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Austria and Switzerland

Basic and Applied Ecology 12 (2011) 590–599

Basic and Applied Ecology

www.elsevier.de/baae

The susceptibility of species to extinctions in model communities

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Received 1 April 2011; accepted 12 September 2011

Abstract

Despite the fact that the loss of a species from a community has the potential to cause a dramatic decline in biodiversity, for example through cascades of secondary extinctions, little is known about the factors contributing to the extinction risk of any particular species. Here we expand earlier modeling approaches using a dynamic food-web model that accounts for bottom-up as well as top-down effects. We investigate what factors influence a species' extinction risk and time to extinction of the non-persistent species.

We identified three basic properties that affect a species' risk of extinction. The highest extinction risk is born by species with (1) low energy input (e.g. high trophic level), (2) susceptibility to the loss of energy pathways (e.g. specialists with few prey species) and (3) dynamic instability (e.g. low Hill exponent and reliance on homogeneous energy channels when feeding on similarly sized prey).

Interestingly, and different from field studies, we found that the trophic level and not the body mass of a species influences its extinction risk. On the other hand, body mass is the single most important factor determining the time to extinction of a species, resulting in small species dying first. This suggests that in the field the trophic level might have more influence on the extinction risk than presently recognized.

Zusammenfassung

Obwohl wir wissen, dass Artensterben durch sekundäre Aussterbefälle weitreichende Verluste von Biodiversität in Artengemeinschaften auslösen kann, ist wenig bekannt über Faktoren, die das Aussterberisiko einer bestimmten Art beeinflussen. Hier erweitern wir frühere theoretische Arbeiten mit Hilfe eines dynamischen Nahrungsnetzmodells, das sowohl top-down als auch bottom-up Effekte berücksichtigt. Wir untersuchen welche Faktoren das Aussterberisiko und die Zeit bis zum Aussterben der nicht persistenten Arten beeinflussen.

Wir identifizierten drei fundamentale Eigenschaften, die sich auf das Aussterberisiko einer Art auswirken. Das höchste Risiko tragen Arten mit (1) niedriger Energiezufuhr (z.B. mit hohem trophischen Level), (2) Anfälligkeit für den Verlust von Energiepfaden (z.B. Spezialisten mit wenig Beutearten) und (3) dynamischer Instabilität (z.B. mit niedrigem Hill Exponenten und Abhängigkeit von homogenen Energiepfaden durch Fraßen ähnlich großen Beutearten).

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Unser Modell zeigt, dass, anders als in Feldstudien festgestellt, nicht die Körpergröße einer Art sondern ihr trophischer Level ihr Aussterberisiko beeinflusst. Für die Zeit bis zum Aussterben auf der anderen Seite ist die Körpergröße der wichtigste bestimmende Faktor. Dies führt dazu, dass die kleinen Arten als Erste aussterben. Somit könnte sich der trophische Level einer Art mehr als bisher angenommen auf ihr Aussterberisiko auswirken.

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Keywords: Extinction risk; Allometry; Dynamic modeling

Introduction

Today, global biodiversity is declining at an alarming rate that matches the rate of historical extinction waves (Pimm, Russell, Gittleman, & Brooks 1995; Barnosky et al. 2011) and is referred to as the sixth wave of extinction. This is especially critical since every extinction has the potential to trigger secondary extinctions, which might in turn lead to extinction cascades, accelerating the rate of biodiversity loss even further (Pimm 1980; Berlow et al. 2004; Dunne & Williams 2009). Declining species numbers, in consequence, endanger an ecosystem's ability to perform certain functions important to mankind (Loreau et al. 2001; Solan et al. 2004; Hooper et al. 2005). This risk of cascading extinctions and degradation of ecological communities makes it vitally important to gather information about the causes of species extinctions. One important task is the development of effective models that can be translated into protection measures for preserving the diversity of natural systems.

There have been a number of studies trying to assess a species' vulnerability to extinction and discussing different individual traits influencing extinction risk (McKinney 1997; Simberloff 1998; Purvis, Gittleman, Cowlishaw, & Mace 2000). These have identified high trophic levels (Purvis et al. 2000; Jackson et al. 2001), low population density (McKinney 1997; Purvis et al. 2000), and large body size as an indicator of the species' life history (McKinney 1997; Jackson et al. 2001) as key factors influencing extinction risk. Unfortunately, many of these studies focus on carnivorous vertebrates, primates (Purvis et al. 2000), birds and mammals (McKinney 1997) with few invertebrate examples, even though invertebrates contribute far more to global diversity. Hence, the crucial question remains whether these results obtained for certain groups of vertebrates can be generalized. As long as high quality empirical data on extinctions is lacking, modeling approaches promise to be the most effective means to gain knowledge that can be universally applied to fit a multitude of species.

Some prior studies have used different mathematical models to predict future biodiversity. The "field of bullets" model assumed a single, fixed extinction rate for all species, rendering the extinctions independent from one another (Raup 1992; Nee & May 1997). This model predicted an exponential decline of biodiversity. Sole and Manrubia (1996) included species interactions into their model to account for changing extinction risks. This resulted in a clustering of species losses into fewer but larger avalanches that were found to make

predictions more difficult. Recently, Ingram and Steel (2010) expanded the field of bullets model and compared the outcome of a version with varying extinction rates ("generalized field of bullets") with one that incorporated food-web topology ("ecology-based field of bullets"). They also found that accounting for food-web dependencies reduces the prediction accuracy of the model. All these studies focused solely on bottom-up effects for extinction risk and did not incorporate top-down processes, which can underestimate the number of secondary extinctions (Ebenman, Law, & Borrvall 2004; Eklöf & Ebenman 2006; Curtsdotter et al. 2011, this special feature).

Berlow et al. (2009) used a dynamic bioenergetic model to investigate the response of one species to the extinction of another. Unlike the other models, theirs accounted for the dynamics in a food web, which include top-down as well as bottom-up effects. They found that the knowledge of individual species traits such as the biomasses of the involved species and the body mass of the extinct species suffice to predict a species' biomass response to an extinction event. Including food web interactions into the model thus makes it easier rather than more difficult to predict the consequences of species extinctions.

Here, we use a dynamic bioenergetic food-web model to assess a species' vulnerability to extinction (extinction risk) and the time to extinction (number of time-steps before extinction) of the species dying out. This model does not use explicit extinction rates for the species but uses the dynamic energy flow within the food web over time to calculate changes in biomass densities. We want to explore a species' intrinsic extinction risk, as depending on network and species parameters. We therefore assemble a variety of food webs and combine them with a variety of dynamic parameters, all within the range found in natural communities (see 'Methods' section). Screening this multitude of combinations enables us to identify a species' basic risk profile as applicable without perturbation of the system. In addition to providing a theoretical framework for studies of extinctions, these risk profiles allow disentangling intrinsic from disturbance-induced extinction risks in future studies. Our findings do not focus on one individual system, but take a broader approach that nonetheless can be helpful for nature conservation.

We address the question of a species' extinction risk in two steps: Step 1: What determines the susceptibility of species to extinction? By incorporating food web structure as well as dynamic interactions between species we identify a simple

combination of traits that are measurable in the field and thus usable for conservationists. Step 2: What determines the time to extinction of the species dying out? Our interest is to see whether it is possible to predict which extinctions will be the first to be observed in the system and which species are “living dead”, doomed to extinction but not yet gone.

Methods

Our data set consists of 1000 size-structured food webs that were dynamically simulated based on an allometric, multi-species version of Yodzis and Innes' (1992) model. The webs were constructed using the rules of the niche model (Williams & Martinez 2000). This model arranges the trophic links (L) in the food web using its species richness (S) and connectance ($C=L/S^2$) as parameters. It has been successfully tested against empirical data (Williams & Martinez 2000). For each web the initial species number and initial connectance were randomly drawn from truncated normal distributions. The mean species number was 40 species, with a standard deviation of 10 species and an upper and lower boundary of 20 and 60 species, respectively. The initial connectance was chosen with a mean of 0.15, a standard deviation of 0.05 and a lower and upper boundary of 0.05 and 0.25, respectively. These values fall within the range found in natural communities (Digel, Riede, & Brose 2011) and ensure a variety of naturally plausible webs to explore and understand.

Following the dynamic model, the rate of change in the biomass through time (\dot{B}) of the primary producers (Eq. (1)) and consumers (Eq. (2)) in the system are given by:

$$\dot{B}_i = r_i G_i B_i - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (1)$$

$$\dot{B}_i = -x_i B_i + \sum_k x_i y_i B_i F_{ik} - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (2)$$

B_{ij} denotes the biomass density of the populations i and j , respectively, r_i i 's mass-specific intrinsic growth rate, G_i is the logistic growth rate, x_{ij} denotes the mass-specific metabolic rate of the populations i and j , y_{ij} the consumer's maximum consumption rate relative to its metabolic rate and e_{ji} is j 's assimilation efficiency when it consumes species i . The suffix k describes the resources of i and the suffix j its consumers.

The logistic-growth model assumes that the growth of each basal species is dependent on the carrying capacity (K) of the population. The term of the logistic growth is

$$G_i = \left(1 - \frac{B_i}{K_i}\right) \quad (3)$$

where G_i describes the deviation of the population i from K_i . To keep the energy content of the food webs constant and the webs comparable we used a system wide carrying capacity ($K_{sys}=5$), calculating each primary producer's share by dividing K_{sys} by the number of plant species in the food web.

Rall, Guill and Brose (2008) studied the effects of enrichment on consumer-resource models and complex food webs by varying the carrying capacity in the system. They found starvation of high trophic level consumers for low K and extinctions due to dynamic instability at high values of K (Rall et al. 2008). A K_{sys} of 5 is somewhere in the middle of these extremes while still maintaining a variety of cases to explore.

F_{ji} , the functional response, describes the resource density dependent feeding of a consumer j on a resource i influenced by all other j 's resources k :

$$F_{ji} = \frac{\omega_{ji} B_i^h}{B_0^h + c B_j + \omega_{ji} B_i^h + \sum_k \omega_{jk} B_k^h} \quad (4)$$

The functional response is described by ω_{ji} , a dimensionless positive weight factor (set to 0.5, see Koen-Alonso 2007, for more details), B_0 , the half-saturation density (i.e. the population density at which half the maximum consumption of the species is reached), the predator interference term, c , and the Hill exponent, h , that regulates the shape of the function. An increasing Hill exponent renders the shape of the curve more sigmoidal, which is interpreted as a refuge effect for prey species at low prey densities (see Williams & Martinez (2004b) and Rall et al. (2008) for more details).

Metabolic theory suggests that the biological rates of production (R), metabolism (X) and maximum consumption (Y) scale with the species' body mass with a negative-quarter power law (Enquist, West, Charnov, & Brown 1999; Brown, Gillooly, Allen, Savage, & West 2004). We used this established scaling coefficient in our simulation, but it should be kept in mind that recently a lower scaling coefficient was found (Ehnes, Rall, & Brose 2011). However, this should not detract from the applicability of our results.

$$R_P = \alpha_r M_P^{-0.25} \quad (5)$$

$$X_{C,P} = \alpha_x M_{C,P}^{-0.25} \quad (6)$$

$$Y_C = \alpha_y M_{C,P}^{-0.25} \quad (7)$$

where the suffixes C and P indicate consumer and producer parameters, respectively, α_r , α_x and α_y are allometric constants. In our model, these biological rates are normalized by the mass-specific intrinsic growth rate of the smallest basal species j , (R_j). This results in different growth rates for j and all other basal species, i , and defines the time scale of the system:

$$r_j = \frac{R_j}{R_j} = 1 \quad (8)$$

$$r_i = \frac{R_i}{R_j} = \left(\frac{M_i}{M_j}\right)^{-0.25} \quad (9)$$

Accordingly, the mass-specific metabolic rates (Eq. (6)) are normalized by the production and thus the time scale (Eq. (5)), leading to:

$$x_i = \frac{X_{C,P}}{R_P} = \frac{\alpha_x}{\alpha_r} \left(\frac{M_{C,P}}{M_P} \right)^{-0.25} \quad (10)$$

The maximum consumption (Eq. (7)) is normalized by the metabolic rates (Eq. (6)):

$$y_i = \frac{Y_C}{R_C} = \frac{\alpha_y}{\alpha_x} \quad (11)$$

Inserting Eqs. (9)–(11) into Eqs. (1) and (2) results in a population dynamic model with parameters that are allometrically scaled.

We used the following assimilation efficiencies: $e_{ij} = 0.85$ for carnivore links, $e_{ij} = 0.45$ for herbivore links. The maximum consumption rate of the species was kept at ($y = 8$). The normalized metabolic rate (α_x/α_r) was set to 0.314 (Brose, Williams, & Martinez 2006). The predator interference term was randomly chosen from a truncated normal distribution with a mean of 0.1 and a lower boundary of zero, the hill exponent from one with the mean of 1.1 and lower boundary of 1. Both had a standard deviation of 0.05 and an upper boundary of 2. Again, these values fall well within the range of natural communities while providing a range of parameter combinations to screen (Yodzis & Innes 1992; Brose et al. 2006; Vucic-Pestic, Rall, Kalinkat, & Brose 2010). The initial abundances of the species were randomly chosen between 0.1 and 1.

The body masses of the species increase with the species' trophic level, modified by a factor sampled from a normal distribution with a mean of 10 and a standard deviation of 10. This stochastic factor yields variation in body masses within trophic levels while preserving the increase in mass with trophic level that can be found in natural systems (Riede et al. 2011). Trophic level and body mass are thus highly correlated variables but can influence a species' extinction risk and time to extinction independently.

All food webs were assembled and simulated for 100,000 time steps. A species was considered extinct if its biomass fell below 10^{-30} . Contrary to other studies we did not force any extinctions but only registered the ones occurring "naturally" in the food webs. Throughout the simulation we recorded several variables at time step zero to test for their influence on the species' susceptibility to extinction.

As food-web variables, we recorded the initial species number and connectance of the web. To characterize the species and its relations to the other species in the web we recorded the prey-averaged trophic level of the species (Williams & Martinez 2004a), the Hill exponent, predator interference term, body mass and initial biomass as well as the average body-size ratio of the species to its prey, the standard deviation of this ratio, the average body-size ratio to its predators and the standard deviation thereof.

Also recorded for each species were the generality (number of prey species), the vulnerability (number of predators) and linkedness (number of links). We then calculated for each of these variables the mean and maximum the species shares with all other species in the web. We furthermore calculated the mean and maximum number of "var" each species shares with other species with which it shares at least one "var" where "var" is prey species, predator species or links. We also calculated the number of species each species shares prey species, predator species, or links with.

Additionally, we calculated the similarity of the species to each of the other species in the web as follows: $I = C/(A + B + C)$ where I is the similarity, A the prey, predators or links unique to the species, B the prey, predators or links unique to the other species in the web and C the prey, predators or links that both species share. We recorded the species' maximum and mean prey, predator and link similarity to all other species in the web and its mean prey, predator and link similarity to the species it is sharing at least one prey species or one predator species or one link with.

As dependent variables we recorded whether the species went extinct (1) or not (0) and the extinct species' time to extinction.

Statistics

Step 1: To determine which parameters have the largest influence in determining if a species goes extinct or not we performed a classification tree analysis (Ripley 2010) with all recorded variables plus the log-transformed values of the species' body mass and biomass. This is used for exploratory data analysis and investigates the relative importance of variables in explaining the variance of a dependent variable, in this case the binary variable stating if the species went extinct during the simulation (1) or survived (0). To obtain a more quantitative understanding, the significant explanatory variables of the classification tree analysis were entered in a generalized linear model (R Development Core Team 2009) to see how they influence the extinction probability of the species. We performed this analysis once with all species in the web and once without the basal species. The trends in both cases were the same, but more pronounced when focusing on the consumer species and in this paper we present the results obtained with the basal species excluded.

Step 2: We examined the species that had died out during the simulation. To analyze which parameters influence the time to extinction of these species we ran a generalized additive model (Wood 2006) on the data set and all recorded variables. This model uses a back-fitting smoothing algorithm to link the explanatory variables to the time to extinction. The smoothers

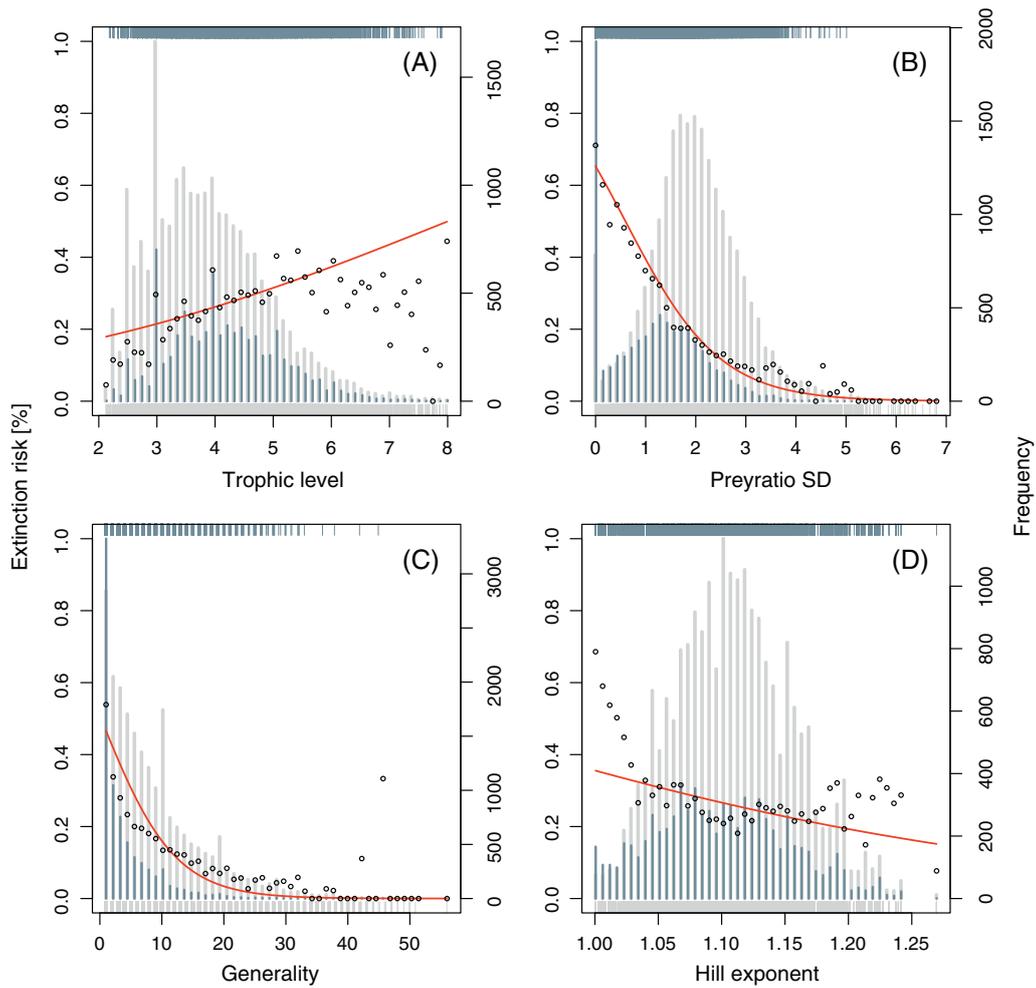


Fig. 1. The variables influencing a species' susceptibility to extinction. Plotted is the extinction risk on the first y-axis (dark-gray lines above $y=1$ correspond to extinct species, light-gray lines below $y=0$ to species being alive at the end of the simulation) and the frequency of observation on the second y-axis (the dark-gray histogram corresponds to dead species, the light-gray histogram to species being alive at the end of the simulation) over the explanatory variable. The red solid line illustrates the extinction probability calculated by the general linear model based on the observed values. The circles denote the fraction of extinctions from the overall data points at that x value. The plots are based on data excluding basal species to make the trends clearer. The explanatory variables are (A) the species' trophic level, (B) the standard deviation of the species' body-mass ratio to its prey items (preyratio SD), (C) the species' generality (number of prey) and (D) the species' Hill exponent, shaping its feeding interactions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are calculated with respect to the best representation of the relationship of the explaining variable and the partial residuals are calculated by removing the effect of all other predictor variables on the dependent variable.

Results

Step 1: *Species with a high trophic level, low variation in prey size, low generality and low Hill exponent are most susceptible to extinction.*

The classification tree analysis identified four out of 35 tested variables as having a significant influence ($R^2 < 0.001$) on a species' extinction risk. Their trends, as calculated by the generalized linear model, are depicted in Fig. 1. The higher the trophic level of the species the greater the chances of that species going extinct during the simulation (Fig. 1A). A trophic level of two is associated with an extinction probability of less than 20% while a trophic level of eight increases the extinction probability to 50% (solid line in Fig. 1A). The proportion of extinct species at the higher trophic levels deviates from the expected extinction risk as calculated by the generalized linear model (the circles below the solid line). This pattern suggests that the generalized linear model might

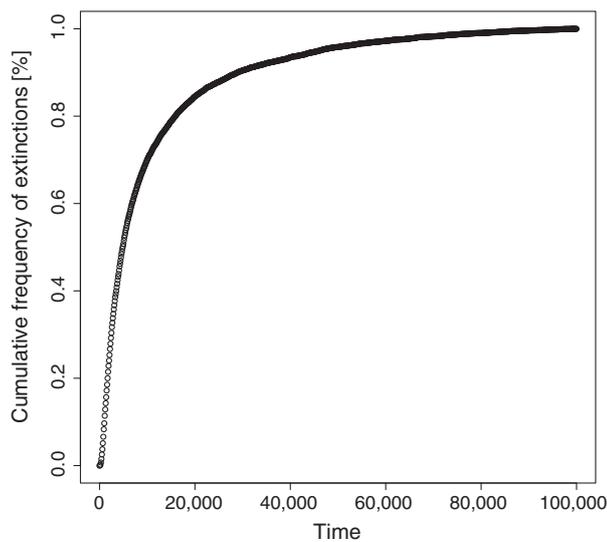


Fig. 2. Cumulative percentage of extinctions over time. The slope of the tangent of the plotted curve gives the extinction rate at that point in time. As the simulation time (x -axis) progresses the extinction rate levels off, indicating that the number of extinctions decreases over time with almost no extinctions at the end of the simulation.

overestimate the frequency of extinctions at the highest trophic levels. However, focussing on the frequency distribution of the data points (histograms in the background of the plot) reveals that the model might be oriented to fit the area with a high density of data points (and therefore high informative value) and extrapolates its curve on that basis.

Fig. 1B shows the influence of the variation in body size of the prey utilized by the focal species, given as the standard deviation of the body-mass ratio between the species and its prey: the more differently sized prey items a species feeds on the lower its extinction risk (Fig. 1B). The extinction risk of a species decreases with increasing generality (number of prey), with almost no extinctions of species with more than 30 prey items (Fig. 1C). The higher the Hill exponent the lower the extinction risk of the species. Interestingly, using natural food web structures and simulating their dynamic behavior for an equivalent of 30 years yields the same results as the simulations using the niche model webs (data not shown).

Fig. 2 shows the cumulative percentage of extinctions over time. As the simulation progresses the extinction rate, as indicated by the slope of the tangent of the plotted curve, decreases and approaches zero at the end of the time-series. Over 80% of all extinctions occur in the first fifth of the time-series and almost none by the end indicating that the vast majority of extinctions that will take place in the food webs we created are within our observed time frame. This clearly separates the data into surviving species and those that went extinct. For the latter, we also addressed the question of which parameters affect the time until extinction.

Step 2: Species with low body mass, large prey and large predators are the first to go extinct.

We identified six parameters that influence a species' time to extinction. All six influencing parameters together explain 61.1% of the variation in the data set. We cannot assess each individual parameters' contribution to the model, but the visualization of the influences of the parameters on the time to extinction (Fig. 3) clearly shows a major influence of the body mass of the species. The higher the body mass of the species the longer it takes that species to go extinct (Fig. 3A). A higher mean body-mass ratio of the species' predators to the species (i.e. having predators that are much larger than itself) decreases the time to extinction (Fig. 3B). A higher mean body-mass ratio of the species to its prey (i.e. having small prey in comparison to its own body size) increases the time to extinction (Fig. 3C). Predator interference, a measure of how much time the species spends competing with con-specifics (Fig. 3D), the maximum number of species the species is sharing prey items with (max preyshared, Fig. 3E) and the generality (number of prey) of the species (Fig. 3F) also contribute to the species' time to extinction, but their individual influence is not great (Fig. 3).

Discussion

In this study, we focused on two questions concerning a species' extinction risk. Step 1 investigated the species' vulnerability to extinction and parameters influencing it. In a second step we explored which parameters affect the time to extinction of the species dying out. Our study shows that a combination of a few factors influence a species' susceptibility to extinction: accessibility of energy, availability of energy pathways and population dynamics. Interestingly, a species' body mass influences its time to extinction, but not its extinction risk.

Step 1: A species' ability and flexibility to gain energy through the web is crucial to determine its susceptibility to extinction.

The trophic position can be seen as a measure of how much the species is separated from the food web's source of energy at the base, such as phytoplankton in marine ecosystems, primary decomposers in soil food webs or vascular plants in terrestrial systems. Each trophic level receives less energy in comparison to the lower levels: the higher the species' trophic level the less energy is available to balance its metabolic needs. This explains the higher extinction risk of high trophic level species. The species' community does not provide enough energy for the species to survive. Already Hutchinson argued that energy transfer limits the length of food chains in food webs (Hutchinson 1959) which found empirical support in microbial systems (Kaunzinger & Morin 1998). Pimm and Lawton disturbed food chains and found that the more trophic levels in the chain the longer it took the system to get back into equilibrium. The population dynamics of the system lead to a higher probability of extinction and

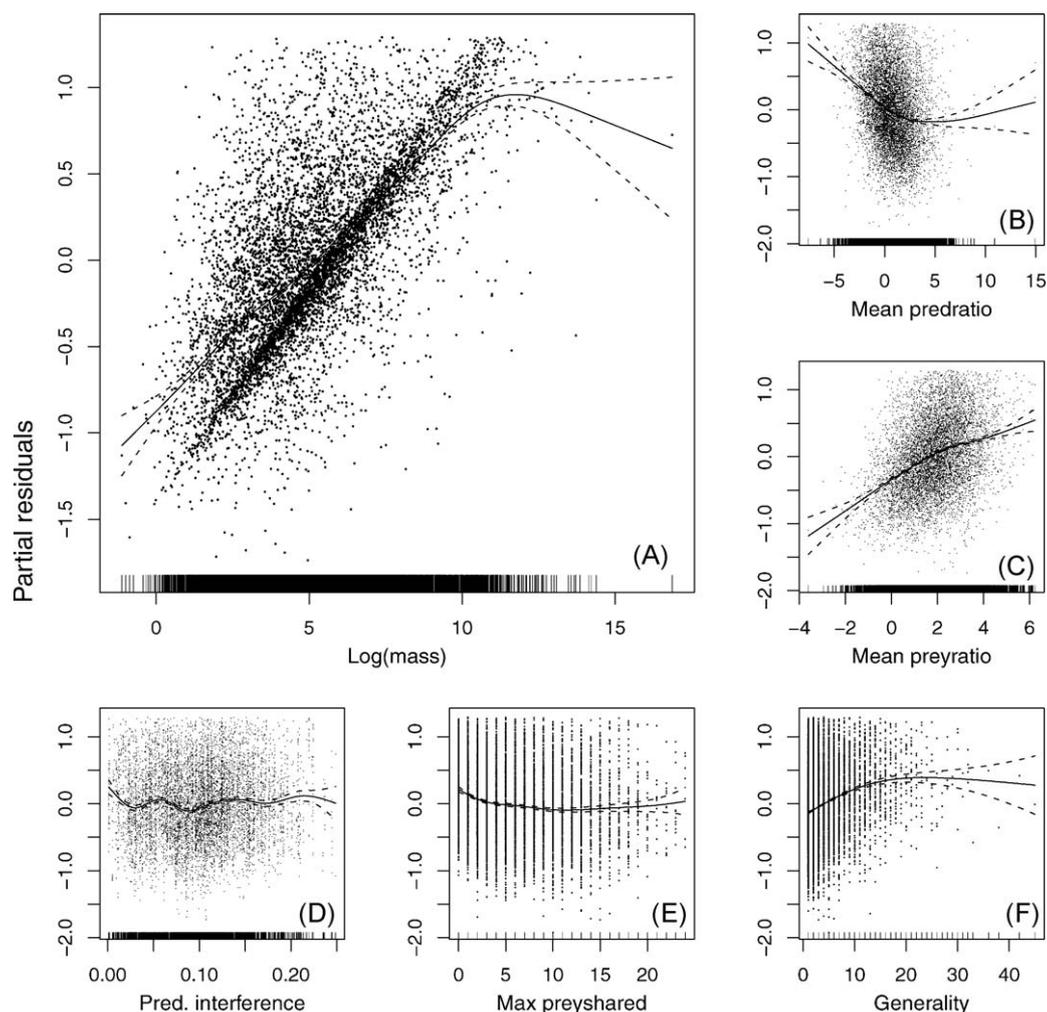


Fig. 3. Variables influencing the species' time to extinction. Plotted are the partial residuals of the model against the explanatory variable. The continuous line is the local regression smoother, the dotted lines the corresponding 95% point-wise confidence bands. The dashes on the x-axis give the distribution of observed values. The influencing variables are: (A) the log body mass of the species ($\log(\text{mass})$), (B) the average body-mass ratio of the predators to the species (mean predratio), (C) the average body-mass ratio of the species to its prey (mean preyratio), (D) the predator interference term, (E) the maximum number of prey shared with other species in the web (max preyshared) and (F) the generality (number of prey) of the species.

therefore decreases stability (Pimm & Lawton 1977). Later studies emphasized the importance of ecosystem size to the number of feasible trophic levels in a system (Post, Pace, & Hairston 2000; Post 2002). Unfortunately our model does not incorporate effects of spatial patterns. Also, species at higher trophic levels might suffer the cumulative effects of disturbance and oscillatory dynamics of the species situated lower in the web, leaving them more vulnerable to extinction (Purvis et al. 2000). This wide variety of reasons can cause the higher risk of extinction we found for species with higher trophic levels.

Here we find that the trophic level and not the body mass of the species determine the species' risk of extinction. In empirical studies body mass is often identified as a major driving factor of extinction risk (Cardillo et al. 2005). However, empirical studies usually do not measure a species' trophic level because it is more complicated to measure compared

to the species' body mass. Our results indicate that even if correlated, trophic level and body mass are not equivalent in predicting a species' extinction risk and time to extinction. This introduces the possibility that trophic level might be more important to the risk of extinction of a species in natural systems than hitherto imagined and important to take into account as a separate parameter in models of food web and extinction dynamics.

The size variability of the prey items of a species (here expressed as the standard deviation of its size-ratio) is a measure of the species' specialization on specific size classes, and consequently a measure of the flexibility of the species to obtain energy from different preys. Species with a broader prey size spectrum can subsist on other prey to obtain energy from and escape extinction more easily. At the same time, variation in prey sizes means that the species is gaining energy through different pathways with different

dynamics. In the case of a perturbation these energy channels act complementary and thus save the species from extinction. This is in line with findings from (Rooney, McCann, Gellner, & Moore 2006) who stated that a predator preying on differently sized prey links multiple asymmetric energy channels with fast (small prey) and slow (large prey) dynamics, which ultimately enhances stability in the chains and the food web. While space constraints prevent own analyses of these population dynamics, they are well documented in prior publications (Yodzis & Innes 1992; Brose et al. 2006).

The generality of a species characterizes its ability to modify its energetic income and is linked to its vulnerability to bottom-up extinctions. A species with only a few prey items is more at risk when loosing prey than one with more prey. Generality and variation in prey size are highly correlated in our data set but emphasize different aspects of a species energy availability. Generality is a safeguard against loss of energy channels and a species trait pertaining to the structure of the food web. Variability in prey size relates to the dynamics between species because it influences the availability of energy for the feeding species throughout time. Our model analyses are thus in line with classic food-web analyses stating that specialization lowers food web stability and increases species efficiency (MacArthur 1955). Our results suggest that a high rate of specialization of a species does not only decrease the food web's stability but also decreases that very same species' ability to survive. A high Hill exponent causes effective top-down control to low equilibrium densities. This dampens the biomass oscillation of consumer and resource and increases dynamic stability, thus reducing a species extinction risk. Interestingly, our results are thus entirely consistent with prior studies demonstrating the importance of type-III functional responses (high Hill coefficients) for food-web stability (Williams & Martinez 2004b; Rall et al. 2008). Dynamic stability in a food web is influenced by species traits such as the Hill exponent as well as food-web properties such as the dynamic of energy channels.

Overall our results suggest that it is most important for a species to be able to obtain enough energy to be able to survive, whereas other factors play only a minor role. Certainly, this is an expected result in a purely trophic network and future extensions of our approach should also include other interaction types. The data suggests that there are a few key concepts that minimize a species' extinction risk. (1) A high energy supply through the food web. In our scenario this translates into a low trophic level and thus less energy loss through trophic levels that separate the species from the energy supply at the base. (2) Security against the loss of energy pathways. A species with a high generality, feeding on many species, is less likely to lose all sources of energy than a species preying on only a few species. (3) Dynamic stability. A higher Hill exponent stabilizes a species' population dynamic and thus decreases its extinction risk. The same is true for species with a high variation in prey sizes that couple different energy pathways.

Step 2: *A species' metabolism (energy need) determines its time to extinction.*

Metabolic theory links the metabolism of a species to its body mass, indicating that with increasing mass the species' metabolism is increasing with a power-law exponent of 0.75 (Enquist et al. 1999) or slightly lower (Ehnes et al. 2011). This implies that with increasing body mass a species' metabolism becomes more efficient, resulting in a lower per-unit body mass metabolism for larger species in comparison to smaller ones. In our simulated scenario this explains the huge influence of the species' body mass to its time to extinction: a smaller species needs proportionally more energy per unit biomass to stay alive than a larger species resulting in a shorter time to extinction in the case of an energy cut-off. As the same rules apply to natural ecosystems this implies that even if only small-species extinctions can be observed quickly after a perturbation there might be larger species already doomed to extinction but still present in the system. In our simulations these "living dead" are high trophic level and therefore high body mass species. It is these that depress the observed extinction rate below that predicted by the model (Fig. 1A). We expect those species to constitute the few extinctions that would take place if the time-series would be prolonged.

Conclusion

Our data set suggests three fundamental processes that minimize a species' extinction risk: high energy accessibility, availability of energy pathways and stable population dynamics. A species' body mass does not influence its extinction risk, but its time to extinction. This shows that extinction events in natural systems are not random. Instead we see that specialists (species with low generality and little variation in prey size) with a high trophic level are most vulnerable to extinction. Studies dealing with consequences of extinctions should consider these scenarios as the most likely (Curtsdotter et al. 2011, this special feature). Basic individual species' traits and simple measures of interaction between species provide good estimates of its susceptibility to extinction. Our model furnishes researchers in the field with simple predictors, giving them easy-to-use indicators (such as body mass and trophic level of a species) to assess a species' risk of extinction and helping them to focus their conservation attention. Simulating natural food web structures with the same dynamics yielded the same results, indicating a congruency of our model with reality. At the same time it should be kept in mind that our model does not provide information about any individual system, but takes a wider approach, trying to assess a species intrinsic extinction risk that is independent from specific ecosystems and the basis on which disturbance experiments should be evaluated.

Acknowledgements

This work has been carried out as part of the ESF-funded SIZEMIC Working Group led by Owen L Petchey and Ute Jacob. UB and AB are funded by the German Research Foundation (BR 2315/13 and BR 2315/11-1, respectively).

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