Food web structure and interaction strength pave the way for vulnerability to extinction

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Abstract

This paper focuses on how food web structure and interactions among species affects the vulnerability, due to environmental variability, to extinction of species at different positions in model food webs. Vulnerability is here not measured by a traditional extinction threshold but is instead inspired by the IUCN criteria for endangered species: an observed rapid decline in population abundance. Using model webs influenced by stochasticity with zero autocorrelation, we investigate the ecological determinants of species vulnerability, i.e. the trophic interactions between species and food web structure and how these interact with the risk of sudden drops in abundance of species. We find that (i) producers fulfil the criterion of vulnerable species more frequently than other species, (ii) food web structure is related to vulnerability, and (iii) the vulnerability of species is greater when involved in a strong trophic interaction than when not. We note that our result on the relationship between extinction risk and trophic position of species contradict previous suggestions and argue that the main reason for the discrepancy probably is due to the fact that we study the vulnerability to environmental stochasticity and not extinction risk due to overexploitation, habitat destruction or interactions with introduced species. Thus, we suggest that the vulnerability of species to environmental stochasticity may be differently related to trophic position than the vulnerability of species to other factors.

Earlier research on species extinctions has looked for intrinsic traits of species that correlate with increased vulnerability to extinction. However, to fully understand the extinction process we must also consider that species interactions may affect vulnerability and that not all extinctions are the result of long, gradual reductions in species abundances. Under environmental stochasticity (which importance frequently is assumed to increase as a result of climate change) and direct and indirect interactions with other species some extinctions may occur rapidly and apparently unexpectedly. To identify the first declines of population abundances that may escalate and lead to extinctions as early as possible, we need to recognize which species are at greatest risk of entering such dangerous routes and under what circumstances. This new perspective may contribute to our understanding of the processes leading to extinction of populations and eventually species. This is especially urgent in the light of the current biodiversity crisis where a large fraction of the world’s biodiversity is threatened.

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1. Introduction

Many factors may lead to a reduction in abundance of a species, including demographic variability, genetic, ecological, and anthropogenic factors and environmental stochasticity (Shaffer, 1981). Of these, the first two factors operate predominantly in small populations, characteristically with one factor reinforcing the effect of the other in a positive feedback-process commonly labelled as the “extinction vortex” (Gilpin and Soulé, 1986), with the potential of driving a species to extinction. Fagan and Holmes (2006) analyzed the decline to extinction using data from natural populations and found that initial population decline to quasi-extinction levels and final decline to actual extinction are different (with the latter being characterized by increasing population variability caused...
by the processes representative of the extinction vortex). This implies that it is important to stop species from reaching “extinction vortex levels” where population dynamics become very unpredictable but further declines are difficult to prevent (Pimm et al., 1993) because the driving forces are no longer the same as the ones that initiated the decline. Consequently, we need to prevent populations from entering the first road of decline that could lead to the extinction vortex and eventually result in extinction.

If the cause for the initial decline of a population is known, then the actions needed to prevent further decline should, in theory at least, be easy to recognize. Diamond (1989) introduced the “evil quartet” (habitat loss, over-exploitation, introduced species, and chains of extinctions) as the main causes for modern extinctions. However, not all extinctions are the result of long and gradual declines in abundance before entering the extinction vortex phase. Under the influence of environmental stochasticity and direct and indirect interactions with other species, many extinctions could potentially occur rapidly and apparently unexpectedly. In a sense, the IUCN has integrated this kind of scenario into the A.1 criterion of endangered species (EN) (IUCN, 2001), and we use a comparable set of conditions (observed rapid decline in abundance) to investigate which species, in model food webs, are most at risk of becoming endangered. That observed decline in abundance is correlated to extinction risk is supported by O’Grady et al. (2004) who, in a modelling study on 43 vertebrate taxa, found that trend in population size was an important predictor of vulnerability for large, not already threatened populations. Here, the objective is to identify characteristics that increases population vulnerability to environmental stochasticity (which importance frequently is assumed to increase as a result of climate change, Karl and Trenberth, 2003) in a food web setting and thus shed new light on the extinction process. Although climate change is one of the most important global threatening processes, to our knowledge no study has analyzed and tried to predict which species, in a multispecies setting, will respond most strongly to increased environmental variability.

It has been hypothesized that various intrinsic traits of species may lead to increased vulnerability of a population (Cardillo, 2003; Jennings et al., 1998; Johnson, 2002; Luckinbill and Fenton, 1978; Purvis et al., 2000). For example, species with slow life histories (long generation time, gestation length, etc.) should be less able to compensate for increased mortality with increased fecundity and thus, ought to be more vulnerable to extinction due to anthropogenic factors. Fisher and Owens (2004) however, in a thorough review of studies looking at the effect of various factors on the extinction risk of species, noted that fewer than half of all studies (that have taken a phylogenetic comparative approach) found a positive correlation between slow life history and extinction risk. Theoretical studies (Borrall et al., 2000) as well as field records (Cardillo et al., 2004, 2005) have indicated that species at higher trophic levels more frequently go extinct than species at the basal level. Furthermore, the spatial dimension of habitats, e.g. fragmentation (Bascompte and Solé, 1996; Davies et al., 2000; Tilman et al., 1994), and regimes of stochasticity (Halley, 1996) have been suggested to affect species vulnerability. Brook et al. (2006) found that commonly used predictors of population vulnerability (such as body size, geographical range, human impact, etc.) correlated with the recorded IUCN threatened status of a large set of species analyzed but not with estimated minimum viable population sizes (i.e. MVPs). Under the assumption that an estimated MVP is an indication of the vulnerability of a species, this means that traditionally used predictors of population vulnerability at least are not telling the whole story. Put another way, there seem to be more factors affecting the vulnerability of species than simple species characteristics. At the same time, new threats to population persistence, caused by increased environmental variability, is rising and challenging old wisdom on what factors correlate with increased extinction risk of species. Jonsson et al. (2006) studied multi-species food web models subjected to uncorrelated degrading stochasticity and found that various metrics of food web structure and the location of a strong interaction in a web were tightly linked to species extinctions. Furthermore, Karlsson et al. (unpublished) have shown that the spectral colour of the time series of species in food web models subjected to environmental stochasticity is correlated to extinction risk.

Interactions between species are known to modify population dynamics and abundances. For example, McCann et al. (1998) showed that strong direct effects of consumers on their resources increase the variability in population abundance, which could imply increased risk of reaching endangered levels of a species. The effect of indirect interactions is less well understood. It has been argued that direct interactions should be stronger than indirect interactions, and that strong direct effects are a prerequisite of indirect interactions, since many indirect interactions appear only as a result of strong direct interactions (Schoener, 1993). From this argument follows that the strength of indirect interactions should diminish with distance from the strong direct effect (but see Brown et al., 2001; Paine, 1966). Based on this, it could be hypothesized that population vulnerability should be higher for species directly involved in strong trophic interactions than for species affected only indirectly by strong interactions.

Here, the objective is to study the vulnerability to environmental stochasticity of trophically interacting populations. We analyze the extent to which sudden large drops in abundance of species (in line with the IUCN criterion of EN) is affected by characteristics of food web structure and strong trophic interactions. More specifically, we investigate

(a) the type of species that experiences rapid declines in abundance when exposed to environmental stochasticity
and thus could be likely to reach endangered population levels first,
(b) if some metrics of food web structure and the position and direction of strong interactions are related to high probabilities of rapid decline in abundance, and
(c) if species reaching endangered population levels do so predominantly as a result of strong direct or indirect effects.

In accordance with previous studies, we predict that population vulnerability will increase with trophic level and we hypothesize that population vulnerability to environmental stochasticity is higher for species directly involved in strong trophic interactions than for species affected only indirectly by strong interactions.

2. Methods

2.1. Construction of model communities and food web metrics

Seven network types were constructed from a basic triangular-shaped community module with six species at three trophic levels (three basal species, two intermediate species and one top species) by varying the number of trophic links from 5 to 11. By varying the position of the trophic links in each network type, in total 68 different food webs were produced. The number of species and number of trophic links were constant among the food webs in each network type. Within each food web one strong interaction between two species, ten times greater in magnitude than the basic parameter setting (see below and Table 1), was added and its position was varied to produce different subwebs. In total this procedure generated 757 different subwebs, which all had the same number of species but varied in the number of trophic links and position of one strong interaction. Thus, network types differ in the number of trophic links, food webs within a particular network type differ in the position of the trophic links, and subwebs within a food web differ in the position of one strong interaction. As a reference to study the effect of having one strong interaction, for each food web we also created one subweb without any strong interaction. Altogether this resulted in a total of 825 different subwebs.

Species vulnerability is here defined as the risk (probability) of experiencing a rapid decline in abundance (see below). In order to characterize the structure of a food web and enable an analysis of the relationship between vulnerability of species and food web structure a number of food web metrics were calculated for every model web (Table 2). Here, connectance, proportion of weak interactions and average generality of consumer species (average number of resource species per consumer) were perfectly positively correlated to the number of trophic links (this is due to the method used here to construct model communities, i.e. varying the number of links and not the number of species). Thus, the effect of these web metrics on vulnerability of a species cannot be separated here and we use number of links in the analyses of our results.

2.2. The model

The dynamics of the species were modelled by coupled differential equations of Lotka–Volterra type with stochasticity:

$$\frac{dN_i}{dt} = N_i \left( b_i + \sum_{j=1}^{n} a_{ij} N_j \right) - \beta_i(t).$$ (1)

Here, $N_i$ is the abundance of species $i$, $b_i$ is the density independent per capita growth or mortality rate of species $i$, $a_{ij}$ is the per capita effect of species $j$ on the per capita growth rate of species $i$ (being negative if $j$ is a predator on $i$, positive if $j$ is a prey to $i$) and strictly negative if $j = i$. Direct (interference) competition, mutualism or migration was not included in the model. Environmental stochasticity was included as an additive term in the deterministic model, describing the growth rate of species. That is,

$$\beta_i(t) = \delta(t) \sum_i \prod_j$$ (2)

Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Trophic level involved and type of parameter</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_i$</td>
<td>$i = 1, 2, 3$</td>
<td>Producer growth rate $+200$</td>
</tr>
<tr>
<td></td>
<td>$i = 4, 5$</td>
<td>Primary consumer mortality rate $-0.01$</td>
</tr>
<tr>
<td></td>
<td>$i = 6$</td>
<td>Secondary consumer mortality rate $-0.0035$</td>
</tr>
<tr>
<td>$a_{ii}$</td>
<td>$i = 1:6$</td>
<td>Intraspecific effects of all species $-0.025$</td>
</tr>
<tr>
<td>$a_{ij}$</td>
<td>$i = 1, 2, 3, j = 4, 5$</td>
<td>Effect of primary consumers on producers $-0.08$</td>
</tr>
<tr>
<td></td>
<td>$i = 1, 2, 3, j = 6$</td>
<td>Effect of secondary consumer on producers $-0.07$</td>
</tr>
<tr>
<td></td>
<td>$i = 4, 5, j = 6$</td>
<td>Effect of secondary consumers on primary consumers $-0.016$</td>
</tr>
<tr>
<td>$a_{ji}$</td>
<td>$j = 4, 5, i = 1, 2, 3$</td>
<td>Effect of producers on primary consumers $+0.00003$</td>
</tr>
<tr>
<td></td>
<td>$j = 6, i = 4, 5$</td>
<td>Effect of primary consumers on secondary consumer $+0.00002$</td>
</tr>
<tr>
<td></td>
<td>$j = 6, i = 1, 2, 3$</td>
<td>Effect of producers on secondary consumer $+0.00003$</td>
</tr>
</tbody>
</table>

Parameters that represent interactions that were not present in a particular model community configuration were set to zero.
Table 2

Food web metrics ($X_1$–$X_{33}$) and presence or absence of particular strong trophic interactions ($X_{12}$–$X_{33}$) used to characterize the structure of 726 model webs

<table>
<thead>
<tr>
<th>Definition</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food web metrics</td>
<td></td>
</tr>
<tr>
<td>$X_1$: Irregularity$^a$</td>
<td>$0$–$0.50$</td>
</tr>
<tr>
<td>$X_2$: Kurtosis$^b$</td>
<td>$-1.90$–$6.00$</td>
</tr>
<tr>
<td>$X_3$: Skewness$^c$</td>
<td>$-2.40$–$2.40$</td>
</tr>
<tr>
<td>$X_4$: Trophic height$^d$ of secondary consumer in a food web.</td>
<td>$2.25$–$3$</td>
</tr>
<tr>
<td>$X_5$: No. of trophic links</td>
<td>$5$–$11$</td>
</tr>
<tr>
<td>$X_6$: Average number of consumers$^e$</td>
<td>$1.0$–$2.5$</td>
</tr>
<tr>
<td>$X_7$: No. of trophic links$^f$</td>
<td>$1$–$5$</td>
</tr>
<tr>
<td>$X_8$: No. of omnivorous links$^g$</td>
<td>$0$–$3$</td>
</tr>
<tr>
<td>$X_9$: No. of specialist consumers$^h$</td>
<td>$0$–$2$</td>
</tr>
<tr>
<td>Presence of strong trophic interactions</td>
<td></td>
</tr>
<tr>
<td>$X_{12}$: $a_{41}$</td>
<td>Absence or presence of $a_{41}$</td>
</tr>
<tr>
<td>$X_{13}$: $a_{51}$</td>
<td>Absence or presence of $a_{51}$</td>
</tr>
<tr>
<td>$X_{14}$: $a_{61}$</td>
<td>Absence or presence of $a_{61}$</td>
</tr>
<tr>
<td>$X_{15}$: $a_{42}$</td>
<td>Absence or presence of $a_{42}$</td>
</tr>
<tr>
<td>$X_{16}$: $a_{62}$</td>
<td>Absence or presence of $a_{62}$</td>
</tr>
<tr>
<td>$X_{17}$: $a_{43}$</td>
<td>Absence or presence of $a_{43}$</td>
</tr>
<tr>
<td>$X_{18}$: $a_{53}$</td>
<td>Absence or presence of $a_{53}$</td>
</tr>
<tr>
<td>$X_{19}$: $a_{63}$</td>
<td>Absence or presence of $a_{63}$</td>
</tr>
<tr>
<td>$X_{20}$: $a_{44}$</td>
<td>Absence or presence of $a_{44}$</td>
</tr>
<tr>
<td>$X_{21}$: $a_{54}$</td>
<td>Absence or presence of $a_{54}$</td>
</tr>
<tr>
<td>$X_{22}$: $a_{64}$</td>
<td>Absence or presence of $a_{64}$</td>
</tr>
<tr>
<td>$X_{23}$: $a_{45}$</td>
<td>Absence or presence of $a_{45}$</td>
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<tr>
<td>$X_{24}$: $a_{55}$</td>
<td>Absence or presence of $a_{55}$</td>
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<tr>
<td>$X_{25}$: $a_{65}$</td>
<td>Absence or presence of $a_{65}$</td>
</tr>
<tr>
<td>$X_{26}$: $a_{46}$</td>
<td>Absence or presence of $a_{46}$</td>
</tr>
<tr>
<td>$X_{27}$: $a_{56}$</td>
<td>Absence or presence of $a_{56}$</td>
</tr>
<tr>
<td>$X_{28}$: $a_{66}$</td>
<td>Absence or presence of $a_{66}$</td>
</tr>
<tr>
<td>All variables ($X_1$–$X_{33}$) were used in a regression tree analysis of the effect of food web structure on the risk of a species to experience a rapid decline in abundance (see methods). Range indicates the minimum and maximum values of food web metrics for the set of model food webs used in this study (or presence/absence of strong trophic interactions). The variables have the following meaning: $L_1$: number of links connected to species $i$; $L$: mean number of links connected to species in a web; $s$: number of species in a web; $\sigma$: standard deviation in number of links per species; $T_w$: trophic level of secondary consumer in food chain $w$; $N$: number of food chains from any producer species to the secondary consumer in a web; $L$: number of trophic links in a web; $S_{prey}$: number of prey species in a web; $L_{prey}$: number of prey links of a particular predator species $i$. $X_7$, $X_8$, and $X_9$ indicate generality of species 4, 5, and 6, respectively. Variables $X_{12}$–$X_{33}$, indicate the absence or presence (0 or 1, respectively) of a strong interaction at the specified location with $a_{ij}$ describing a strong impact of species $j$ on species $i$.</td>
<td></td>
</tr>
</tbody>
</table>

$^a$Irregularity (Sokal and Rohlf, 1995) describes the coefficient of variance in the number of links per species.

$^b$Kurtosis (Sokal and Rohlf, 1995) is here used to describe the peakedness in the distribution of number of links per species (relative to a normal distribution).

$^c$Skewness (Sokal and Rohlf, 1995) is here used to describe the asymmetry in the distribution of number of links per species (relative to a normal distribution).

$^d$Trophic height is here used to describe the degree of omnivory of the secondary consumer (or the average number of links from the secondary consumer to a producer).

$^e$Average number of consumers describes the average number of predators per prey species (Schoener, 1989).

$^f$Species-specific generality describes the number of prey of a particular predator species $i$.

$^g$No. of omnivorous links describe the number of predatory links from the secondary consumer to producer species.

$^h$No. of specialist consumers describe the number of consumer species with only one predatory link.
is the stochastic mortality of species \(i\) (with \(\tau\) being the integer value of \(t\)). \(\delta(t)\) is a time-specific number drawn at random (each integer time step) from a symmetric beta probability distribution (mean zero and variance 0.111), which was not significantly different from a normal distribution (Lilliefors and Jarque-Bera tests of normality, \(p < 0.05\)), but restricted random values to the interval \([-1, 1]\). \(z\) is a constant (here set to the value 0.28) and \(\Pi_i\) is the “equilibrium gross production of species \(i\)”, representing the biomass inflow to a species at equilibrium (i.e. the gross production rate at equilibrium). In effect, this procedure scales the effect of environmental stochasticity relative to the potential growth rate of a species. For producers the equilibrium gross production of a species is

\[
\Pi_i = b_i \times N_i^* \tag{3}
\]

(where \(N_i^*\) is the abundance of species \(i\) at equilibrium). For consumers, equilibrium gross production is

\[
\Pi_i = N_i^* \left( \sum_{j=1}^{i-1} a_{ij} N_j^* \right), \tag{4}
\]

where the summation is across all prey species of consumer species \(i\). Without stochastic mortality the biomass inflow to a species is, at equilibrium, exactly matched by an outflow of biomass due to mortality (predation, density-dependent and density-independent intraspecific mortality). Here, \(z\) was set to 0.28, which resulted in either an enhancement or depression of the growth rate of each species by at most 28% of the gross production at equilibrium at a single time step.

**2.3. Parameter values and simulations**

Table 1 shows the basic parameter setting used to simulate Eq. (1). All producer species have the same growth rate \(b_i\) and in absence of interspecific competition they only differ in which predator species they are consumed by. To reflect the longer generation times often served, estimated, inferred or suspected’’ to have experienced “a reduction of \(\geq 70\%\) over the last 10 years or three generations, whichever is the longer...”).

Results did not differ qualitatively for other values of \(\gamma\), i.e. for the range of values of \(\gamma\) where \(\gamma\) was large enough to label at least some species as vulnerable but low enough to not label any variability in abundance as vulnerability to extinction. Only the first drop in abundance to endangered levels was recorded, i.e. no more than one species was considered vulnerable in a single simulation replicate. Thus, for each species, vulnerability in a particular subweb was calculated as the fraction out of 100 replicates where a species experienced a rapid decline in abundance according to the criteria defined above. We have not explicitly considered the effects of demographic and genetic stochasticity operating in small populations (i.e. the EN). Instead our focus is on whether there exists a relationship between food web structure and the risk that a species apparently unexpectedly may reach endangered levels where the effects of demographic and genetic stochasticity may set in under...
the influence of stochasticity (e.g. due to environmental change).

2.5. Direct and indirect strong effects

In this study, an indirect strong effect took place whenever a species was recorded as vulnerable (as defined above) and *not* directly involved in a strong interaction (i.e. when the strong interaction was situated somewhere else in the web). A direct strong effect was defined as when a species that was directly involved in a strong interaction was recorded as vulnerable. Direct strong effects could be divided into two subcategories based on if the species noted as vulnerable took part in a strong interaction from a predator to a prey ($a_{ij}$) or in a strong interaction from a prey to a predator ($a_{ji}$).

2.6. Data analyses

We used regression tree analyses to explore how one single response variable (the risk of experiencing a rapid decline in abundance) could be explained by 33 explanatory variables describing food web structure (numeric) and the absence/presence of a strong interaction at a specific location in the food web (categorical) (Table 2). CART (classification and regression tree analyses) is an efficient method to analyze complex ecological data with many variables that may hold nonlinear relationships, which are then presented in a simple and easily interpretable way (see Deeth and Fabricius, 2000). The regression tree analyses were implemented in Matlab using methods described in Martinez and Martinez (2002). Regression trees for subwebs with one strong interaction were generated using 10-fold cross validation, and for subwebs without any strong interaction test sample validation was used (test sample fraction = 50%). In both cases, the final best tree was chosen as the smallest tree that had a prediction error within one standard error of the prediction error of the tree with minimum prediction error. Validation methods differed between the two sets of subwebs, primarily due to dissimilarities in sample size. A simplified version (Fig. 2a) of the full regression tree of species 1 (Appendix, Fig. A1) was generated by grouping the response variable into 4 classes (risk of a rapid decline in abundance: 0–25%, 26–50%, 51–75%, and 76–100%). This produced a less complex tree (more easy to interpret) albeit with a high proportion of variance explained and identifying the same primary explanatory variables as the full regression tree. This procedure was used for species 2 and 3 as well with the same result (i.e. the same primary explanatory variables were identified in the full as well as the simplified analysis).

3. Results

In summary, the species vulnerability was related to (i) its trophic position in the food web, (ii) the position of the strong trophic interaction, and (iii) food web structure. More specifically, (i) the risk of a species experiencing a rapid decline in abundance was negatively related to trophic height. Thus, producer species (species 1–3) was noted as vulnerable more frequently than primary consumers (species 4–5) (Fig. 1). The secondary consumer (i.e. top predator) was never noted as vulnerable in this study. Furthermore, (ii) direct strong effects (i.e. the risk of experiencing a rapid decline in abundance when involved in a strong interaction) were more frequent than indirect strong effects (Fig. 1) and the direction of the strong interaction causing most direct strong effects differed between species at different trophic levels. Finally, (iii) food web structures that correlate with high probabilities of rapid decline in abundance were identified but differed somewhat between groups of species (Fig. 2a–c).

In all subwebs with ($n = 726$) as well as without any strong interaction ($n = 67$) species experienced rapid declines in abundance in at least one replicate. The number of replicates of a subweb where a species was recorded as vulnerable was normally distributed among subwebs without any strong interaction (mean = 50), but was not so among subwebs with one strong interaction (median = 69) (Lilliefors test, $p < 0.05$, and Jarque-Bera test, $p < 0.05$, for goodness-of-fit to a normal distribution). In subwebs with one strong interaction all species but the secondary consumer (species 6) were noted as vulnerable in at least some subwebs. Most frequently a producer species (species 1–3) experienced rapid declines in abundance, both in terms of proportion of subwebs (100%) and in terms of number of replicates within a subweb (median = 53). In 29.2% of the subwebs with one strong interaction a primary consumer (species 4–5) was recorded as vulnerable, with a median of 27 replicates among these subwebs. Within 40.2% of the subwebs with one strong interaction only one species experienced a rapid decline in abundance. Within the remaining 59.8% of the subwebs ($n = 434$) several species were noted as vulnerable (but in different replicates). Among these, within 212 subwebs with one strong interaction (29.2% overall) species from different trophic levels experienced a rapid decline in abundance. In subwebs without any strong interaction only species 1 experienced a rapid decline in abundance.

3.1. Direct and indirect strong effects

In this study an indirect strong effect took place whenever a species *not* involved in a strong interaction was noted as vulnerable. Only producers were subjected to indirect strong effects (Fig. 1). Overall, indirect strong effects of producers or primary consumers were less common than direct strong effects. On average, producers were noted as vulnerable in 79.7% of the subwebs where they were involved in either type of strong interaction ($a_{ij}$ or $a_{ji}$), whereas indirect strong effects occurred in 24.9% of the subwebs where a producer did not take part in a strong interaction (Fig. 1). Primary consumers experienced rapid
or less of its equilibrium abundance (in abundance) was based on the A.1 criteria of IUCN and here a species abundance due to an indirect strong effect was 73% for a producer species in a single subweb. Population vulnerability (risk of experiencing a rapid decline in abundance) was higher in subwebs when the producer was involved in a strong interaction (direct strong effect) or not involved in a strong interaction (indirect strong effect). Results for separate species were not qualitatively different. The secondary consumer was never recorded as vulnerable in this study. Direct strong effects were further divided based on the direction of the strong interaction, such that $a_{ij}$ indicates a strong interaction from a predator on a prey, and $a_{ji}$ indicates a strong interaction from a prey on a predator. Error bars denote maximum risk of experiencing a rapid decline in abundance in a subweb (i.e. the maximum proportion of replicates in a subweb where a species experienced a rapid drop in abundance). Numbers above error bars denote sample size. Pie charts: the black area represents the proportion of subwebs where a species is noted as vulnerable in at least one replicate (i.e. ≥1% risk of experiencing a rapid decline in abundance) of that sample. Note that among indirect strong effects both producers and primary consumers had a median value of 0% risk of being recorded as vulnerable in a subweb (thus no bars), but that the distribution of risks was highly skewed for producers. As a result, the maximum risk of experiencing a rapid decline in abundance due to an indirect strong effect was 73% for a producer species in a single subweb. Population vulnerability (risk of experiencing a rapid decline in abundance) was based on the A.1 criteria of IUCN and here a species $i$ was considered vulnerable if the population ($N_i$) experienced a reduction to 25% or less of its equilibrium abundance ($N_i^e$) within a period of ten time steps.

decreases due to direct strong effects in, on average, 36.1% of the subwebs (compared to 0% for indirect strong effects) (Fig. 1). Thus, both direct and indirect strong effects were more common among producers than among primary consumers. The position of the strong interaction influenced the incidence of indirect strong effects for producers. Characteristically, producers did not experience indirect strong effects in one case—when there was a strong interaction from a primary consumer to another producer species, but indirect strong effects could occur when a strong interaction was situated elsewhere.

Within the two subcategories of direct strong effects, producers were noted as vulnerable in a larger fraction of the subwebs when they took part in a strong interaction from a predator to a prey ($a_{ij}$; 97.2%), than vice versa ($a_{ji}$; 62.3%) (Fig. 1). Similarly, the median number of replicates where a producer experienced a rapid decline in abundance was higher in subwebs when the producer was involved in a strong interaction from a predator to a prey, than vice versa (Fig. 1). Direct strong effects of producers frequently occurred irrespective of a strong interaction with a primary or a secondary consumer.

The pattern above was strikingly different for primary consumers. Direct strong effects arose mainly in subwebs when a primary consumer was involved in a strong interaction from a prey on a predator ($a_{ji}$; 67.1%), and only seldom in the opposite direction ($a_{ij}$; 2.7%) (Fig. 1). More specifically, primary consumer populations were noted as vulnerable in subwebs where they took part in a strong interaction from a producer species (Fig. 2b), but only in a few subwebs where a primary consumer was directly involved in a strong interaction from a secondary consumer.

3.2. Effects of food web structure and interaction strength

The final best trees of the regression tree analyses on subwebs with one strong interaction explained 92.1–96.2% of the variance in risk for a sudden decline in abundance of a species at a certain trophic level using the ungrouped response variable (Fig. 2b and Appendix, Fig. A1–A4), whereas the level of explanation was only 41% for species 1 in subwebs without any strong interaction (Fig. 2c).

The regression trees for each of the producers in subwebs with one strong interaction showed a consistent pattern; a strong impact from a primary consumer was identified as the most important explanatory variable and indicated a higher risk of experiencing a rapid decline in abundance for the specified producer species (Fig. 2a and Appendix, Fig. A1–A3). Next, increased generality of primary consumer species and a strong impact from the secondary consumer seemed to result in increased vulnerability of producer species (Fig. 2a and Appendix, Fig. A1–A3). For example, presence of a strong interaction from species 4 to species 1 ($X_{21} = 1$) was associated with a higher vulnerability of species 1, and when this aspect was accounted for, increased vulnerability of species 1 was associated with increased generality of species 4 (Fig. 2a).
The regression trees of primary consumers in subwebs with one strong interaction also showed a consistent pattern; vulnerability of primary consumers appeared to be most strongly affected by the presence or absence of a strong interaction from a producer to the primary consumer (Fig. 2b and Appendix, Fig. A4). For example, species 5 never experienced a rapid decline in abundance in subwebs with no strong $a_{52}$-interaction ($X_{16} = 0$) that had no strong $a_{53}$-interaction ($X_{19} = 0$) or strong $a_{51}$-interaction ($X_{13} = 0$). Instead, the vulnerability of a primary consumer appeared to be strongly affected by the combination of a strong interaction from a producer to the primary consumer and an increase in its own generality (rightmost branch, Appendix, Fig. A4).

In subwebs without strong interactions, producer species seemed to be more prone to reaching endangered levels when generality of primary consumers increased. Furthermore, increased number of consumers of species 1 indicated a significantly increased risk of species 1 being noted as vulnerable (Pearson’s product moment correlation, $r = 0.42, n = 67, p = 0.0004$). Thus, food web structure seemed to affect the vulnerability of species in both subwebs with and without one strong interaction.

4. Discussion

Contrary to our initial expectations, we found that the risk of a population experiencing a rapid decline in abundance...
decreased with trophic level in food webs experiencing stochasticity with zero autocorrelation (Fig. 1). Furthermore, we show that food web structure as well as interaction strength affects the risk of experiencing a sudden drop in abundance and thus may indicate the vulnerability of populations to environmental stochasticity (Fig. 2). We also demonstrate that indirect strong effects occur for some species in our model webs, but, as hypothesized, they are less common than direct strong effects (Fig. 1).

Our simulations show that species at the basal trophic level (producers) most frequently experienced sudden declines in abundance. Intermediate species (primary consumers) also expressed population dynamics that could put them in the danger zone of extinction. However, the
top species (the secondary consumer) was never labelled as vulnerable. This result rejects our initial hypothesis and contrasts sharply with some empirical findings (e.g. Spencer et al., 1999) and theoretical suggestions (e.g. Ebenman et al., 2004; Holt et al., 1999), which posit that predators, preferably those with larger bodies and slow life histories, are more prone to extinction than smaller species at lower trophic levels. However, fewer than half of all comparative studies (that have used a phylogenetic comparative approach) have found a positive correlation between slow life history or body size and extinction risk (see Fisher and Owens, 2004, and references therein).

The difference in extinction risk among trophic levels between the study presented here and other studies could potentially be a corollary of skewed empirical research attention towards vulnerability to extinction of species from the animal kingdom (but see Petchey et al., 1999; Thomas et al., 2004). However, a more plausible explanation is that, contrary to previous studies, here we explicitly focus on the vulnerability of trophically interacting populations to environmental stochasticity. Thus, although species with high trophic positions (often species with slow life history) may be more vulnerable to extinctions due to factors causing sustained increased mortality (such as habitat destruction, overexploitation or interactions with introduced species) they may at the same time be more buffered against temporal variability in mortality. In other words, large body size and high trophic position could mean that a species is less vulnerable to extinction due to environmental stochasticity. Also, it may very well be the case that producer species (or species with low trophic position) on average display more variable population dynamics and thus more frequent rapid declines than species at higher trophic levels, but at the same time often a quick return to safe levels of abundance. Larger species at higher trophic levels on the other hand should, when subjected to a dramatic decline, have more difficulties in returning to safe levels, and thus, should spend longer time at low levels of abundance following a dramatic decline. Consequently, a high probability of a dramatic decline is not necessarily a good correlate of extinction risk (although O'Grady et al., 2004, suggest that it is).

The population sizes of producer species in this study expressed a larger variability earlier in the time series, due to higher per capita growth and mortality rates than the consumers, and thus expressed more violent population fluctuations including sudden declines in abundance. It has been shown that autocorrelation of time series (i.e. spectral redness) increases with trophic level when species are subjected to uncorrelated stochasticity (Karlsson et al., unpublished). This indicates that variability of consumer species increases more rapidly with time than for producers (Halley and Kunin, 1999), which suggests a higher risk of a consumer reaching endangered levels later in the time series; a risk that may be even further enhanced by increased reddened spectrum of contemporary environmental stochasticity (Schiermeier, 2001; Wigley et al., 1998). At the same time, it has been shown that environmental variability may promote coexistence among producer species (Adler et al., 2006). Furthermore, populations are more likely to persist in a variable environment when the average abundance is large, recovery from low abundance is rapid and the fluctuation in abundance is small (Lande, 1993). The first two traits agree with features of smaller species at lower trophic levels (Lawton, 1995), and the second trait suggests that the producers in this study may recover more easily from the sudden drops to extinction-prone levels.

Recent research have shown that species in many communities today experience stress, from habitat destruction and global warming (e.g. Thomas et al., 2004), which may take the form of “degrading perturbations” where recruitment is subjected to long-run stochastic reduction. Based on this line of reasoning Jonsson et al. (2006) studied extinction risk in model populations subjected to degrading stochasticity (i.e. at each time step the reproductive rate was stochastically reduced) and showed that consumers, but rarely producers, went extinct.

The regression tree of species 1 in subwebs without any strong interaction (Fig. 2c) had much less explanatory power than the tree for species 1 in subwebs with one strong interaction (Fig. 2a). One possible explanation for this is the smaller variation in the risk of experiencing rapid declines in abundance for species 1 among subwebs without any strong interaction (minimum risk = 37, maximum risk = 61), which make separation into nodes (groups) with different levels of population vulnerability more difficult than for species 1 in subwebs with one strong interaction (min risk = 0, max risk = 99). Nevertheless, all regression trees indicated that food web structure was related to the risk of experiencing rapid declines in abundance for species.

The food web metric generality of a consumer (number of prey per predator, Table 2) communicates predatory pressure on prey, since increased generality of consumers increases the likelihood that a resource will interact with several consumers. This presumably explains the increased vulnerability of producer species with increased generality of primary consumers. The food web metric number of omnivorous links (Table 2) was positively related to vulnerability of species 4. This result coincides with earlier findings (Jonsson et al., 2006) and the suggestion of Pimm and Lawton (1978) that intermediate species should suffer doubly from both competition and predation from omnivorous species at higher trophic levels, and thus are more prone to extinction.

Theory predicts that the effect of a particular interaction should diminish with distance from the source, and that strong direct interactions are needed to produce indirect interactions (Schoener, 1993). From this and other arguments, it has been concluded that detecting indirect interactions may be a difficult task (Bender et al., 1984; Menge, 1997). However, empirical studies have shown that
strong effects of species may travel via indirect pathways (Paine, 1966; Vandermeer, 1980; Wootton, 1994) and that indirect interactions may actually be stronger than direct interactions (Abrams, 1992; Power, 1990; Wootton, 1992). In this study, only producers experienced indirect strong effects. In agreement with our hypothesis, the indirect strong effects were less common than direct strong effects. For producers indirect strong effects occurred in approximately 1/4 of the subwebs where a producer did not take part in a strong interaction, but the great range indicates that indirect strong effects may be very significant in certain webs. However, the exact location of strong interactions producing indirect strong effects offered little prognostic insight, since almost all positions of a strong interaction in our model webs were associated with increased vulnerability of producers, which indicates that indirect effects caused by environmental stochasticity is very unpredictable.

The great majority of theoretical food web studies (including this one) have used a fixed set of interaction strengths. But interaction strengths need not be constant (Berlow, 1999), instead they may change over time by, for example, alterations in characteristics of species (e.g. body size, diet, Werner and Peacor, 2003) or the environment (Post et al., 1999). Navarrete and Berlow (2006) showed that the spatial and temporal variability in trophic interaction strengths, in an intertidal community exposed to environmental stochasticity, was an important mechanism behind a temporally invariant community structure. Thus, variable interaction strengths seemed to increase the resilience in community patterns rather than the reverse. Here, we show that environmental stochasticity and food web structure interact and expose species differently to the risk of becoming endangered. A very interesting next step would be to analyze how the patterns in vulnerability discovered here are affected by variability in interaction strengths and if such variability could decrease the extinction risk of species in the type of models used here.

Today species are going extinct at an unprecedented rate, predominantly as a consequence of anthropogenic disturbances and activities (Ehrlich, 2002; Myers et al., 2000; Pimm and Raven, 2000). This is an alarming fact that has spawned vast amounts of research that tries to explain the proximate (Lawton, 1995) and ultimate causes (e.g. Cardillo et al., 2004, 2005; Fisher and Owens, 2004; Hanski, 1998; Polis and Merow, 2002; Ripa and Lundberg, 2000) of extinction in variable environments. Population viability analysis has been suggested as a reliable method to provide useful projections of dynamics of a singular threatened species (Brook et al., 2000, but see Coulson et al., 2001). But how do we detect warning signs of imminent decline and subsequently vulnerability to extinction among the natural variability in abundance among populations in real multi-species settings? As a first step, Karlsson et al. (unpublished) showed that the spectral colour of time series was correlated to extinction risk of producers subjected to stochasticity with zero autocorrelation. However, the risk of extinction depended on the exact location of the strong interaction in the model webs. To better understand which species are more susceptible to become endangered and enter the unsafe domain where demographic and genetic variability increase the risk of extinction, and in what circumstances, we need to continue studies of larger communities under different regimes of stochasticity. Here, we have taken the next step in analyzing the effect of stochasticity on the population vulnerability of species in a food web setting by showing how properties of food web structure and the position (and direction) of strong trophic interactions may predict those species that rapidly may enter dangerous routes towards endangered population levels (according to the IUCN criterion of EN). We chose to use a criterion for population vulnerability to extinction that combines the time over which a decrease has occurred with a threshold level of abundance (≤25% of equilibrium abundance remaining) that is greater than the so-called quasi-extinction levels used in many other studies. The reason for the model setup used here is that initial decline to extinction vortex levels and final decline to extinction appear to be very different (Fagan and Holmes, 2006) and governed by different mechanisms which implies that a model describing the entire route to extinction needs to include different mechanisms that are activated at various abundance levels. Here, our objective was to study the effect of environmental stochasticity on population vulnerability in a food web setting and to focus on the initial decline in abundance (which may result in small populations exposed to demographic and genetic stochasticity that eventually puts a population at the risk of extinction).

Ecological forecasting has been suggested as an urgent measure to slow down the process of accelerating species extinctions (Clark et al., 2001), i.e. to be able to predict future severe declines of population size. Forecasting of population dynamics in ecology is probably a daunting task due to the uncertainties associated with complex networks, nonlinearities and stochasticity, but better knowledge of the traits and structures that govern population dynamics in multi-species settings may be necessary first steps towards this goal. The work presented here could aid in the formulation of appropriate simulation or correlation models that in the future may help in identifying features that signal regime shifts (Kleinen et al., 2003).

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Appendix

Figs. A1–A4 show the final best regression trees for explaining the risk of experiencing a rapid decline in
abundance (vulnerability) for three producer species and one primary consumer species in a six-species Lotka–Volterra food web model exposed to stochastic perturbations. Contrary to Fig. 2a, that show a simplified regression tree for species 1 where the response variable was grouped into four discrete categories, the regression trees in Figs. A1–A4 are all based on a full CART analysis using 33 explanatory variables (Table 2) and a continuos response variable.

Risk of experiencing a rapid decline in abundance for species 1 in webs with one strong interaction

![Regression Tree Diagram]

Fig. A1. The final best regression tree for species 1 in subwebs with one strong interaction. The proportion of variation explained is denoted by PVE. At each node of the tree the number and short name of the explanatory variable (see Table 2 for a list) used for a binary split of the data is displayed. In each terminal node, the expected (average) risk of experiencing a rapid decline in abundance (E) and number of observations (n) are given. To highlight an increased vulnerability, the terminal nodes are tinted from white to black (white: 0–25%; light grey-black text: 26–50%; dark grey-white text: 51–75%; black: 76–100%).
Risk of experiencing a rapid decline in abundance for species 2 in webs with one strong interaction

PVE = 92.1%

Fig. A2. The final best regression tree for species 2 in subwebs with one strong interaction. For explanations to notations see Fig. A1.
Risk of experiencing a rapid decline in abundance for species 3 in webs with one strong interaction

PVE = 95.5%

Fig. A3. The final best regression tree for species 3 in subwebs with one strong interaction. For explanations to notations see Fig. A1.
Risk of experiencing a rapid decline in abundance for species 5 in webs with one strong interaction

![Diagram](FigA4.png)

Fig. A4. The final best regression tree for species 5 in subwebs with one strong interaction. For explanations to notations see Fig. A1.

References


