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Modelling the unpredictability of future biodiversity in ecological networks

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ABSTRACT

We consider the question of how accurately we can hope to predict future biodiversity in a world in which many interacting species are at risk of extinction. Simple models assuming that species' extinctions occur independently are easily analysed, but do not account for the fact that many species depend on or otherwise interact with each other. In this paper we evaluate the effect of explicitly incorporating ecological dependencies on the predictive ability of models of extinction. In particular, we compare a model in which species' extinction rates increase because of the extinction of their prey to a model in which the same average rate increase takes place, but in which extinctions occur independently from species to species. One might expect that including this ecological information would make the prediction of future biodiversity more accurate, but instead we find that accounting for food web dependencies reveals greater uncertainty. The expected loss of biodiversity over time is similar between the two models, but the variance in future biodiversity is considerably higher in the model that includes species interactions. This increased uncertainty is because of the non-independence of species—the tendency of two species to respond similarly to the loss of a species on which both depend. We use simulations to show that this increase in variance is robust to many variations of the model, and that its magnitude should be largest in food webs that are highly dependent on a few basal species. Our results should hold whenever ecological dependencies cause most species' extinction risks to covary positively, and illustrate how more information does not necessarily improve our ability to predict future biodiversity loss.

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1. Introduction

Prediction is very difficult, especially about the future.

Niels Bohr, Danish physicist (1885–1962)

1.1. Predicting future biodiversity

We are in the midst of a major biodiversity crisis, with many species either extinct or threatened by extinction (Pimm et al., 1995). To predict how much of present biodiversity will be lost in the future, and to evaluate the ability of conservation strategies to slow this decline, we need estimates of species' risk levels and a framework in which to model how these risks will translate to extinctions. By expressing threat levels as extinction rates—or probabilities that species will be lost over a given period of time—we can model the expected loss of biodiversity. A common approach is to envision a 'field of bullets' (Nee, 1997; Raup, 1992) in which species go extinct stochastically over time.

A drawback to this modelling approach is the assumption that species' extinctions are independent of one another. If species are members of the same ecological communities this assumption is likely to be invalid. The extinction of any one species has the potential to affect the extinction rate of other species that it interacts with directly or indirectly. If secondary extinctions—extinctions caused at least in part by the extinction of other species—are common, diversity should decline more rapidly than if species were independent. Furthermore, the non-independence of interacting species may affect the precision with which we can predict biodiversity loss. We might expect information about species interactions to improve prediction, but this is not necessarily the case. The non-independence of interacting species could increase uncertainty if it causes species' extinctions to be clustered into extinction cascades rather occurring independently through time.

1.2. Incorporating ecological interactions into models of extinction

The original field of bullets (FOB) model assumed a single extinction rate for all species, leading to a Poisson process of extinction and an exponential decline of future biodiversity

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(Raup, 1992). This simple approach can be generalized to situations where extinction rate varies among species or over time. Species may have different extinction rates because they differ in traits such as body mass that make some species intrinsically more vulnerable (Purvis et al., 2000). Extinction rates may change over time if threat factors intensify or are ameliorated by conservation measures; this change in extinction rate may be uniform or may itself vary among species. Rate variation among species and with time can be incorporated into a generalized field of bullet ('g-FOB') model, in which extinction is modelled as a non-stationary Poisson process. Despite this added realism, the g-FOB model still makes the key assumption that extinction events occur independently among species, such that the extinction of one species does not change the extinction rate of any another.

In a first step toward incorporating species interactions, Solé and Manrubia (1996) devised a model in which species have both positive and negative interactions of varying strength, and go extinct when extinctions of interacting species drive the sum of their interactions with surviving species below a threshold value. The addition of these interactions causes the waiting times to extinction and the size of 'extinction avalanches' (simultaneous extinction of multiple species) to shift from an exponential to a power-law distribution. In biological terms, this implies that species losses will be clustered into fewer, larger avalanches. This should make future biodiversity inherently less predictable when species depend on each other, as the rate of species loss will depend on a few critical events. While this model represents progress toward incorporating ecology into extinction models, the arbitrary topology of the interaction network makes its relevance to real communities unclear.

A second line of theoretical research has focussed on one important interaction type—predation—to model the extinction of species interacting in food webs (networks that map who eats who in ecological communities). A primary goal of these studies is to determine whether robustness (resistance to secondary extinctions) can be predicted by the topology of food webs. A common approach is to simulate the collapse of real or model food webs by sequentially deleting species, and test whether robustness varies with food web diversity, complexity, or other features (Dunne et al., 2002). These topological analyses have shown that robustness can indeed be predicted by food web structure, often increasing with connectance (density of links) or redundancy (frequency of trophically identical species) (Borrvall et al., 2000; Dunne et al., 2002; Dunne and Williams, 2009; Petchey et al., 2008; Quince et al., 2005). Subsequent work has identified features such as bottlenecks and important individual links that make food webs prone to extinction cascades (Allesina and Bodini, 2004; Allesina et al., 2009). This work has contributed to the longstanding argument about the relationship between complexity and stability (May, 1973; McCann, 2000) by showing that aspects of food web complexity may confer resistance to ecosystem collapse.

Topological analyses are informative about the relationship between food web interactions and extinction cascades, but the method of sequential deletion does not provide a timescale on which to estimate either the mean or variance of future biodiversity. A model by Amaral and Meyer (1999) organizes species into different trophic levels in a food web and tracks the fate of species over time. As in the previous models, extinctions are deterministic (i.e. a species goes extinct immediately when its final prey becomes extinct). In most cases the effects of incorporating ecological dependencies are similar to those identified by Solé and Manrubia (1996), although in highly connected food webs the distribution of extinction avalanche sizes may be even more skewed toward a few large events (Pekalski et al., 2008).

To our knowledge, the effect of ecological dependencies on our ability to predict future biodiversity has not yet been studied explicitly. In the topological analyses described above this unpredictability could in principle be quantified as the variance in robustness among different deletion sequences, but we are unaware of this having been done. It is perhaps more appropriate to model this uncertainty using a framework related to the g-FOB model that includes explicit extinction rates rather than sequential deletions. This approach allows us to model a species' extinction rate as an increasing function of the proportion of its prey that have gone extinct, in contrast to the usual assumption that extinction rate does not change until the extinction of the final prey species, whereupon extinction is immediate. In our approach, the extinction rate of a predator begins to increase as soon as some of its prey begin to go extinct, reflecting the likelihood of lower population sizes and decreased foraging success. When all of a species' original prey have gone extinct, its extinction rate is higher but finite, allowing some capacity for switching to novel prey types. Here, we develop a framework that uses food web topology to model extinction rates that change following other extinctions. In this context, we use 'extinction' to refer to the permanent extirpation of a species from the community, as the effect on the food web should be the same whether the extinction is local or global.

2. Model presentation

Here we summarize the properties of the field of bullets class of models, and discuss extensions that allow for secondary extinctions by incorporating ecological dependencies. We examine how these dependencies affect our ability to predict future biodiversity. We measure biodiversity as the number of species remaining (though we discuss other possibilities), and quantify our uncertainty as the variance in future biodiversity.

2.1. Modelling extinction I: generalized 'field of bullets' (g-FOB) models

Consider a finite set X of species. First, suppose each species $x \in X$ undergoes extinction independently according to a non-stationary death process, at rate $r_x(t)$. We suppose that the present time is $t=0$, and that biodiversity declines under a 'pure death' process, assuming that any contribution from speciation is negligible over the time frame involved. Allowing $r_x(t)$ to vary with time allows for (i) changing environmental conditions (e.g. climate change) that may alter extinction risk, and (ii) changes in the timing or intensity of conservation measures. Let $p_x(t)$ denote the probability that x is extant (has not gone extinct) at time $t \geq 0$. This is given by the well-known formula for a non-stationary Poisson process:

$$p_x(t) = \exp\left(-\int_0^t r_x(u) du\right). \quad (1)$$

Notice that $p_x(t)$ decreases monotonically with increasing t , and it converges to zero—meaning that species x is guaranteed to eventually go extinct—if and only if $r_x(t)$ converges to zero slowly enough that $\int_0^t r_x(u) du$ tends to infinity (e.g. if $r_x(t) = (t+1)^{-\gamma}$ for $\gamma \leq 1$, but not for $\gamma > 1$). This process induces a continuous-time non-stationary Markov process Y_t on the state space 2^X (the set of all subsets of X) defined by $Y_0 = X$ (with probability 1) and

$$\mathbb{P}(Y_t = Y) = \prod_{x \in Y} p_x(t) \cdot \prod_{x \in X-Y} (1-p_x(t)),$$

where $p_x(t)$ is given by Eq. (1). In this extension of the generalized field of bullets (g-FOB) model from Faller et al. (2008), extinction

rates can vary among taxa and with time, but we still assume independence of extinction events between taxa.

2.2. Modelling extinction II: ecology-based 'field of bullets' (eco-FOB) models

We incorporate ecology by using food web topology to define species' dependencies on one another. A food web can be represented as a directed graph (X, A, w) where the set of arcs is A (a subset of $X \times X$) and an arc (y, x) is drawn from each prey y to each of its predators x . w is a weighting function $w : X \times X \rightarrow \mathbb{R}$ that satisfies the constraint:

$$\text{for each } x \in X, \sum_{y \in P(x)} w_{xy} = 1,$$

where $P(x)$ denotes the set of prey species of x —that is $P(x) := \{y \in X : (y, x) \in A\}$. The weight w_{xy} describes the proportional importance of y to x . We can assume that each prey species y has equal weight, or w_{xy} can be quantified as the proportional numerical or energetic contribution of y to the diet of x . It is convenient in what follows to introduce a root vertex ρ (outside of X) that corresponds to the external environment (Allesina and Bodini, 2004). For each source species x that has no incoming arc (i.e. the primary producers in the food web), we add an arc from ρ to x . For an example of a food web topology, see Fig. 1, which shows the Chesapeake Bay estuarine food web (Baird and Ulanowicz, 1989) used for simulations later in this manuscript.

In an ecological network, it is reasonable to assume that the extinction risk of a species x at any time t depends not only on its intrinsic response to threat factors and conservation efforts (collectively described by $r_x(t)$) but also on the fate of the other species with which it interacts. Thus, we can use (X, A, w) to define a modified continuous-time non-stationary Markov pure death process, Y_t on 2^X defined by $Y_0 = X$ (with probability 1) and with

$$\mathbb{P}(Y_{t+\delta} = Y - x | Y_t = Y) = r_x(t, Y)\delta + o(\delta) \tag{2}$$

for each $x \in Y$, and for some rate function $r_x(t, Y)$ and

$$\mathbb{P}(Y_{t+\delta} = Y | Y_t = Y) = o(\delta) \tag{3}$$

for any set Y' that is not a one-element deletion of Y , or equal to Y . Informally, what these last two equations express is that over a sufficiently short period of time (of duration δ), the only possible outcomes are that either there is no new extinction or one of the

species extant at that moment becomes extinct. Moreover, the probability that a particular extant species becomes extinct in that moment depends on which other species are extant.

Like most previous studies of extinctions in food webs (Allesina and Bodini, 2004; Amaral and Meyer, 1999; Dunne et al., 2002), ours focuses on bottom-up extinctions (secondary extinction of predators following extinction of some or all of their prey). This means we do not account for any changes in extinction rate caused by other interaction types, such as top-down effects of predators on prey, exploitation competition or mutualism. Models with explicit population dynamics can allow extinctions driven by other interaction types, and indicate that a focus on bottom-up extinctions underestimate the total number of secondary extinctions (Ebenman et al., 2004). However, these models require detailed knowledge (or many more assumptions) about how these interactions influence extinction rates (Ebenman and Jonsson, 2005). For example, following the extinction of its predator, the extinction rate of a prey species may decrease if it was limited by predation or increase if the predator was suppressing a competing prey species. We focus on the more straightforward bottom-up interactions for the analyses and simulations in this paper, and explore the possible implications of doing so in the Discussion.

The model described by Eqs. (2) and (3) is very general, and without further restrictions it would require a huge number of parameters to fully specify the model for even a moderately sized network. Thus it is helpful at this point to propose a simple parametric description for the rate function $r_x(t, Y)$. We assume that only the prey taxa of x are directly involved in determining its extinction rate, and that the rate function $r_x(t, Y)$ in (2) can be written as

$$r_x(t, Y) = r_x(t) + (q_x(t) - r_x(t)) \cdot (1 - s_{x,Y})^b \tag{4}$$

for a constant $b > 0$ and where $r_x(t) \leq q_x(t)$ and $s_{x,Y} = \sum_{y \in P(x) \cap Y} w_{xy}$ (Fig. 2). Thus the extinction rate of x increases as the proportion of its prey remaining $s_{x,Y}$ decreases. We refer to $r_x(t)$ as the *intrinsic extinction rate* of species x at time t , and to $r_x(t, Y)$ as the *effective extinction rate* of species x at time t (this latter rate is a random variable as it depends on the status of $P(x)$ at time t). The quantity $q_x(t)$ is the maximum rate of extinction of x when all of its prey are extinct; this rate may be very high but we assume it is finite. b is a curvature parameter determining how a predator's extinction rate increases as more of its prey go

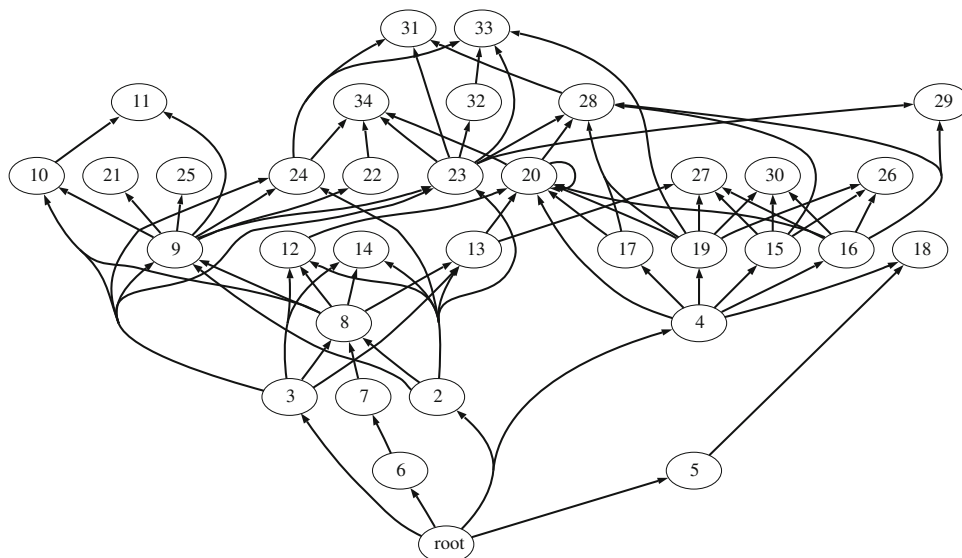


Fig. 1. Structure of the Chesapeake Bay food web (Baird and Ulanowicz, 1989). Trophic links are represented as arrows pointing from prey to predator.

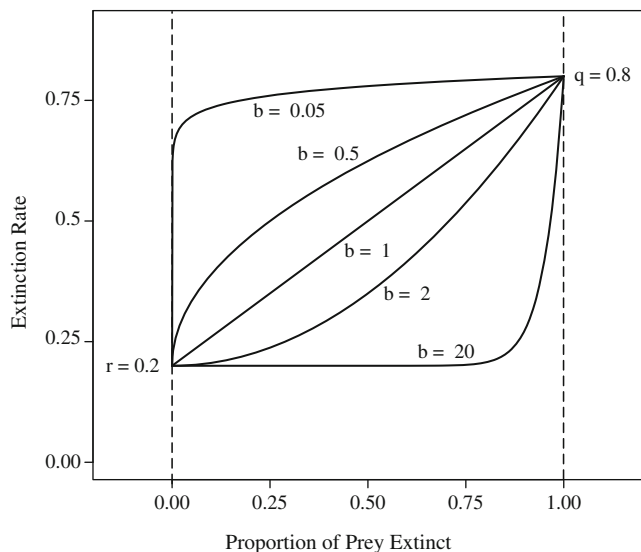


Fig. 2. Parameters of the eco-FOB model. The parameter b (five values shown) determines the trajectory from r (the intrinsic rate of extinction) to q (the maximum effective rate of extinction).

extinct. When $b = 1$, the effective rate of extinction $r_x(t, Y)$ increases linearly from $r_x(t)$ to $q_x(t)$ as the prey of x go extinct. Values of $0 < b < 1$ mean that most of the increase in $r_x(t, Y)$ occurs with the first prey extinctions, while $b > 1$ mean that $r_x(t, Y)$ increases most with the last prey extinctions (Fig. 2). We will assume throughout that for the root vertex ρ does not go extinct, so that $r_\rho(t) = 0$ for all $t \geq 0$. We will refer to this model (defined by (2)–(4)) as the *eco-FOB model*.

The model is now sufficiently well-specified that it can easily be simulated, allowing us to study the effect of including ecology on the distribution of quantities of interest. While the distribution of Y_t (the actual subset of species that are extant at time t) will typically be difficult to measure by simulation when X is large, real-valued quantities that are dependent on Y_t (such as the number of species extant at time t) will generally be much easier to estimate reliably. We can therefore examine how ecological dependencies influence the mean, the variance, or the entire distribution of measures of biodiversity.

3. Analytic properties of a simple eco-FOB model and a matching g-FOB model

We have now defined a model that incorporates species dependencies, but to evaluate the effect of these dependencies we require a suitable formulation of the g-FOB model as a basis for comparison. We are most interested in the variance in future biodiversity, so we would like the g-FOB model to match the trend for mean future biodiversity under the eco-FOB model, allowing differences in variance to be isolated. We could in principle parameterize a single-rate g-FOB model by fitting an exponential function to the expected decline in biodiversity through time. However, this decline can diverge considerably from an exponential under the eco-FOB, so a g-FOB using this rate estimate leads to a poor match to the expected biodiversity decline and inappropriate calculations of its variance.

Our solution is to use the results of the eco-FOB model itself to construct a ‘matching’ g-FOB model. We calculate the trend in mean extinction rate over time for each species in the food web. We then use these rates to simulate extinctions under a g-FOB model in which extinction rates vary among species and with time. This model produces trends for mean future biodiversity

that closely match the eco-FOB model, allowing variances to be compared and the effect of ecological dependencies on variance to be isolated.

In this section, we consider a special case of the eco-FOB model in which:

- $b = 1$;
- $r_x(t) = r$ for all species $x \in X$ and $t \geq 0$;
- $q_x(t) = q$ for all species $x \in X$ and $t \geq 0$;

where $q \geq r$. Under these conditions, Eq. (4) simplifies to

$$r_x(t, Y) = q - (q - r) \cdot s_{x, Y}. \tag{5}$$

As in the g-FOB setting, let $p_x(t)$ denote the probability that species x is extant at time t in this eco-FOB model. Thus, if the random variable T_x is the time until the extinction of species x , $p_x(t) = \mathbb{P}(T_x > t)$. We will derive equations for $p_x(t)$ under the eco-FOB model, and a matching g-FOB model.

Let $\bar{r}_x(t)$ be the expected value of the instantaneous extinction rate $r_x(t, Y)$ of species x . From Eq. (5), we have

$$\bar{r}_x(t) = q - (q - r) \cdot \sum_{y \in P(x)} w_{xy} p_y(t), \tag{6}$$

where $p_y(t)$ is the probability that y is extant at time t .

Similarly, let $\bar{r}_x^x(t)$ denote the expected value of the instantaneous rate $r_x(t, Y)$ of species x conditional on x being extant at time t . From Eq. (5) we have

$$\bar{r}_x^x(t) = q - (q - r) \cdot \sum_{y \in P(x)} w_{xy} p_y^x(t), \tag{7}$$

where $p_y^x(t)$ is the conditional probability that y is extant at time t given that x is extant at time t .

Note that, in general, we have

$$p_x(t) \neq \exp\left(-\int_0^t \bar{r}_x(u) du\right) \neq \exp\left(-\int_0^t \bar{r}_x^x(u) du\right) \neq p_x(t), \tag{8}$$

as we will show by a simple example below.

3.1. Example: two special cases

We now consider two very special cases of the eco-FOB model that are simple enough that we can explicitly calculate the relevant rate functions ($\bar{r}_x(t)$ and $\bar{r}_x^x(t)$) and see how they are related.

- First, suppose that either (i) the network is arbitrary and $r = q$, or (ii) the network consists only of the root vertex and the first trophic level, so that species’ extinctions are independent. In either case, the eco-FOB model is stochastically identical to a g-FOB model with a single extinction rate r .
- Second, consider a network that consists of a directed chain $0 \rightarrow 1 \rightarrow 2 \rightarrow \dots \rightarrow n-1 \rightarrow n$, where 0 is the root vertex (with extinction rate 0 as usual) and where all other vertices have intrinsic extinction rate $r < q$ for all $t \geq 0$. In this case, it can be shown that, for all integers $x \geq 1$:

$$p_{x+1}(t) = e^{-rt} p_x(t) - e^{-qt} \int_0^t e^{(q-r)u} p_x'(u) du. \tag{9}$$

A formal justification of Eq. (9) is provided in the Appendix.

To specialize this second case even further, suppose that $n = 2$ (a chain of length 3, including the root node 0). Thus we have the simplest possible non-degenerate ecological network. For $x = 1$ we have $p_x(t) = e^{-rt}$, while, for $x = 2$, Eq. (9) gives

$$p_x(t) = e^{-2rt} + \frac{r}{2r-q} (e^{-qt} - e^{-2rt}). \tag{10}$$

The unconditional and conditional rate functions $\bar{r}_x(t)$ and $\bar{r}_x^x(t)$ for $x=2$ are given from (6) and (7) as

$$\bar{r}_x(t) = q - (q-r)e^{-rt} \quad \text{and} \quad \bar{r}_x^x(t) = q - \frac{q-r}{1+Y_x(t)},$$

where $Y_x(t) = (r/(2r-q))(e^{2r-qt} - 1)$, and where Eq. (10) and Bayes' rule is used to derive the conditional probability $p_y^x(t)$ in (7) for $x=2, y=1$. This example suffices to establish the inequalities recorded in (8). An interesting contrast between $\bar{r}_x^x(t)$ and $\bar{r}_x(t)$ is that, as $t \rightarrow \infty$:

$$\bar{r}_x(t) \rightarrow q \quad \text{while} \quad \bar{r}_x^x(t) \rightarrow \min\{2r, q\},$$

because $\bar{r}_x^x(t)$ is based only on the extinction rates of x conditional on its having survived to time t .

3.2. Alternate measures of biodiversity

The biodiversity of an ecosystem can be measured in a variety of ways. Recalling that Y_t is the random subset of species in X extant at a future time t , we can consider the number $N_t = |Y_t|$ of species extant at time t , as we have done in this paper. Depending on the unit of interest to conservation, X may refer to levels of biological organization below (population or subspecies) or above the species level (e.g. genus or aggregated 'trophospecies' that occupy the same role in the food web). We can also generalize from species richness to the sum ψ_t over those species in Y_t of species-specific weights (e.g. weighting species by trophic level or some other quantity of interest). That is

$$\psi_t = \sum_{x \in X} \lambda_x \theta_x(t),$$

where the Bernoulli random variable $\theta_x(t)$ is defined by

$$\theta_x(t) := \begin{cases} 1 & \text{if } x \in Y_t \text{ (i.e. species } x \text{ is extant at time } t), \\ 0 & \text{otherwise;} \end{cases}$$

and where the species-specific weights λ_x are non-negative. The special case $\psi_t = N_t$, corresponds to setting $\lambda_x = 1$ for all $x \in X$.

Another option is phylogenetic diversity (PD), which describes how much evolutionary history is captured by a group of species (Faith, 1992; Gernhard et al., 2008; Hartmann and Steel, 2007; Steel et al., 2007; Witting et al., 2000). Future biodiversity can be measured as the PD_t of the extant species at a future time t in some evolutionary tree—in this case, a phylogenetic X -tree $T=(V,E)$ with branch lengths λ . PD_t is the sum of the branch lengths of the subtree that is spanned by the leaves in Y_t and the root of the tree. Formally

$$PD_t = \sum_{e \in E} \lambda_e Z_e(t),$$

where the random variable $Z_e(t) = 1$ precisely if at least one species in Y_t is a descendant of e , and $Z_e(t) = 0$ otherwise. Note that ψ_t is also a special case of PD_t where the tree is a 'star tree' with one interior vertex and weighted edges.

3.3. Comparing the distribution of ψ_t under eco-FOB and a matching g-FOB

We wish to compare the mean and variance of ψ_t under two matching models:

1. An eco-FOB model of the special type considered in this section where $b=1, r_x(t)=r, q_x(t)=q > r$.
2. A matching g-FOB model where the extinction rate of each species x at time t is set equal to a mean rate derived from the eco-FOB model. For our purposes we focus on the conditional mean rate $\bar{r}_x^x(t)$, which provides the best match to mean ψ_t .

The eco-FOB model: Under this model, the mean and variance of ψ_t are given by

$$\mathbb{E}[\psi_t] = \sum_{x \in X} \lambda_x p_x(t) \tag{11}$$

and

$$\text{Var}(\psi_t) = \sum_{x \in X} \lambda_x^2 p_x(t)(1-p_x(t)) + \sum_{x, x' \in X, x \neq x'} \lambda_x \lambda_{x'} \text{Cov}[\theta_x(t), \theta_{x'}(t)], \tag{12}$$

where Cov refers to covariance ($\text{Cov}[\theta_x(t), \theta_{x'}(t)]$ is the probability that both x and x' are extant at time t minus the product of the two separate probabilities that each are extant at time t).

The matching g-FOB model: In this model, ψ_t has mean:

$$\mathbb{E}[\psi_t] = \sum_{x \in X} \lambda_x \bar{p}_x(t) \tag{13}$$

and variance

$$\text{Var}[\psi_t] = \sum_{x \in X} \lambda_x^2 \bar{p}_x(t)(1-\bar{p}_x(t)), \tag{14}$$

where

$$\bar{p}_x(t) = \exp\left(-\int_0^t \bar{r}_x^x(u) du\right),$$

substituting $\bar{r}_x(t)$ for $\bar{r}_x^x(t)$ if one wished to use the unconditional mean rate.

Regarding the distribution of ψ_t at a given time t under the matching g-FOB model, we can apply the Central Limit Theorem provided that (i) the number of species is large, (ii) any variation in the $\bar{p}_x(t)$ values with x is not too severe, and (iii) t is not so large that most diversity has died out. In that case, ψ_t will be approximately normally distributed, with its mean and variance given by (13) and (14), respectively.

The analysis of phylogenetic diversity (PD_t) results in only slightly more complex formulae—we have

$$\mathbb{E}[PD_t] = PD_0 - \sum_{e \in E} \lambda_e \cdot \prod_{x \in C(e)} (1-\bar{p}_x(t)),$$

where $C(e)$ is the set of leaf taxa (subset of X) descendant from e (this formula, and one also for the variance are provided in Faller et al., 2008). A similar asymptotic normal distribution holds for future phylogenetic diversity (PD_t), though the conditions and proof are more complex (Faller et al., 2008).

Although the expected value of ψ_t under the two models is very close (but not identical), the variance is quite different and typically much larger under the eco-FOB model. To understand this difference, it is helpful to compare Eqs. (12) and (14).

Recall that under the matching g-FOB model, $\text{Cov}(\theta_x(t), \theta_{x'}(t)) = 0$ for all distinct pairs $x, x' \in X$ because of the independence assumption implicit in the g-FOB model. For the eco-FOB model, we also have that $\text{Cov}(\theta_x(t), \theta_{x'}(t)) = 0$ if there is no species y that has both a directed path to x and a directed path to x' (this follows because in the eco-FOB model, the effective extinction rate $r_y(t, Y)$ of any species y at time t is determined (just) by the random variable Y , which consists of the subset of the prey species of x that are extant at time t). However, in contrast to the matching g-FOB, in the eco-FOB, many of the covariance terms will typically be positive, because of the dependencies between pairs of species under the eco-FOB model. This in turn which will tend to inflate the variance of ψ_t over what it would be in a matching g-FOB model.

We end this section by formally describing how pairs of species are stochastically dependent in the eco-FOB model, as this is relevant to the covariance issue that we have just discussed. We will assume, for the remainder of this section, that the ecological network is acyclic (i.e. it has no directed cycles). Given a subset S of X , define the history of S up to time t , denoted $h_t(S)$, to be the

random variable that assigns to each species $s \in S$ the value $\max\{t' \leq t : s \in Y_{t'}\}$. That is, s is assigned the value t if s is extant at time t ; otherwise, s is assigned the time at which it becomes extinct. For any two species, the joint probability that both are extant (or not) at time t is determined by the history of a particular subset of species that lies below the two species in the network, as the following proposition makes precise:

Proposition 1. For any two species x and x' in X let $C_{x,x'}$ be a set of species $y \in X$ for which (i) there is a path from y to x and a path from y to x' , and (ii) y is maximal with this property (i.e. if y' is any other element of X with this property then there is no path from y' to y). Then under the eco-FOB model, the random variables $\theta_x(t)$ and $\theta_{x'}(t)$ are conditionally independent given $h_t(C_{x,x'})$.

4. Simulated extinctions in complex food webs

The arguments above demonstrate that incorporating ecological dependencies into models of extinction can increase our uncertainty about the rate of biodiversity loss. To evaluate the magnitude of this effect in complex ecological networks that cannot be treated analytically, we simulated extinctions in real and model food webs using the eco-FOB and matching g-FOB models. First, we examined the effect of ecological dependencies on variance in future biodiversity using a well-studied empirical food web—the Chesapeake Bay estuary. We also used this food web to explore how varying the assumptions of the eco-FOB model influence the outcome. Second, we applied the eco-FOB model to a large number of simulated food webs to assess which structural properties of food webs make them likely to show this effect of ecological dependencies.

The Chesapeake Bay estuarine food web (Fig. 1) contains 33 species and includes estimates of edge weights (interaction strengths between species) that are based on multiple seasons of data collection (Baird and Ulanowicz, 1989). Previous simulation studies have predicted that this food web is neither especially prone nor especially resistant to secondary extinctions (Allesina and Bodini, 2004; Dunne et al., 2002).

For each analysis, we simulated 2000 extinction sequences under the eco-FOB model, using Eq. (4). We divided time into discrete intervals of 0.01 units and calculated the conditional extinction rate $\bar{r}_x^x(t)$ for each species at each time interval as the average over all simulations in which the species was extant at time t . We then used these time-varying conditional rates for 2000 simulations under the g-FOB. This results in a trend for mean richness through time that is very similar to the eco-FOB (Fig. 3), allowing us to isolate the difference in variance. We

quantified the magnitude of increased variance due to ecology as the maximum difference between the variance in species richness under the eco-FOB and matching g-FOB models at any time during the simulations (Fig. 4). We refer to this measure as the 'variance inflation' (VI), referring to the general increase in variance under eco-FOB compared to g-FOB (as defined, $VI \geq 0$, although it is possible for variance to be lower under the eco-FOB at some time during the simulation). VI was highly correlated with other possible measures such as the average difference in variance across all time steps.

We first simulated the eco-FOB model with parameter values $r = 0.2$, $q = 0.8$ and $b = 1$ and all links weighted equally. We then explored parameter space by carrying out simulations at a range of combinations of b ($\log b = -3, 2.6 \dots 2.6, 3$) and q ($q = 0.2, 0.4 \dots 1.8, 2.0$), all with $r = 0.2$. We also examined two interesting variants of the eco-FOB model. First, we used the first set of parameters above ($r = 0.2$, $q = 0.8$ and $b = 1$) but weighted links by each consumer's empirical diet proportions (meaning a species' extinction rate increases more when prey making up a greater proportion of its diet go extinct). Next, we calculated each species' trophic position following Levine (1980), and performed simulations assuming that the extinction rates r and q are

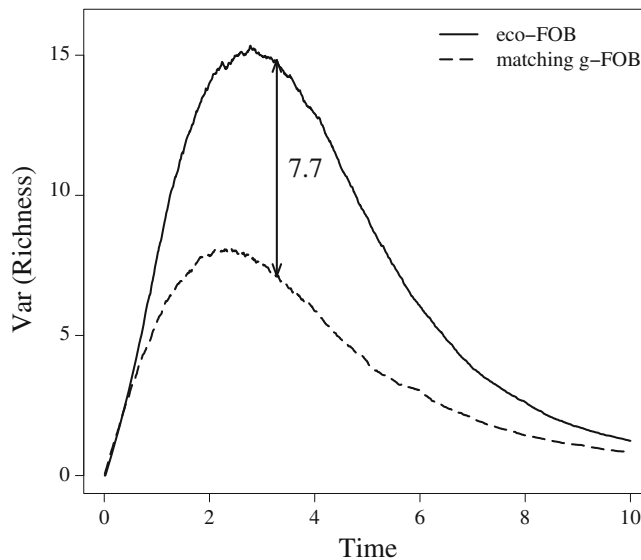


Fig. 4. Variance in species richness through time under the eco-FOB and matching g-FOB models. The double-headed arrow indicates the magnitude of variance inflation (VI).

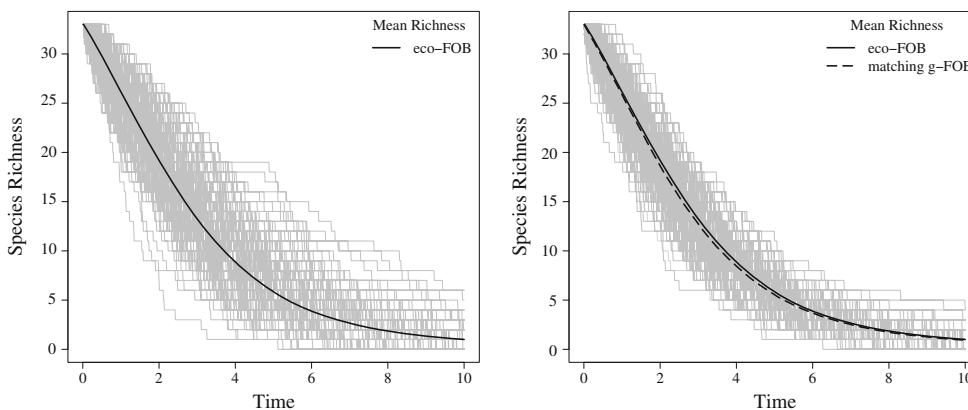


Fig. 3. Species richness through time under the eco-FOB (left) and matching g-FOB (right) models. The trajectories for 200 individual simulations (grey lines) and the mean richness through time are shown. Note the similar trends for mean richness (the trend under the eco-FOB model is also shown on the right for comparison) and the greater spread around the mean under the eco-FOB model.

proportional to trophic position ($r_x = 0.08 * TP_x$; $q_x = 0.6 + 0.08 * TP_x$). These coefficients lead to average rates across species matching the $r_x = 0.2$ and $q_x = 0.8$ used in other simulations, making the expected decline in mean biodiversity comparable.

We found that the general result of variance inflation under the eco-FOB model is robust to variations in many of its assumptions. VI occurs unless $q = r$ (in which species extinctions are independent as under the g-FOB model). Increasing q while keeping r constant led to substantial increases in VI , while varying the parameter b had subtler effects. Generally, at any given q , smaller values of b (i.e. a saturating rather than an accelerating increase in the predator's extinction rate as its prey become extinct) led to slightly larger VI (Fig. 5). Weighting edges by empirical diet proportions led to a slight increase in VI , while VI decreased when we assumed that the extinction rates r and q were positive functions of trophic position (Fig. 6).

These simulations indicate that while the magnitude of VI can vary, the effect is robust to many assumptions of the eco-FOB model. To identify features of food webs that lead to greater variance inflation, we constructed food webs from a simple stochastic model that is similar (but not identical) to the evolutionary model of Amaral and Meyer (1999). This model is

more complex than stochastic models such as the niche model (Williams and Martinez, 2000), allowing us to independently manipulate more aspects of food web structure. The input parameters for the model are the initial number of species S , the number of trophic levels TL_{max} , the expected number of prey species per predator nw , the expected proportion of omnivorous interactions pO and the expected proportion of basal (source) species pB .

We fixed $S = 30$ for all simulations, focussing on generating variability in features other than species number. We repeated the following process 200 times, generating a wide variety of food web structure. First, we randomly assigned $TL_{max} = 2, 3$ or 4 (with probabilities 0.2, 0.3 and 0.5), sampled integer nw from 2 to 5 with all probabilities = 0.25, sampled pO from a uniform distribution between 0 and 0.3 and sampled pB from a beta distribution with shape parameters 1.5 and 3. Given these input parameters we assigned the S species to trophic levels with probability pB for the first trophic level and $(1 - pB)/(TL_{max} - 1)$ for higher trophic levels. We sampled each species' niche width (number of prey) from a Poisson distribution with parameter nw . Finally, we assigned prey to each predator with trophic level TL_i , sampling its prey from trophic level $TL_i - 1$ with probability $1 - pO$

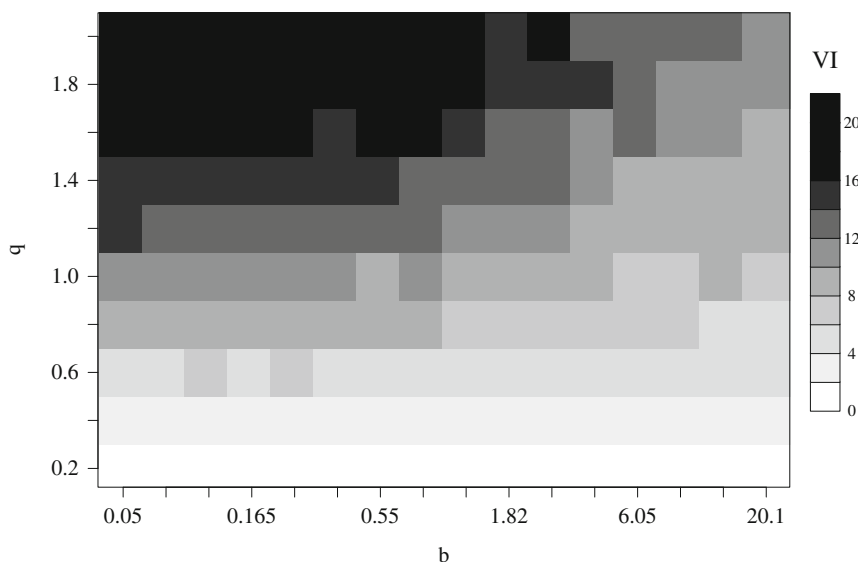


Fig. 5. Strength of the variance inflation effect across the parameter space of the eco-FOB model. Simulations were performed (see text for details) at 10 values of the maximum extinction rate q and 16 values of the curvature parameter b (spaced evenly in log space). In all simulations $r=0.2$, so the bottom row of values ($q = 0.2$) is equivalent to the g-FOB model. Dark shading indicates a greater magnitude of VI , as shown on the scale to the right.

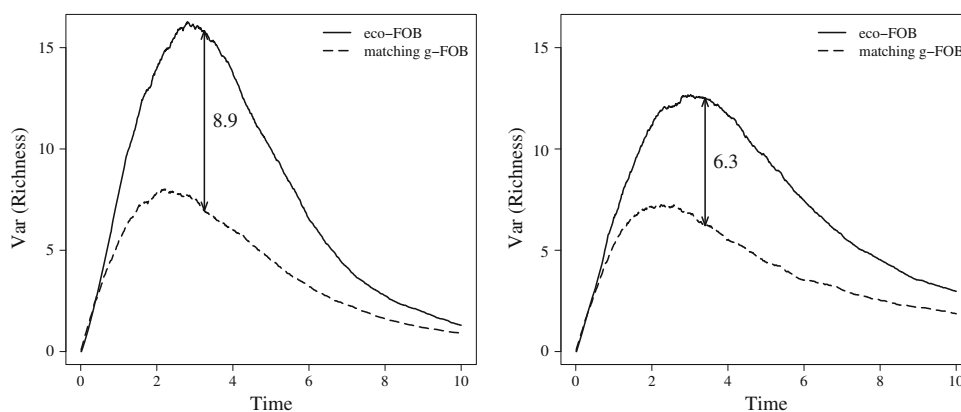


Fig. 6. Variance inflation effect under two particular versions of the eco-FOB model. In the left panel, links in the food web were weighted by diet proportions, so the extinction of energetically important prey had a greater impact on a predator's extinction rate. In the right panel, extinction rates were made proportional to trophic position as described in the text.

and from trophic levels TL_i and $TL_i - 2$ with probabilities $pO/2$. For each model food web, we simulated extinctions as in the first simulation with the Chesapeake food web ($r = 0.2, q = 0.8, b = 1$ and links weighted equally) and calculated VI .

We quantified structural variables thought to affect food web robustness, to assess whether they also influence variance inflation. For each of the 200 food webs we calculated connectance ($C = L/S^2$, where L is the total number of links), B (the proportion of basal species), and $VulSD$ (the standard deviation of species' 'vulnerability', or their number of predators normalized by L/S). $VulSD$ will be small if species tend to have similar numbers of other species depending on them, and large if some species are depended on by many more species than others (Williams and Martinez, 2000). We quantified *redundancy* as the proportion of trophically identical species sharing all predators and prey (Quince et al., 2005). We also calculated an index that directly quantifies how prone food webs should be to secondary extinctions by identifying bottlenecks (species whose extinction leads to the loss of many species above them). First, we computed dominator trees following Allesina and Bodini (2004), which identify species that are wholly dependent on other species to remain connected to the food web. We then calculated the 'error susceptibility' index (ES), which quantifies the probability that a randomly chosen species will become extinct following the extinction of another randomly chosen species. This is a useful index because food webs with low ES values should have high robustness as defined in topological analyses of extinctions in food webs (Dunne et al., 2002; Dunne and Williams, 2009).

These variables showed numerous correlations both with each other and with VI (Table 1, above diagonal). The proportion of basal species, B , was most strongly correlated with VI ($r = -0.937$, Fig. 7). Of the other variables investigated, C and ES were positively correlated with VI and *redundancy* was negatively correlated with VI . However, these relationships are confounded by the strong correlations of these variables with each other and with B . It should be noted that the largest values of B in the simulated webs were outside the range of values (0.04–0.32) observed in a sample of empirical food webs (Williams and Martinez, 2000), while distributions of the remaining variables were generally similar to observed distributions.

Rather than attempt to statistically remove the effect of B to evaluate the other variables, we elected to simulate a second set of 200 food webs that each had three basal species ($B = 0.1$). We did this by setting $pB = 0.1$, varying the other input parameters as before, and rejecting any food webs with $B \neq 0.1$. In this second set of food webs, relationships between VI and the other variables were considerably weaker (Table 1, below diagonal), suggesting that most of the correlations in the first set were driven by variation in B . By far the strongest correlate of VI in this set of food webs was $VulSD$, the standard deviation of species' normalized predator number ($r = 0.517$, Fig. 7).

5. Discussion

Our findings demonstrate that accounting for ecological dependencies may reduce our ability to predict future biodiversity.

Table 1
Pearson correlations among VI and several structural properties of simulated food webs^a.

	VI	C	ES^b	<i>redundancy</i> ^b	$VulSD^b$	B
VI	–	0.604^c	0.421	–0.575	0.049	–0.937
C	–0.036	–	–0.239	–0.580	–0.403	–0.657
ES	–0.031	–0.835	–	–0.088	–0.082	0.279
<i>redundancy</i>	0.153	–0.282	0.279	–	0.370	0.727
$VulSD$	0.735	–0.386	0.324	0.367	–	0.108
B^c	–	–	–	–	–	–

^a Correlation coefficients within the first set of 200 simulated food webs (above diagonal) and for the set with all $B=0.1$ (below diagonal). Boldface indicates statistically significant correlation at a Bonferroni-adjusted $\alpha = 0.0033$ (0.05/15, above diagonal) or $\alpha = 0.005$ (0.05/10, below diagonal).

^b Log-transformed for analysis.

^c Invariant for second set of simulated food webs.

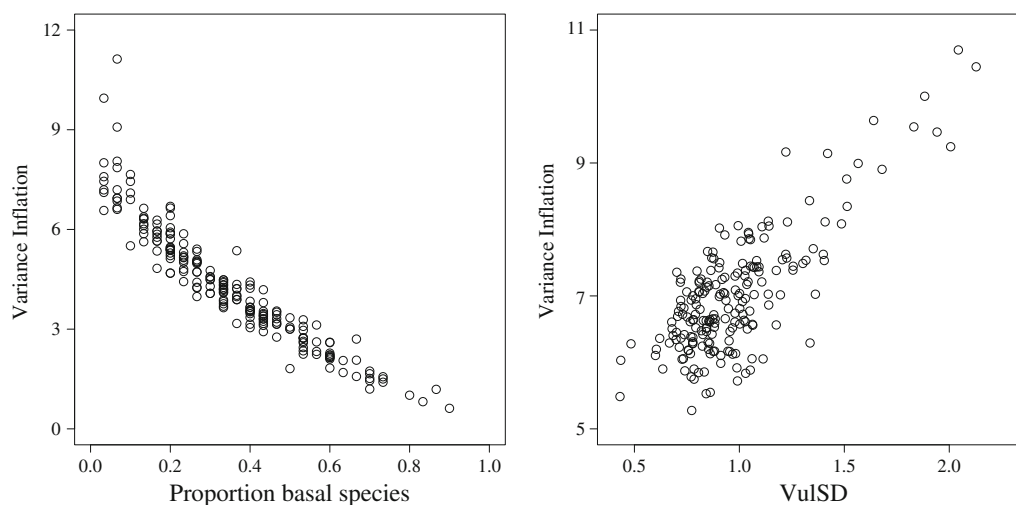


Fig. 7. Relationships between VI and structural features of simulated food webs. Left, VI vs. B based on the first set of simulations. Right, VI vs. $VulSD$ based on the set of simulations with all $B=0.1$.

Of course, the act of identifying these dependencies itself does not change the true variance; it simply exposes the intrinsic unpredictability of food web collapse. An intuitive explanation of variance inflation is that interacting species in a food web are not independent, and the extinction of one makes further extinctions more likely. We will first discuss the significance of the variance inflation we have described, then discuss the potential implications of considering only bottom-up secondary extinctions.

The generalized field of bullets model makes the crucial assumption that the fate of one species does not affect the probability that any other species will go extinct. Thus, while the flexibility of this model allows for time- and taxon-varying extinction rates, it ignores the potentially important effects of species interactions. The most obvious implication of the process investigated here—bottom-up secondary extinction—is that biodiversity will decline more rapidly than if predator extinction risk did not increase when prey went extinct. In the eco-FOB model we present here, this simply means that for a given r_x , biodiversity will decline faster if $q_x > r_x$ than if $q_x = r_x$, an outcome that is implicit in most analyses of secondary extinctions in food webs. In this paper we have identified a less obvious consequence of species dependencies: the increased uncertainty around predictions of future biodiversity, which we quantify as VI . While real estimates of r_x , q_x and b would be necessary to estimate VI in real systems, we are able evaluate which features of the model and which features of food webs are associated with relatively larger variance inflation. Our ‘matching g-FOB’ approach allows us to account for the faster loss of biodiversity due to dependencies, and to isolate the effect of dependencies on the variance in future biodiversity.

Our analyses of the Chesapeake Bay food web show that variance inflation is robust to changes in the parameterization and assumptions of the eco-FOB model. VI occurs whenever there is scope for extinction rate to increase as prey go extinct (i.e. if $q_x > r_x$), and its magnitude increases strongly with the maximum extinction rate q_x . There were subtler but potentially interesting effects when we varied the curvature of the function describing how a species’ extinction rate increases as progressively more of its prey go extinct. VI tended to be higher when extinction rate increased fastest with the first few prey extinctions. This scenario implies that species have a low resistance to the loss of any prey species, perhaps because different prey provide non-substitutable resources. Conversely, VI was lower when extinction rate increased fastest with the final few prey extinctions, as we might expect if species are flexible foragers that can switch effort to alternate prey types. At this point we can only speculate as to how real species’ extinction rates change when their prey go extinct, but variance inflation should occur under any increasing function where $r_x < q_x$.

Two variants on the eco-FOB model yielded interesting patterns. In the Chesapeake Bay food web, incorporating empirically estimated link strengths led to a slightly higher VI . If certain prey species make up a large part of the diet of many predators, the rate of species loss will largely depend on when these important species go extinct, similar to the effect of large $VulSD$. It remains to be seen whether other food webs also have link strength distributions that tend to increase VI .

We found that when the extinction rates r_x and q_x were positive functions of trophic position, VI was notably smaller. This reduction in VI can be explained by the tendency of predators to go extinct before their prey in this scenario. When the more basal species on which most other species depend also have the lowest extinction rates, they will tend to outlive most of the other species and thus reduce the number of secondary extinctions. This version of the model is consistent with the evidence in both

aquatic and terrestrial ecosystems that species with higher trophic position have higher extinction risks or threat levels (Pauly et al., 1998; Purvis et al., 2000). This tendency of predators to have higher extinction rates than their prey—usually attributable to a combination of their higher rates of exploitation by humans, larger body sizes and lower population sizes—should reduce but certainly not eliminate the variance inflation effect we have described.

Our simulations with model food webs allowed us to identify structural features of food webs that affect the magnitude of variance inflation. Of a number of interrelated variables, the strongest correlate of VI was the proportion of basal species in the food web (B). This can be interpreted as both an ecologically meaningful result and a mathematical banality. On the one hand, food webs with many basal species will tend to contain fewer of the bottlenecks in energy flow that make more top-heavy food webs highly sensitive to the loss of particular species. On the other hand, source species in the eco-FOB model have no prey aside from the root, so their fates are independent of any other species just as they would be under the g-FOB. As B increases, the eco-FOB model thus converges on the g-FOB model, making it unsurprising that VI tends toward zero.

The second set of simulations accounted for the relationship between VI and B by forcing B to be equal for all food webs. We found that when there was no variation in B , relationships between VI and other variables such as connectance and redundancy effectively disappeared, and $VulSD$ was the only strong correlate of VI . This result is also intuitive and biologically intriguing. Food webs with high $VulSD$ have some (typically basal) prey species with many predators, and others with very few, while food webs with low $VulSD$ have a more equitable distribution of numbers of predators. Food webs with high $VulSD$ should therefore tend to feature ‘keystone’ species on which many other species ultimately depend. The dynamics of species loss in these food webs will be highly dependent on precisely when these important species go extinct, leading to high VI . It is perhaps surprising that there was no relationship between VI and ES , the variable that attempts to measure the occurrence of bottlenecks directly (Allesina and Bodini, 2004). However, ES only includes information about ‘dominators’, species whose extinction would leave another species disconnected from the food web. $VulSD$, while a crude measure of food web structure, may better account for the fact that many species partly depend on species that do not meet the dominator criteria. As there was no relationship between connectance and VI , the magnitude of variance inflation seems to depend on how links are distributed among species rather than on link density per se.

Before we conclude, it is necessary to discuss the implications of our focus on bottom-up food web interactions in this study. This practice, which is common in analysis of extinction in food webs, is due to our ignorance about how other interaction types affect extinctions in complex food webs, rather than any belief that secondary extinctions due to other interactions types do not occur. Ebenman et al. (2004) found that moving from a topological, bottom-up analysis to one that incorporates population dynamics (and thus the potential for top-down or other types of coextinctions) increased the total number of secondary extinctions. However, it remains unknown how such interactions would impact the variance in future biodiversity. Of particular importance for our model is the fact that when all secondary extinctions are transmitted ‘up’ the food web—from prey to predator—all covariances between species’ fates are necessarily either zero or positive. If most covariances were negative, species interactions will actually tend to reduce variance in future biodiversity. Incorporating processes other than bottom-up secondary extinctions could lead to more negative covariances

(decreased extinction rate following the extinction of a competitor or predator) or positive covariances (increased extinction rate following the extinction of a mutualist or a predator that allowed coexistence of competing prey species). We can predict that VI will be highest in communities heavily biased toward positive interactions—such as plant-pollinator mutualism networks—and lowest in highly competitive communities with mainly negative interactions.

While a full, empirically driven parameterization of the eco-FOB model is likely to remain out of reach, it may be possible to estimate properties such as the relationship between extinction rate and trophic position, or the functional form of the increase in extinction rate due to prey extinctions (Fig. 2). When we reach a point of being able to properly estimate the variance in future biodiversity in food webs, we can evaluate the practical implications and plan conservation strategies to account for this level of uncertainty. In the meantime, we should remember that more information may not improve our predictive ability in the case of intrinsically variable processes such as the collapse of food webs.

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Appendix A. Proof of Eq. (9)

Recall that T_x is the random variable that measures the time to extinction of species x . We have

$$p_{x+1}(t) = \mathbb{P}(T_{x+1} > t) = \int_0^\infty \mathbb{P}(T_{x+1} > t | T_x = u) f_x(u) du,$$

where $f_x(u)$ is the probability density function for T_x . Splitting up the range of integration into the two intervals $[0, t)$ and $[t, \infty)$ and noting that $\mathbb{P}(T_{x+1} > t | T_x = u) = e^{-rt}$ when $u > t$, gives

$$p_{x+1}(t) = \int_0^t \mathbb{P}(T_{x+1} > t | T_x = u) f_x(u) du + e^{-rt} p_x(t). \quad (15)$$

Now, $\mathbb{P}(T_{x+1} > t | T_x = u) = e^{-q(t-u)} \cdot e^{-ru} = e^{-qt} \cdot e^{(q-r)u}$ and $f_x(u) = (d/ds)\mathbb{P}(T_x \leq s)|_{s=u} = -p'_x(u)$. Substituting these into Eq. (15) gives Eq. (9).

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