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Using community viability analysis to identify fragile systems and keystone species

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Owing to interdependences among species in ecological communities, the loss of one species can trigger a cascade of secondary extinctions with potentially dramatic effects on the functioning and stability of the community. It is, therefore, important to assess the risk and likely extent of secondary extinctions. Community viability analysis is a new technique that can be used to accomplish this goal. The analysis can also be used to identify fragile community structures and keystone species and, hence, to provide guidelines for conservation priorities. Here, we describe the principles underlying community viability analysis and review its contributions to our understanding of the response of ecological communities to species loss.

Climate change, overexploitation of natural resources and the destruction and fragmentation of natural habitats are predicted to cause unprecedented rates of population and species extinction in terrestrial and aquatic environments in the near future [1,2]. To find out which species are most likely to face extinction and to put appropriate conservation measures in place to prevent these events are thus matters of great urgency. But of equal importance is to predict how ecological communities will respond to forecasted rates of species loss.

Mechanisms that enable the coexistence of interacting species can break down when a species is lost from a community, leading to a sequence of secondary extinctions (Figure 1). Such secondary extinctions have been observed in many natural communities [3–6] and, in the worst case, the loss of a single species can lead to a community collapse [3,4,6]. For example, the extinction of sea otters from the Pacific coasts of North America led to the collapse of kelp forest communities [3], and formerly specious communities were replaced by barren habitats. The numbers of the preferred prey of sea otters (sea urchins) increased dramatically in the absence of their predator and overgrazed their resource, the giant kelp. The local extinction of kelp led, in turn, to the loss of numerous species of fishes and invertebrates inhabiting the kelp forests. This collapse illustrates an extinction cascade resulting from the absence of top-down regulation

(i.e. predators limiting herbivores and thereby preventing them from overgrazing primary producers). Similar situations have also been documented in terrestrial ecosystems: the local extinction of wolves and grizzly bears has led to high population densities of moose that, in turn, have caused dramatic changes to the vegetation [7]. Experiments have also shown that the deletion of
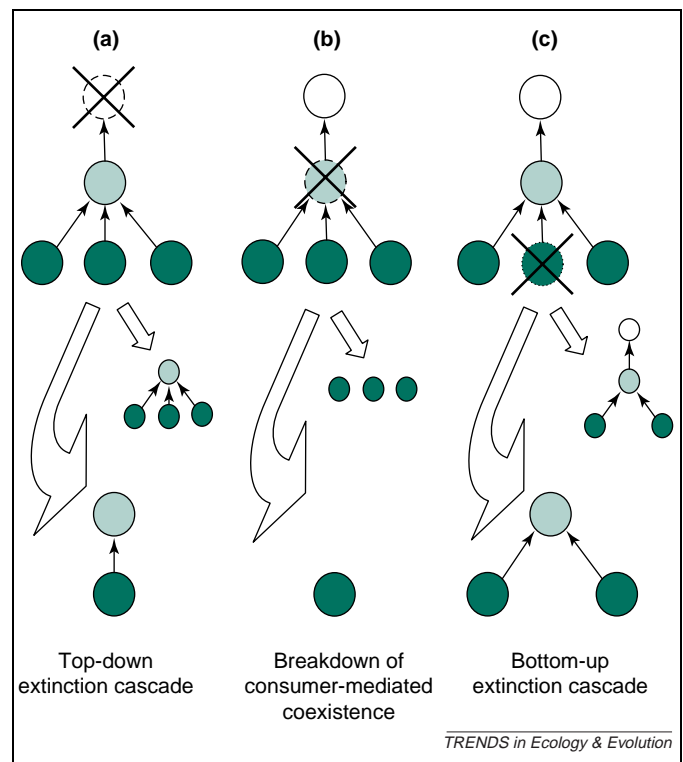
Figure 1. Mechanisms of secondary extinctions following the loss of a species (crossed out circles). The large arrow points at the actual post-extinction community that is predicted using a community viability analysis where changes in species densities are accounted for. The small arrow points at the post-extinction community that would have been predicted using a community viability analysis where the dynamics of species is not taken into account. Dark green, light green and white circles represent primary producers, primary consumers (i.e. herbivores) and top predators, respectively. **(a)** Loss of a top predator unleashing a top-down extinction cascade. This is the mechanism at play in the collapse of kelp forest communities following the loss of sea otters [3]. **(b)** Loss of a consumer (e.g. herbivore) leading to the breakdown of consumer-mediated coexistence among prey (e.g. plants). Dominating resource species out-compete subordinate ones in the absence of the consumer. An illustration of this mechanism is the secondary extinctions of algal species in marine intertidal communities following the loss of the herbivorous periwinkle snail [9]. **(c)** Loss of a primary producer triggering a bottom-up extinction cascade.

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Glossary

Compartmentalization: the degree to which a community is organized into subunits (modules) within which interactions are strong, but between which interactions are weak.

Connectance: the proportion of possible trophic links that are realized in a binary food web with L number of links and S species ($C = L/S^2$).

Internal stability: inverse of variability in population densities over time (variability can be internally or externally driven).

Local and global asymptotic stability: the ability of a system to recover from small and large temporary (pulse) perturbations, respectively; assumes that long-term persistence requires that the system is approaching an equilibrium point. Thus, complex dynamics that might be consistent with community persistence, such as periodic and chaotic attractors, are excluded.

Permanence: a global criterion of persistence (long-term coexistence of interacting species) that makes no assumptions about the dynamic behaviour of the system; equilibrium behaviour as well as more complex dynamic behaviour is allowed. Thus, persistence does not require the interior fixed point(s) to be locally or globally stable.

Post-extinction community: the species remaining in a community once secondary extinctions have occurred. Consider a community with S species initially that have lost one species (thus consisting of $S-1$ species). The criterion of permanence can be used to find the post-extinction community. First, the community with $S-1$ species is checked for permanence: it is the post-extinction community if it is permanent. If not, the post-extinction community is determined by examining all of the subsets of the $S-1$ species community for one that is permanent and uninvadable by species that are absent from the subset and present in the $S-1$ species community. The subset that fulfils these conditions is the post-extinction community.

Quasi-collapse risk: the probability that the number of species falls below some value following the loss of a species. For example, the probability that the number of species in a ten-species community falls below 9, 8, 7,..., 2 or 1 species following the loss of a given species. A complete collapse means that all species vanish. The graph of quasi-collapse risks constitutes the risk curve for the community.

Resistance: measures the degree of change in the structure of a community following a sustained (i.e. press) perturbation, the smaller the change the greater the resistance. For example, if the loss of a species does not result in secondary extinctions, the system is resistant with respect to species composition.

Secondary extinction: the extinction of a species caused by the loss (primary extinction) of another species.

consumers (herbivores or predators) can lead to large reductions in species diversity at the next trophic level below [6,8–10]. Here, the mechanism involves the breakdown of coexistence of species within a trophic level following the loss of consumers (consumers limit the growth of dominant resource species and thereby prevent them from excluding weaker competitors). Several theoretical studies also predict that the loss of a species (a primary extinction) can trigger a cascade of secondary extinctions [11–17].

Are the examples mentioned here typical of the response of ecological communities to species loss or will most communities be only marginally affected? Are some ecological communities, such as those with few species and/or few interaction links, more (or less) liable to be adversely affected by species loss? Are there particular kinds of species (keystone species) whose loss is likely to have serious effects on the continued existence of other species and, hence, on the long-term persistence of the ecosystem? Are some species, such as top predators, more vulnerable to going secondarily extinct than are others? To what extent is the keystone status and vulnerability of a species context dependent; that is, a function of the trophic structure of the community where it is embedded? Answers to these questions are crucial to predict the response (i.e. number of secondary extinctions) of ecological communities to species loss. The use of community

viability analysis [13] could provide answers to these questions and could help us to understand the response of communities to species loss. Here, we describe the principles underlying community viability analysis and review how it has affected our understanding of the response of ecological communities to species loss.

Principles and methods of community viability analysis

It has been argued that conservation biology could benefit significantly from adopting a more community-oriented research approach [18]. Community viability analysis is a step in that direction. The principle aim of such an analysis, in its present state, is to predict the response of ecological communities to species loss, more specifically to assess the risk and extent of secondary extinctions. The first step in the analysis is to construct a model of a community, a model that should reflect the trophic structure of real ecosystems. The response of the system to species loss is then investigated by performing numerical experiments using the model. As such, community viability analysis is the community analogue of population viability analysis [19]. Community viability analysis can be used in two ways, either to quantify the risk and extent of secondary extinctions in a particular real community exposed to an actual species loss, or to study the relationship between community resistance to species loss and food web structure, from a theoretical perspective, using simple generalized model communities (e.g. how does species richness affect the risk and extent of secondary extinctions in a community).

Two approaches to community viability analysis

There are two main ways to perform a community viability analysis (either by dynamic or static analysis), each of which has their own pros and cons and require different kinds of community data. A static (or topological) approach focuses only on the link structure of a community [12,17,20] and is not concerned with the dynamics of species (Box 1). In a dynamic analysis, changes in species densities through time, and the indirect effects that these changes have on the abundance of other species, are taken into account. Thus, growth rates of species and interaction strengths between species must be specified [11,13,15,16].

Secondary extinctions revealed by a static analysis are consumer species that become disconnected from all of their resource species following the initial loss of one species. Thus, the effects of the loss of top predators on other species cannot be investigated using this approach and potential secondary extinctions of primary producer species following the loss of any other species cannot be revealed (Figure 1). Therefore, the secondary extinction of kelp following the loss of sea otters, or secondary extinctions of plant species following the loss of herbivores, would not have been predicted using this static approach. Important mechanisms, such as the indirect effects of top predators on primary producers (e.g. sea otters on kelp) or indirect effects of herbivores on competing plant species (e.g. rabbits on plants) are not accounted for.

Secondary extinctions revealed by a dynamic analysis can be of any species and the result of direct as well as

indirect effects. A dynamic community viability analysis can be applied to natural communities if we can find ways to estimate intrinsic growth rates of species and the strength of interactions among species. A possible way to estimate these parameters is to infer them from the body sizes of species using allometric scaling relationships [21–24] or to estimate them using numerical abundance data and an equilibrium assumption [25].

The strength of the static approach is that it can be applied more easily to complex real food webs for which estimates of interaction strengths and growth rates of species are difficult to come by. Moreover, it makes no assumptions about the kind of dynamics involved. However, a community viability analysis based on food webs without dynamics can underestimate the risk and number of secondary extinctions (see also [26]). A dynamic community viability analysis is therefore to be preferred wherever possible.

Quantifying the response to species loss: quasi-collapse risk

A quantitative measure is needed to describe the extent of secondary extinctions in ecological communities following the loss of a species. One such measure is the so-called 'quasi-collapse risk' [13], which is defined as the probability that the number of species in a community falls below some value within a fixed period of time following the loss of a species. The quasi-collapse risk of a community is a counterpart to the so-called 'quasi-extinction risk' of single species in a population viability analysis (i.e. the risk that the number of individuals in a population falls below some level within a fixed period of time [27]). Using the quasi-collapse risk, risk curves for the community can be constructed (Box 2).

Applying community viability analysis to identify fragile community structures

Community viability analysis can be applied to identify fragile community structures. Here, a fragile community is one in which the loss of a species, on average, causes a large number of secondary extinctions or a high risk of quasi-collapse. Several structural properties of ecological communities can affect their fragility to species loss. Here, we focus on (i) species richness; (ii) the number of trophic links and their distribution among species (connectance and compartmentalization); and (iii) the distribution of interaction strengths. These are properties that have been found, by earlier work, to be important in the general relationship between the structure and stability of ecological communities (e.g. [28]).

Species richness

The question of the form of the relationship between species richness (diversity) and stability has a long history in ecology (reviewed in [29]). A recent study [30] shows that, in marine reefs, ecological stability is positively related to taxonomic diversity on million-year timescales, supporting the hypothesis that species richness promotes stability. However, there are few empirical studies that have formally analysed how species richness in a community affects its response to species loss in terms of secondary extinctions (but see [11–14,16,31] for theoretical studies).

Some theoretical studies [13–15] predict that resistance to species loss (i.e. the probability that there will be no secondary extinctions following a species loss) should decrease with increasing species richness. However, recent theoretical work [13] also predicts that species-poor communities run the risk of losing a greater proportion of species following a species deletion (Figure 2a). In this sense, species-poor communities are more vulnerable to species loss than are species-rich ones. In the work above, species richness was varied while connectance (the fraction of the possible number of links that are realized) was kept constant. This means that the number of links per species increased with increasing species richness. MacArthur [32] proposed that consumers feeding on many resource species should be less vulnerable to variations in resource abundance than should consumers feeding on fewer resource species. He based his conclusion on a

Box 2. Applying community viability analysis

Here, we give an example of how community viability analysis can be used to assess the risk and extent of secondary extinctions following the loss of a predator in a community. Consider a community with two plant species, two herbivores and two predators (s_o = six species in original community). Suppose that 1000 permanent replicates of this community have been generated by drawing parameters (i.e. intrinsic growth rates of species and interaction strengths) at random from appropriate distributions. The mean and range of these distributions can be estimated using body sizes of species [21,22,24]. Now suppose that, in each replicate community, one of the predators has been deleted and that the post-extinction community has been determined using one of the methods described in Box 1. To visualize the risk and extent of secondary extinctions following the loss of the predator, a risk curve for the community is generated. Generating a risk curve starts with calculating the frequency of community replicates with 0 to $s_o - 1$ number of species remaining (s_r). From this, the cumulative number of replicates with $< s_o - 1$, $s_o - 2$,..., 2 and 1 species remaining is obtained and rescaled (dividing by the total number of replicates), to get the probability that loss of the predator will result in a post-extinction community with less than s species. This is the quasi-collapse risk $P(s_r < s)$. The graph of quasi-collapse risks is the risk curve (Figure I).

This kind of analysis could have been applied to assess the risk and extent of secondary extinctions in kelp forest communities following the loss of sea otters, given that data on the body sizes of species and the link structure of the community were available.
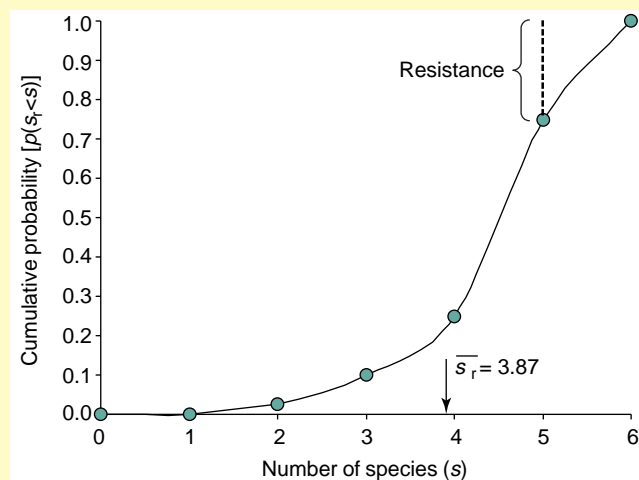
Figure I. Risk curve for a community of six species where one of the predators has been lost. The flip side of the quasi-collapse risk, $1 - P(s_r < s)$, is the probability that the community will have at least s species. For instance, if, $s = s_o - 1$, then $1 - P(s_r < s)$ is the probability that there will be no secondary extinctions following the loss of the predator, shown as the vertical dashed line in the figure (here equal to 0.26). In earlier work, this probability has been called species deletion stability [15], or resistance [11]. The mean number of species remaining in the post-extinction community is indicated by the arrow. Redrawn, with permission, from the Ecological Society of America [13].

verbal argument: if a consumer feeds on many resource species, it will be less affected if one of them declines markedly in numbers than if it feeds only on that single resource species. Extinction of consumers, following the loss of a resource, should therefore decrease as the number of resource species per consumer increases. Consistent with this is the fact that consumers feeding on many resource species show less temporal variation in their densities than do those feeding on few resource species (see [33] and references therein).

Furthermore, empirical observations indicate that trophic cascades are weaker in natural terrestrial communities with a high diversity of herbivore species [34] or predator species [35] and in complex aquatic communities than in simple ones [36]. It has also been suggested [4] that high diversity of consumers feeding on sea urchins delayed the collapse of kelp forest communities in southern California following the loss of sea otters compared with Alaska, where consumer diversity was relatively low. This is consistent with theoretical studies showing that top-down and bottom-up extinction cascades following the loss of top predators and basal species, respectively, are less common in species-rich theoretical model communities than in species-poor ones [13].

Community viability analysis based on deterministic models of ecological communities suggest that high species richness within trophic levels enables more species to persist following the loss of a species [13]. At the same time, high species richness has the effect that populations become smaller in size [13]. In other words, there could be an inverse relationship between population density and species diversity. Then, because smaller populations are more prone to stochastic extinction [37] one would expect a higher probability of stochastic extinction in species-rich communities than in species-poor ones. Hence, the property of species-rich communities to have proportionally less secondary extinctions owing to deterministic processes has to be weighted against the tendency for small populations to go to extinction owing to stochastic processes. In an individual-based stochastic model, the benefit of species richness *per se* was largely cancelled out by the effect of decreased population size [13]. An implication of this finding is that, in the construction of nature reserves, the 'deterministic advantages' of high species diversity could be lost if reserves are small in size.

Number of trophic links and their distribution

The relationship between connectance and stability is the subject of several theoretical studies [28,38–44], most of which are concerned with the internal stability of a community or its response to small temporary perturbations. Only a few studies [12,15] have formally explored how connectance of a community affects its response to species loss.

Using a dynamical approach to study the risk of secondary extinctions, Pimm concluded that, on average, highly connected model webs were less resistant to species loss than were webs with low connectance ([15] see also [14]). This was mainly due to a strong negative relationship between connectance and resistance when top predators were deleted. However, community viability analysis of static models of natural food webs suggest that webs with high connectance are more robust to species loss than are webs with low connectance (robustness is defined here as the proportion of species that initially has to be deleted to lead to a subsequent 50% reduction of species richness) [12]. The most probable explanation to the result of the second study [12] is that, in highly connected food webs, the average number of prey species of a consumer is high. This decreases the probability that a consumer will lose all of its resource species (which here is
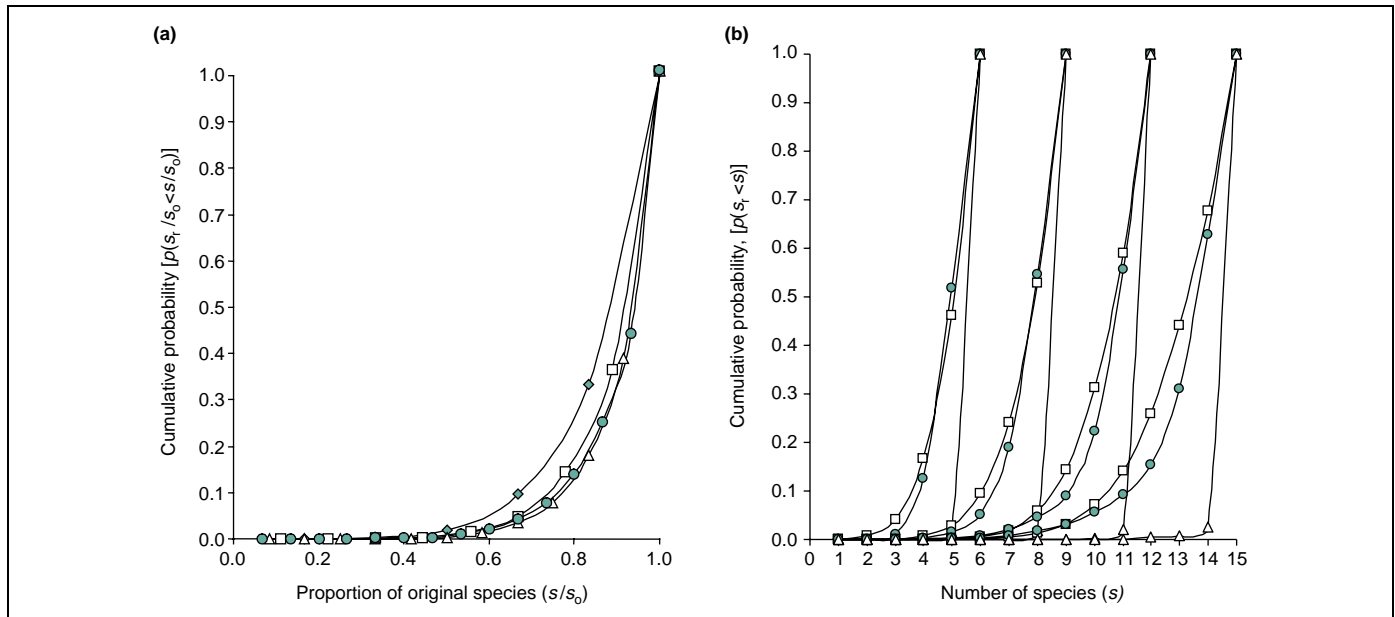
Figure 2. The effect of **(a)** species richness and **(b)** trophic level of deleted species on the extent of cascading extinctions in theoretical model communities. (a) Risk curves showing the cumulative probability that the fraction of species remaining in a community will fall below some level following the loss of one species for four different levels of initial species richness; six species (diamonds); nine species (squares); 12 species (triangles); and 15 species (circles). Each curve is computed from 1000 replicate model communities with a connectance of 0.22. Species-poor communities run the risk of losing a greater proportion of species following a species deletion than do species-rich communities. (b) Risk curves showing the cumulative probability that the number of species remaining in a community will fall below some level following the deletion of primary producer species (squares), herbivores (circles) and top predators (triangles). There is a lower probability of survival of the remaining species when primary producers or herbivores are deleted than when top predators are deleted. For details see [13]. Reprinted, with permission, from The Ecological Society of America [13].

the criterion of secondary extinction) following the loss of a species. However, because of the criterion of secondary extinction used, the loss of top predators in these natural communities is predicted to cause no secondary extinctions.

Distribution of interactions strengths

Not only the number of trophic links in a community, but also their strengths can affect the number of secondary extinctions following the loss of a species. Here, interaction strength means the direct effect of an individual of one species on the growth rate of another species. Theoretical work [21,22,25,28,29,40,41,45–49] suggests that the patterning of interaction strengths is crucial for the stability of ecological communities. For example, a recent study [47] of model communities with only one trophic level (primary producers) found that decreased mean and variance of interaction strengths increased local stability. The study detailed in [47] deals with the response of communities to small temporary perturbations. It is not clear whether the results also apply to large sustained perturbations such as species loss.

The distribution of interaction strengths in natural communities is highly skewed towards weak interactions [21,50]. McCann [29,48] pointed out that, if most species only interact weakly with other species, it follows that, on average, the loss of species will tend to increase the overall mean interaction strength in the community. McCann argues that this, in turn, could increase the risk of destabilization and subsequent collapses, because strong consumer–resource interactions tend to generate population fluctuations [48]. In other words, in a community with many strong interactions, the densities of species

vary more in time, making species more vulnerable to stochastic extinction, than in a community dominated by weak links between species.

The arrangement of weak and strong links can also affect the degree of compartmentalization (modularity) in food webs [51]. A highly compartmented web is organized into strongly integrated modules with weak links between modules. An increased degree of compartmentalization in simple model food webs decreases the variability in population densities over time and increases minimum densities of top predators [51]. Thus, a modular structure could enhance food-web persistence (see also [52]). It is not clear whether this internal stability (no perturbations are applied) ultimately translates into resistance to species loss.

Applying community viability analysis to identify keystone species

The term 'keystone predator' was introduced by Paine [6] to describe the controlling effect of a generalist predator on the structure of intertidal communities. Since then, a keystone species has come to mean any species whose removal has strong effects on community diversity and composition [53]. We chose here to define keystone species as a species whose loss is likely to trigger a significant number of secondary extinctions. Several characteristics of a species can affect its status as a keystone species: trophic position (e.g. top predator versus primary producer); connectivity (number of direct links to other species); and the strength of its interactions with other species. The keystone status of a species might also depend on the structure of the community where it is embedded, as well as on the physical environment [11,15,53–55].

Trophic position
Community viability analysis studies [11,13,15,54] adopting a dynamical approach to investigate the response of theoretical communities to species loss suggest that losses of primary producer species have, on average, more dramatic consequences than do losses of top predators (Figure 2b). These studies also show the context dependency of the keystone status of a species: the consequences of losing a basal species decreases with increasing species richness and connectance whereas the consequences of losing a top species increases with increasing connectance. This indicates the potential keystone role of top predators in complex ecological communities and suggests that

conservation of complex communities should focus on protecting top predators.

Importantly, these studies also indicate that top predators are the species most likely to go secondarily extinct following the loss of a species (a primary extinction). Thus, secondary extinctions, similar to primary extinctions (see [1,56]), are far from random as they primarily affect top predators. This can have important ramifications for the functioning and stability of the resulting post-extinction communities [57,58].

Number and strength of links to other species
Community viability analysis based on static models of communities [12,17,20,59,60] suggests that the sensitivity of communities to species loss is related to the frequency distribution of links among species. Removal of species with a large number of links to other species causes, on average the largest number of secondary extinctions [12,17]; a result indicating the potential keystone role of highly connected species. There are, however, important exceptions. The loss of a species supporting a specialized consumer that, in turn, supports several specialized predators can trigger a cascade of secondary extinctions [12]. It would be interesting to see whether these findings also hold when the dynamics of interacting species are taken into account. A community viability analysis based on dynamic models of communities would answer this question.

Not only the number of interaction links that a species has to other species in the community, but also the strength of these links is likely to affect the consequences of its loss. It has been suggested that there should be a strong positive correlation between the consequences of the loss of a species and the strength of its interactions with other species in the community [40,53]. However, a recent community viability analysis study based on dynamic models of theoretical communities [54] suggests that weakly interacting species can also be keystone species, in the sense that their loss can cause many secondary extinctions. Rare primary producer species and intermediate species that interacted strongly with many consumers, as well as abundant primary producer species and intermediate species that interacted weakly with their consumers, were found to function as keystone species [54]. Keystone species with low population densities might be particularly vulnerable to stochastic extinction. Thus, conservation efforts should be focused on rare keystone species without ignoring the possibility that intense exploitation of more abundant keystone species (see [1,3,4]) can lead to dramatic changes in ecological communities.

Conclusions and future directions
Community viability analysis is still in its infancy and there remain large gaps in our understanding of the response of communities to species loss (Box 3). Perhaps the most important ones are how environmental variation (stochasticity) and spatial heterogeneity affect the response of communities to species loss; both should be incorporated in future developments of community viability analysis. Community viability analysis can be used to

assess the risk and extent of secondary extinctions following the loss of a species and can be applied to identify fragile community structures, keystone species and species that are vulnerable to secondary extinction. Such information is crucial for future effective conservation and management of ecosystems and natural resources.

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