

machinery (proteins), $N_N = N_P = 0.17$, $P_N = P_P = 0$; light-harvesting machinery (chloroplasts), $N_I = 0.113$ and $P_I = 0.0032$ (ref. 6). As a neutral choice, we set the composition of the other biomass to the Redfield ratio, $N_o = 0.0631$, $P_o = 0.00873$; our results are relatively insensitive to these values. Assembly-machinery efficiency was set to $\mu' = 4.0 \text{ day}^{-1} (\text{g (g dry mass)}^{-1})^{-1}$ (ref. 13). Maximum carbon-uptake efficiency was set to $v'_c = w (16.8 \text{ g C day}^{-1} \text{ g}^{-1})$, using $P_{opt}^0 = 20 \text{ mg Chr}^{-1} (\text{mg chl } a)^{-1}$ (ref. 27), where superscript b indicates normalization to biomass, and the proportion of chlorophyll a in chloroplasts being 0.035 (ref. 28). Maximum N- and P-uptake efficiencies were set to $v'_N = w (3.0 \times 10^3 \text{ g N day}^{-1} (\text{g N-uptake protein})^{-1})$ and $v'_P = w (6.7 \times 10^3 \text{ g P day}^{-1} (\text{g P-uptake protein})^{-1})$, based on nutrient-transporter turnover times of 0.01 s (refs 29, 30). The minimum carbon quota was set to $Q_{min,C} = 0.24w$ (ref. 12). The results are independent of cell weight because w cancels from the expression for optimal R_a . The mortality rate was set to $m = 0.01 \text{ day}^{-1}$, chosen from the low end of the observed range to illustrate the lowest feasible value of allocation to assembly machinery. We fix the ratio of uptake machinery types to achieve colimitation during exponential growth, by equating the three terms in the minimum of equation (3). This results in $R_N = 0.00317 R_w$, $R_P = 0.000381 R_w$, and $R_I = 0.996 R_w$, which agrees with the observation that nutrient-uptake proteins are usually a much smaller component of biomass than chloroplasts.

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Food-web interactions govern the resistance of communities after non-random extinctions

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Growing concern about how loss of biodiversity will affect ecosystems has stimulated numerous studies^{1–5}. Although most studies have assumed that species go extinct randomly^{6–8}, species often go extinct in order of their sensitivity to a stress that intensifies through time (such as climate change)⁹. Here we show that the consequences of random and ordered extinctions differ. Both depend on food-web interactions that create compensation; that is, the increase of some species when their competitors and/or predators decrease in density due to environmental stress. Compensation makes communities as a whole more resistant to stress by reducing changes in combined species densities. As extinctions progress, the potential for compensation is depleted, and communities become progressively less resistant. For ordered extinctions, however, this depletion is offset and communities retain their resistance, because the surviving species have greater average resistance to the stress. Despite extinctions being ordered, changes in the food web with successive extinctions make it difficult to predict which species will show compensation in the future. This unpredictability argues for 'whole-ecosystem' approaches to biodiversity conservation, as seemingly insignificant species may become important after other species go extinct.

Interactions among species make it difficult to predict how ecological communities will respond to environmental degradation¹⁰, for two reasons. First, the sensitivity of an individual species to environmental degradation depends not only on the direct impact of degradation on that species, but also on the indirect effects on that species caused by changes in densities of other species^{11–13}. For example, environmental degradation may decrease the density of competitors and/or predators of a species, thereby causing a compensatory increase in the density of that species^{14–17}. Second, as species go extinct, links within the food web are severed, changing the pathways through which indirect effects operate. Changes in food-web structure depend on the order in which species go extinct, making it difficult to extrapolate from studies that assume extinctions are random to real communities facing progressively intensifying stress from environmental degradation¹⁸.

To disentangle the effects of species interactions on the ability of communities to tolerate environmental degradation, we used mathematical simulations to compare how communities resist changes in abundance as species go extinct randomly versus going extinct in order of their sensitivity to an environmental stress. We

considered communities with three trophic topologies that span a range of community types: tritrophic communities with plants, herbivores, and predators; monotrophic communities comprising just competitors; and communities with arbitrary topology containing prey and predators, competitors, and mutualists (Methods). For each topology, we constructed 1,000 communities in which interaction strengths were chosen from random distributions under the constraints of the specified topology. The direct effects of the stressor on each species were also selected at random, but constrained so that the stressor had a negative effect on all species by decreasing their population growth rates.

We defined the tolerance of a species i as the change in its equilibrium abundance, $x_i^*(s)$, relative to a small change in the magnitude of the stressor s :

$$\delta_i(N) = \frac{\Delta x_i^*(s)}{\Delta s} = \frac{x_i^*(s + \Delta s) - x_i^*(s)}{\Delta s} \quad (1)$$

Negative (positive) values of $\delta_i(N)$ indicate that species i decreases (increases) in abundance in response to intensification of the stressor. $\delta_i(N)$ incorporates both direct and indirect effects of the stressor, and N signifies the dependence of tolerance on the number of surviving species in a community. To measure the ability of the community as a whole to maintain abundance in the face of environmental degradation, we use the average tolerance $\bar{\delta}(N)$ of species in the community.

We subjected each simulated community to a 2×2 factorial numerical experiment (random versus ordered extinctions \times absence versus presence of species interactions). For ordered extinctions, we removed species in order of their tolerance $\delta_i(N)$ to the environmental stressor (Methods). We do not consider the effects of demographic stochasticity on extinction risk^{19–21}, because our focus here is on extinctions caused by environmental degradation. To remove species interactions, we set all interspecific interactions to zero, but retained the same intraspecific interactions and direct impacts of the stressor on species population growth rates.

To illustrate several basic results, we begin with the case of a single, tritrophic community experiencing ordered species extinctions (Fig. 1). In the absence of interspecific interactions, species tolerances $\delta_i(N)$ are independent of the number of species that go extinct. Consequently, the abundance of each species declines monotonically through time as the stressor intensifies (Fig. 1a), and the average tolerance of surviving species, $\bar{\delta}(N)$, increases as more species go extinct (Fig. 1c). Not surprisingly, the rank order of species extinction is readily predicted from the initial tolerance of each species in the community before any species has gone extinct (rank correlation, $r_a = 1$; Fig. 1e).

In contrast, when there are strong interactions among species, species in the food web exhibit density compensation, in which one or more species increase in density as other species decline (Fig. 1b). With each extinction, the pathways of indirect effects of the stressor acting through food-web interactions are rearranged. This rearrangement causes a ‘re-shuffling’ of species tolerances after an extinction, which can be seen by the fluctuations in the species-specific values of $\delta_i(N)$ as N decreases (Fig. 1d). Even though values of $\delta_i(N)$ are re-shuffled, indirect effects cause positive values of $\delta_i(N)$ to be as frequent as negative values, so the average tolerance $\bar{\delta}(N)$ of species in the community remains constant as species go extinct. Despite this constancy, the re-shuffling of species tolerances means that the rank order of species extinction is not as well predicted by the initial tolerances of the species ($r_a = 0.83$; Fig. 1f).

The 2×2 factorial experiment, applied to the 1,000 simulated communities of each topology, leads to two important points. First, ordered extinctions generally increase $\bar{\delta}(N)$ relative to the case of random extinctions, regardless of whether there are interspecific interactions (compare solid to dashed lines, Fig. 2). Thus, ordered

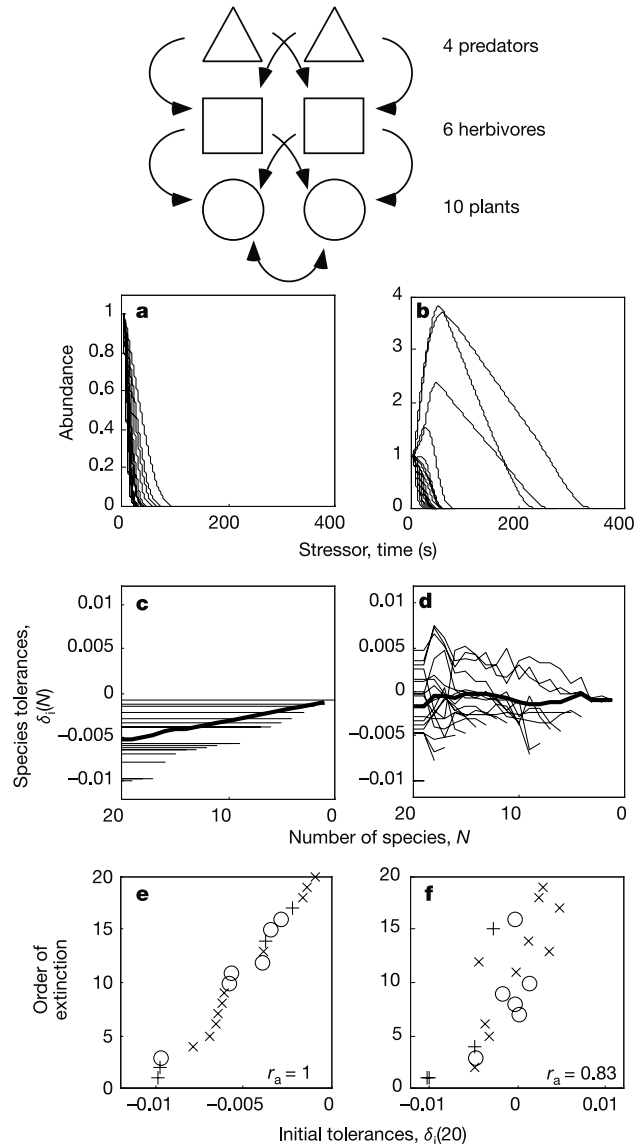


Figure 1 Example of the response of a tritrophic community to environmental stress. **a, b**, Simulations of the dynamics of 20-species communities through time (equation (2)) for food webs with interspecific interactions absent (**a**) or present (**b**). Initial population abundances were scaled to 1, and the stressor was assumed to intensify linearly through time ($s(t) = st$). **c, d**, Species tolerances to the stressor (equation (1)) as a function of the number of species in the communities with interspecific interactions absent (**c**) or present (**d**). Thin lines give $\delta_i(N)$ for individual species, with lines ending at the point of extinction. The heavy line gives the mean tolerance, $\bar{\delta}(N)$, of all surviving species. **e, f**, Rank order of species extinctions versus species tolerances $\delta_i(20)$ in the initial 20-species communities with interspecific interactions absent (**e**) or present (**f**). Plants, herbivores and predators are given by crosses, circles and plus symbols, respectively.

extinctions have a positive effect on the average tolerance of the surviving species. Second, when there are interspecific interactions, the resulting compensation increases $\bar{\delta}(N)$ in the initial 20-species communities (compared to no interactions); $\bar{\delta}(N)$ is zero when $N = 20$ (Fig. 2b–d). However, random extinctions deplete the potential for communities to show density compensation, so $\bar{\delta}(N)$ declines from zero as N decreases. In the presence of interspecific interactions and ordered extinctions (solid lines in Fig. 2b–d), the loss of compensation potential is balanced, almost exactly, by the increase in tolerance associated with the most sensitive species going extinct, leading to little change in $\bar{\delta}(N)$. Finally, food-web inter-

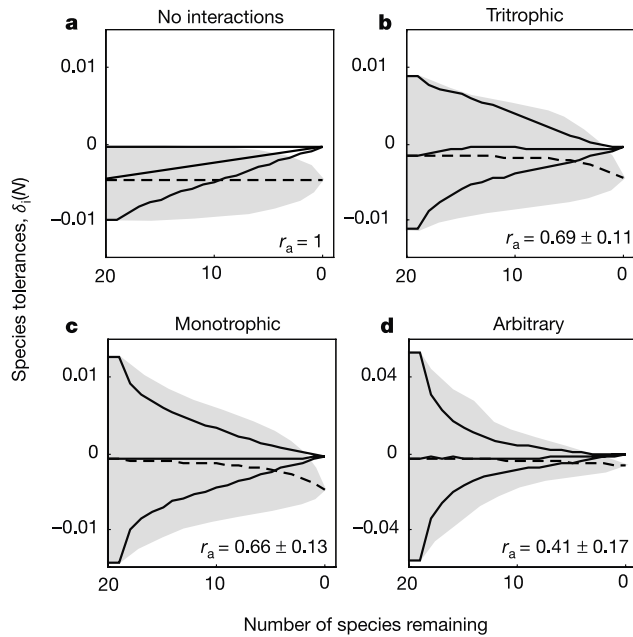


Figure 2 Responses of species tolerances to environmental degradation in various communities. **a**, Communities with interspecific interactions absent; **b**, tritrophic communities; **c**, monotrophic (competitive) communities; and **d**, arbitrarily structured communities. Each panel shows the medians of the minimum, maximum and mean values of $\delta_i(N)$ in each of 1,000 simulations as species went extinct in order of tolerances (solid lines). This procedure was modified by randomly removing species (independently of tolerances), and the resulting medians of minimums and maximums define the shaded region, with the median of the mean values given by the dashed lines. Values for the correlation r_a between the rank order of extinction and species tolerances $\delta_i(20)$ in the initial 20-species communities, for the case of ordered extinctions, are given with their standard deviations.

actions decrease the predictability of extinction, as seen from the reduced correlation between the rank order of initial species tolerances and the rank order of extinction (see r_a in Fig. 2).

To explore the role of interspecific interactions in more detail, we constructed random food webs^{22,23} with 20 species (Methods). We scaled the magnitude of interspecific interactions by p , with $p = 0$ corresponding to no interspecific interactions and $p = 1$ giving interspecific interactions that have on average the same magnitude as intraspecific interactions. Starting with the 20-species communities, we removed the species with the lowest tolerance to the environmental stressor and recomputed the values of $\delta_i(N - 1)$, repeating this procedure until there were only ten surviving species.

Consistent with our previous simulations (Fig. 2), the increase in $\bar{\delta}(N)$ as the most sensitive species go extinct diminishes as the strength of interspecific interactions increases (Fig. 3). This is clear from the change in average tolerance of species, $\Delta\bar{\delta} = \bar{\delta}(10) - \bar{\delta}(20)$, between reduced 10-species communities and the initial 20-species communities. To quantify the re-shuffling of species tolerances caused by extinctions, we computed the correlation r_e between the tolerances of species in the 11- and 10-species communities, $\delta_i(11)$ and $\delta_i(10)$; this correlation drops significantly as p approaches 1. Finally, the impact of interspecific interactions on species tolerances is seen in the correlation r_w between species tolerances in the 10-species community, $\delta_i(10)$, and the values that would have occurred in the absence of interspecific interactions. These results show that even moderately weak interspecific interactions ($p < 0.5$) are sufficient to generate the patterns we have described. The consequences of interspecific interactions can be verified and generalized analytically (Supplementary Information).

We have shown that the consequences of species extinctions for

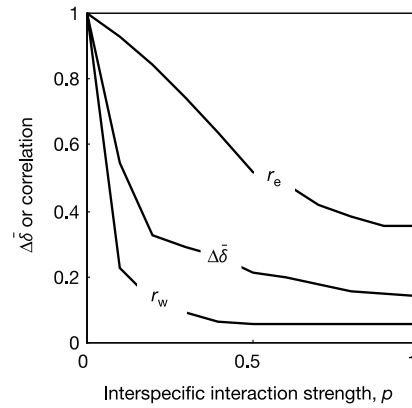


Figure 3 Effect of interspecific interaction strength on the change in mean tolerance of species, $\Delta\bar{\delta}$, when a 20-species community is reduced to a 10-species community through ordered extinction of the most sensitive species. r_w , The correlation between $\delta_i(10)$ for a species and the value of $\delta_i(10)$ that would occur without interspecific interactions. r_e , The correlation between $\delta_i(11)$ and $\delta_i(10)$. To generate estimates, p was increased from 0 to 1 in increments of 0.05, and at each increment 10,000 communities were simulated.

communities depend upon the balance of two opposing forces. First, loss of species from communities (either randomly or non-randomly) tends to decrease the potential for a community to exhibit density compensation that can buffer against future environmental degradation. Second, the ordered extinction of species most sensitive to environmental degradation acts to increase the community-wide average tolerance of the surviving species. When the second of these processes dominates the first, the initial flush of extinctions that often follows the onset of environmental degradation may temper the future impacts of degradation. In contrast, when the first process dominates the second, compensatory dynamics help to alleviate the initial flush of extinctions, thereby allowing the retention of species that may become highly sensitive to the stressor following the initial flush of extinctions. The short-term tolerance of the community to environmental degradation provided by compensation may, therefore, disguise the likelihood of future impacts of degradation. Because density compensation is apparently common and often strong in nature^{4,14,15,24–29}, many communities that have already experienced extinctions may remain unexpectedly sensitive to further environmental degradation.

Species interactions that lead to compensatory dynamics also make it difficult to predict the future sensitivity of a given species to further environmental degradation. This unpredictability argues for whole-ecosystem approaches to ecological conservation, because the future contribution of any particular species to compensation and community resistance is uncertain. Even species that are rare and apparently insignificant may play an important part in community resistance after other species go extinct. □

Methods

Simulations were performed using modified Lotka–Volterra equations:

$$x_i(t + 1) = x_i(t)F[(r_i + a_i s(t)) + b_{i,1}x_1(t) + b_{i,2}x_2(t) + \dots + b_{i,N}x_N(t)] \quad (2)$$

where $x_i(t)$ is the abundance of species i at time t , r_i is its intrinsic rate of increase, $b_{i,j}$ is the per capita interaction strength representing the effect of species j on species i (ref. 30), $s(t)$ is the magnitude of an environmental stressor, and a_i governs the direct effect of the stressor on the population growth rate of species i . We assumed that all values of a_i are < 0 , meaning that an increase in the environmental stressor, $s(t)$, leads to a decrease in the per capita population growth rate of every species i . For the discrete-time Lotka–Volterra equations, F is the exponential function, but the results are general for any form of F , provided that species interactions are additive. Although non-additive interactions (either positive or negative) may be common in natural communities, to assume additivity is a reasonable first approximation.

Species tolerances (equation (1)) depend only on values of a_i and $b_{i,j}$, which govern the direct and indirect effects of the stressor (equation (2)); these were selected from uniform random distributions with signs dictated by food-web topology. For tritrophic

communities, values of b_{ij} were selected from uniform distributions between 0 and -0.1 (plant–plant competition), -0.3 (herbivores \rightarrow plants; that is, the effect of herbivores on plants), 0.1 (plants \rightarrow herbivores), -0.1 (predators \rightarrow herbivores), and 0.05 (herbivores \rightarrow predators). Intraspecific interactions were selected at random between -0.1 and -0.2 for plants, and set to -0.2 for herbivores and predators. For competitive communities, interspecific values of b_{ij} were selected uniformly between 0 and -0.1 , and intraspecific values between -0.06 and -0.16 . For the arbitrary topology, the probability of any pair of species interacting was 0.5, and of the interacting pairs of species 45% were competitors, 45% were prey and predators, and 10% were mutualists. The magnitudes of interspecific values of b_{ij} were selected uniformly between 0 and 0.1, with sign dictated by type of interaction, and intraspecific values were selected between -0.06 and -0.16 .

For the random food webs (Fig. 3), we selected intra- and interspecific values of b_{ij} from uniform $(-0.1, 0)$ and $(-0.1, 0.1)$ distributions, respectively. The interaction coefficients b_{ij} were then modified by multiplying interspecific coefficients by p . The vast majority of resulting food webs when $p > 0.5$ were unstable, but comparable analyses constrained to stable food webs gave similar results.

In selecting coefficients, we constrained values for intraspecific interactions b_{ii} to negative numbers. Otherwise, for the case of no interactions (or when communities are reduced to one species) intensifying the stressor increases species abundances. This is because in the absence of species interactions, $\delta_i(N) = -a_i/b_{ii}$, which is positive when $b_{ii} > 0$.

Values of $\delta_i(N)$ were calculated by solving the set of equations satisfied by equation (1) at equilibrium:

$$r_i + a_i s + \sum_j b_{ij} x_j^* (s) = 0 \quad (i = 1, \dots, N) \quad (3)$$

and new values of $\delta_i(N)$ were calculated sequentially as the community size was reduced. Our assumption that the species with the lowest tolerance $\delta_i(N)$ goes extinct first was supported by simulating the full model given by equation (2) (for example, Fig. 1a, b) and categorizing species as extinct once they were reduced in abundance by a factor of 10^{-3} .

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Resonance effects indicate a radical-pair mechanism for avian magnetic compass

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Migratory birds are known to use the geomagnetic field as a source of compass information^{1,2}. There are two competing hypotheses for the primary process underlying the avian magnetic compass, one involving magnetite^{3–5}, the other a magnetically sensitive chemical reaction^{6–8}. Here we show that oscillating magnetic fields disrupt the magnetic orientation behaviour of migratory birds. Robins were disoriented when exposed to a vertically aligned broadband (0.1–10 MHz) or a single-frequency (7-MHz) field in addition to the geomagnetic field. Moreover, in the 7-MHz oscillating field, this effect depended on the angle between the oscillating and the geomagnetic fields. The birds exhibited seasonally appropriate migratory orientation when the oscillating field was parallel to the geomagnetic field, but were disoriented when it was presented at a 24° or 48° angle. These results are consistent with a resonance effect on singlet–triplet transitions and suggest a magnetic compass based on a radical-pair mechanism^{7,8}.

The magnetic compass of birds is light-dependent^{9,10}, and exhibits strong lateralization with input coming primarily from the right eye¹¹. However, the primary biophysical process underlying this compass remains unexplained. Magnetite^{3–5,12} as well as biochemical radical-pair reactions^{7,8} have been hypothesized to mediate sensitivity to Earth-strength magnetic fields through fundamentally different physical mechanisms. In the magnetite-based mechanism, magnetic fields exert mechanical forces³. In the radical-pair mechanism, the magnetic field alters the dynamics of transitions between spin states, after the creation of a radical pair through a light-induced electron transfer. These transitions in turn affect reaction rates and products^{7,8}. Although in most radical-pair reactions the effects of Earth-strength magnetic fields are masked by stochastic fluctuations, model calculations¹³ show that such effects can be amplified beyond the level of stochastic fluctuations in specialized radical-pair receptor systems.

Exploiting the principles of magnetic resonance, we developed a diagnostic tool to identify a radical-pair process as the primary process for a physiological magnetic compass. No change in magnetic alignment of magnetite receptors is expected for weak oscillating fields with frequencies larger than 100 kHz (ref. 14).