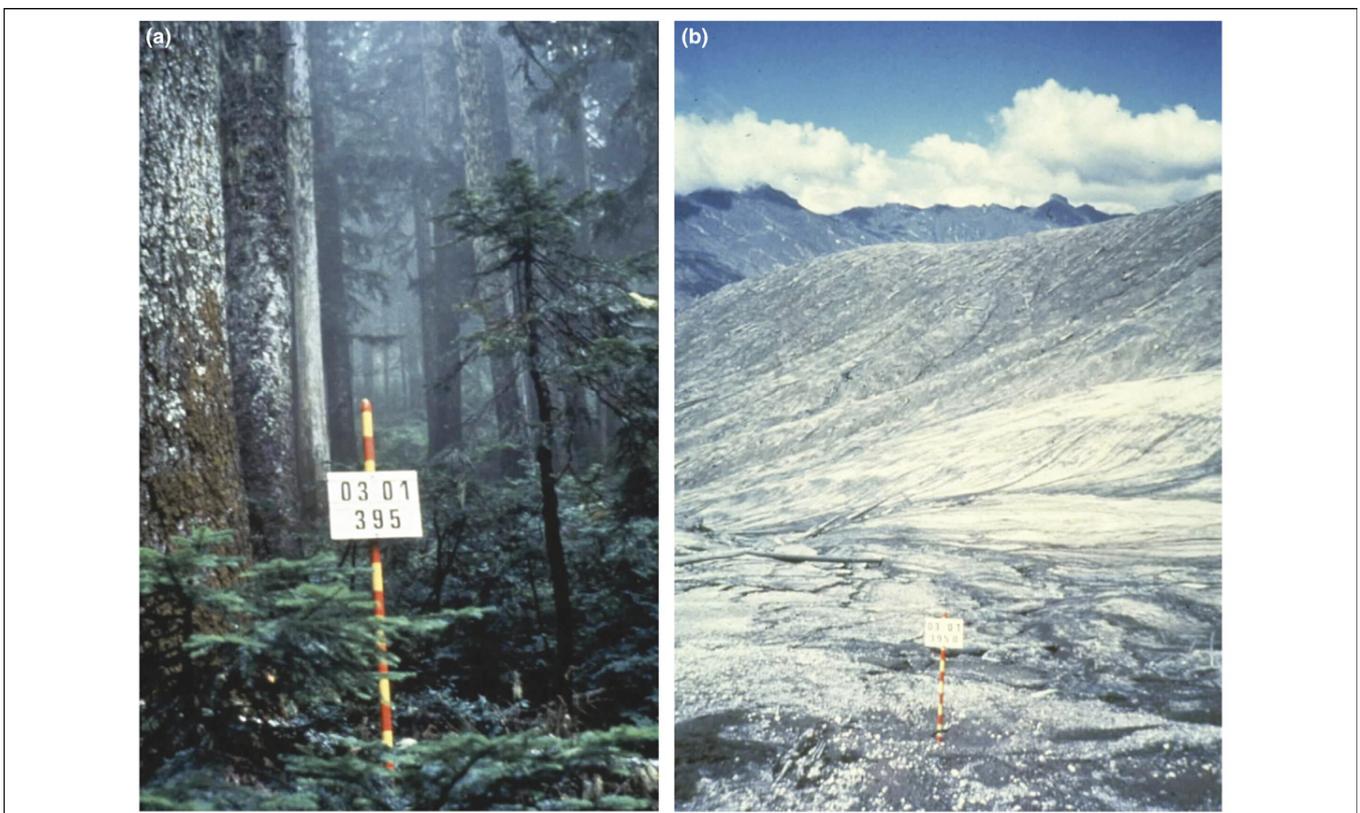
Figure 2. Old growth forest on Mount St. Helens (a) before and (b) after its eruption in 1980. The sign in each photo is in the exact same location. Each time the volcano has erupted over the millennia, the models of Sinha and co-authors predict that the ecological community rebounds to roughly the same network structure (i.e. number of species and distributions of links between species) even though the specific species might be somewhat different each time. Images courtesy of M. Hemstrom and the USDA Forest Service, Mount St. Helens national volcanic monument.

resulting network will undergo a series of extinctions until it too reaches a size of N_{active} (Figure 1). Species extinctions and declines in biodiversity are commonly observed in the joining of two previously unconnected ecosystems, such as occurred through the joining of land masses through tectonic drift (e.g. the joining of North and South America), climate change (e.g. the joining of Asia and North America during glacial periods) and human activity (e.g. the exchange of organisms through ballast water, farm animals, etc.). That such extinctions are predicted purely on the basis of a simple network model suggests that there are fundamental limits to biodiversity based on the strength of species interactions and niche breadth (i.e. how many species a typical species interacts with). Similarly, if a portion of an ecosystem loses its biodiversity as a result of some catastrophic event, such as a hurricane or a volcanic eruption, it will eventually regain N_{active} species through linkage with an adjacent ecosystem (Figure 2).

Sinha and Sinha also find that the asymptotic number of links between species is independent of both the initial size and connectivity of the network, and only weakly related to average interaction strength. In fact, the average number of links per species in the asymptotic community state (3–10 links) is equivalent to the characteristic range of links per species observed across different environments (3–5 links) [14]. This weak dependence of species link distributions on initial conditions and concordance with empirical data suggests that the number of species that interact with each other in real ecosystems is a fundamental property of network structure, and not of particular biotic or abiotic conditions. It also reveals that species that interact with too many other species are destabilizing to network persistence. This is perhaps not surprising given the current loss of biodiversity owing to one species that interacts so strongly with so many others, *Homo sapiens*.

The work of Sinha and collaborators is especially important because they explicitly incorporate dynamics into ecosystem network models. In doing so, they corroborate May's, and other's, previous work on static networks, and extend these results to gain new insights on the factors by which biodiversity is maintained and lost. Their results warn that as we modify the global environment, we should be particularly wary of joining previously unconnected ecosystems.

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The evolution of obligate mutualism: if you can't beat 'em, join 'em

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***Wolbachia* is best known as a facultative endosymbiotic parasite, manipulating host reproduction. However, it has also evolved as an obligate mutualist at least twice. In a recent paper, Pannebakker *et al.* identify a possible mechanism for such a transition from facultative parasitism to obligate mutualism in a parasitic wasp in which *Wolbachia* are required for producing eggs (oogenesis).**

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Their proposed mechanism suggests that compensatory evolution in the host to counter the harmful effects of *Wolbachia* is the basis of this evolutionary transition.

Mutualistic symbiosis
Symbiotic interactions range from reciprocally beneficial (mutualistic) to parasitic and are omnipresent in the living world at various levels of biological organization. The evolution of mutualistic interactions is difficult to explain: