Quantization of ecological interactions yields insights into food web assembly and dynamics

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abstract goes here

Introduction

Amazing words. The best words.

Model Description

The ENIgMa Model We aim to examine how interdependencies between species in communities either aid or inhibit both assembly and extinction over long timescales, and specifically how ecosystem engineers contribute to these dynamics. We approach these questions by considering both multiple types of interactions between species – including but not limited to trophic interactions – as well as indirect interactions between species and 'objects' that are introduced by the presence of ecosystem engineers. Introduced objects are to be considered in the abstract, and serve to represent either resources, habitat, or environmental alterations that are introduced by the engineers that make them, and can be utilized by others.

The ENIgMa model consists of four directed interactions: e: eat, which specifies a dependency involving biomass flow, n: need, which specifies a dependency that does not involve biomass flow, i: ignore, the null interaction, and m: make, which connects a species to an object that it engineers. 'Objects' are interactive components that can be made by ≥ 1 species, and eaten, needed, or ignored by the others. Objects can represent actual molecules or tissues that a species introduces into the environment (e.g. oxygen respired by plants) or a habitat that a species provides (e.g. as an elephant clears savannas of trees, facilitating shrubs).

The four directed interaction types describe specific dependencies that one species/object has on another, however it is the coupling of two opposing directed interactions that describe traditional and familiar ecological relationships (listed in Table 1). For example, an $e \leftrightarrow i$ interaction describes a typical predator-prey relationship, where species 1 eats species 2, whereas species 2 ignores species 1. Of course, a prey's abundance does not *ignore* the effects of predation, however our framework operates at the scale of presence-absence rather than abundance, and we assume that if both species are in the system, they have positive population densities, such that the state of the prey's occurrence effectively ignores the predator. The $e \leftrightarrow n$ and $n \leftrightarrow n$ interactions describe service-resource and service-service mutualisms, respectively. In
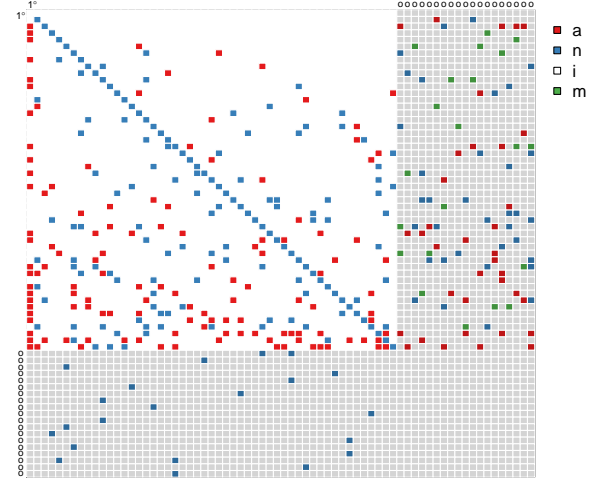

Figure 1: An example of the source pool interaction matrix where $\mathcal{S} = 50$. Species and objects are aligned across the rows and columns; objects are shaded and labeled by 'o' to distinguish them from species. The interaction recorded in row i and column j describes the directed interaction from species/object i to species/object j. The first row/column represents the basal resource; species that assimilate the primary resource are capable of primary production. Species interact with other species and/or objects; objects only interact with their engineers by 'needing' them; objects do not interact with other objects.

the case of the former, one species interacts by way of a trophic interaction, whereas the other is provided a non-trophic need, such is the case in a plant-pollinator relationship. Unique to models of ecological networks, the $m \leftrightarrow n$ interaction describes ecosystem engineering, where a species makes an object, whereas the presence of the object 'needs' the presence of the species that makes it to exist. Objects can be utilized by other species in the community, providing an indirect dependency that could be facilitated by multiple species (many engineers produce the same object) and/or used by multiple species (many species assimilate or need the same object).

We examine the assembly process of a novel community that emerges from a species pool. The pool is a composite of species and objects that seeds the community, and may be imagined to be multiple pools that needn't be capable of coexisting. In the following sections we will describe 1) how we build the species and their interactions within the source pool, and a set of simple rules for

2) species assembly, and 3) local extinction.

Building the source pool The source pool is generated by first setting the number of species $\mathcal{S}$ and calculating how many objects $\mathcal{O}$ will be generated, which is stochastic from one source pool to the next as a function of the mean number of objects expected per species, $\mathrm{E}\{\mathcal{O}_i\} = \eta$. For each species, a set number of objects is drawn from $\mathrm{Poiss}(\eta)$, such that the expected proportion of species that are engineers (species that make objects such that $_i > 0$) is $1 - \mathrm{e}^{-\eta}$. If each species makes unique objects, the number of possible objects is $\mathcal{O}_{\max} = \mathcal{S}\eta$, however because multiple species can make the same object, $\mathcal{O} \leq \mathcal{O}_{\max}$. To determine whether objects are uniquely made or made by multiple engineers, we assign objects by randomly drawing independently object IDs from $[1 : \mathcal{O}_{\max}]$ without replacement for each engineer; unassigned objects are discarded. The expected total number of objects is thus

$$\mathrm{E}\{\mathcal{O}\} = \mathcal{S}\eta \left(1 - \frac{1}{\mathrm{e}}\right). \tag{1}$$

where e is Euler's number. The $m \leftrightarrow n$ interactions are thus determined upfront, and the proportion of 'make' interactions in the $\mathcal{S} + \mathcal{O} \times \mathcal{S} + \mathcal{O}$ interaction matrix is calculated as

$$\mathrm{E}\{p_m\} = \frac{\eta}{S\left(1 + \eta - \frac{\eta}{\mathrm{e}}\right)^2}. \tag{2}$$

For a given species-object interaction, the species 'makes' the object, and the object 'needs' the species that makes it.

Eat and Need interaction probabilities (p_e and p_n, respectively) are model inputs, the Make interaction probability (p_m) is calculated as described above, and the Ignore interaction probability is given by $p_i = 1 - p_a + p_n + p_m$. Pairwise interaction probabilities between both species and objects are then calculated as shown in Table I.

We build the interaction matrix for the source pool (figure 1) according to the following steps: We impose the rule that row/column 1 of the pool interaction matrix is the basal resource from which primary producers derive their energy. Thus, an eat interaction in row i of column 1 means that consumer i is capable of primary production; conversely, it is assumed that the basal resource does not interact with any species/objects. The basal resource is assumed to be always available, and cannot be removed during the assembly process. Next, we randomly assign species-species and species-object interactions with eat, need, and ignore dependencies based on the pairwise probabilities described in Table I. Species that do not have an eat interaction after assignments are made are assumed to be primary producers. The only input to build the interaction matrix of the source pool includes 1) the expected number of objects per species η, and 2) the probabilities p_e and p_n.

Colonization and Extinction The interaction matrix for the source pool specifies how each species inter-
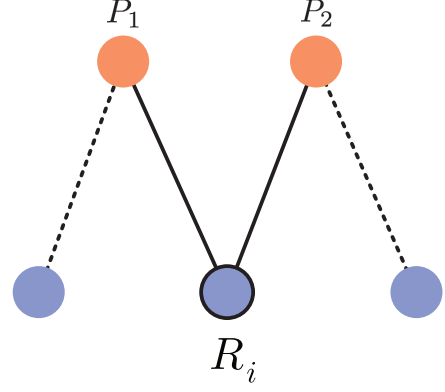

Figure 2: Non-specialist predators ($q = 2$) consume a shared resource i, while each has alternative resources to fall-back on. Assuming Lotka-Volterra dynamics and equivalent attack rates of the predators β, the non-dimensional steady state density for the shared resource is $r_i^* = R_i^*/\kappa_i = 1 - q\epsilon_i$ where $\epsilon_i = \beta P^*/\alpha_i$. We use this relationship between resource density and the number of predators q to calculate extinction probabilities as a function of the number of predators $\omega_i(q)$

acts with every other. Assembly of a species community is the result of both local colonization and extinction of species that are drawn from the source pool. The realized interactions within the assembled community are thus a subset of the potential interactions observed if every species were present, though not all species can necessarily coexist in an assembled community at a given time. We determine the colonization potential for a given species into a community as a function of two threshold conditions: 1) the colonizing species must eat *at least one* species/object including the basal resource, and 2) the colonizing species must satisfy a proportion of its need interactions, given by the threshold n_t; higher values of n_t means that entry into the community is more difficult as a higher proportion of need interactions must be satisfied. If the assimilate and need threshold conditions are both satisfied, colonization is possible. At each time-step, we select one potential colonizer at random and add it (and the objects it makes) to the community. Thus, in the first time-step, only species that consume the primary resource (row 1; figure 1) and do not have any 'need' interactions can initiate the assembly process.

We explore three potential drivers of species extinction: 1) extinction via increased resource competition, 2) extinction via increased predator pressure, and 3) extinction via both resource competition and predator pressure.

Local extinction of a species due to competitive exclusion occurs when it shares a significant proportion of its resources with one or multiple competitors. In this case, we assume that the probability of extinction increases with a consumer's mean resource overlap, $\mathrm{RO} \in [0, 1]$, defined as *the mean proportion of potential competitors sharing a species' resources*, where resources are defined

as anything (species and objects) that are linked to the consumer by eat or need interactions. We calculate RO according to the method described in Appendix 1, where RO = 0 for a consumer means that the consumer eats/needs resources that are not eaten/needed by any other consumer, whereas RO = 1 means that every resource that a consumer eats/needs is consumed by every other species in the community. The probability of extinction due to resource overlap ω_{RO} is assumed to increase sigmoidally with RO, where the location of the increase and the steepness of the increase are parameters and set to ensure that the steady state richness of the community is on average equal to 100 species.

Local extinction of a species due to predator pressure is less commonly invoked, but frequently occurs following invasions (REFS), especially of parasites and novel diseases (REFS). Because the ENIgMa model explores an assembly-through-invasion dynamic, we explore the ramifications of this potential extinction driver relative to that due to resource overlap. The extinction of a resource species due to predation (where we use the term predation generally so as to include parasitism) occurs when a single species accumulates too many predators, increasing its predator load, $PL \in [0, S-1]$. In Appendix II, we show that as the number of predators increase, the steady state of the resource abundance decreases, and we use a Lotka-Volterra framework to calucalte the probability of extinction as a function of the number of predators ω_{PL}. As before, we assume that ω_{PL} is a sigmoid function, this time increasing with the number of predators that consume a given resource species.

Primary extinctions can trigger secondary extinctions, as elimination of prey – and any objects that an eliminated species uniquely engineers – may then result in consumers falling below either or both of the assimilate and need threshold conditions. Accordingly, extinctions can cascade until the threshold conditions for every remaining species are satisfied. Wether extinction is implemented as a function of resource overlap or due to predator load, species that go extinct at time-step t may re-colonize at $t + 1$. In this respect, each time-step is a colonization event and needn't be assumed to represent an equivalent length of time.

Taken together, the community dynamics occur from a minimal set of rules:

1. Colonization: At time-step t, determine whether eat/need threshold conditions are met for each species in the source pool that isn't currently in the community. Those passing the eat/need threshold conditions are *potential colonizers*

2. Select at random a colonizing species and its attendant objects from the subset of potential colonizers

3. Extinction: Assess the probability of extinction for all species in the assembling community due to either resource overlap or predator load

4. Independently draw extinctions from a binomial distribution with a success probability equal to the extinction probabilities. Eliminate these species and any uniquely made objects from the community. These are *primary extinctions*.

5. Re-assess whether eat/need threshold conditions are satisfied in the post-extinction community. Eliminate those species and any uniquely made objects from the community that do not meet threshold conditions. If further extinctions occur, continue to re-assess threshold conditions until all species meet the requirements. Combined, these are *secondary extinctions*.

6. Time advances as t=t+1 and the process is repeated.

Results & Discussion

Appendices

Extinction via Resource Overlap The matrix $\boldsymbol{A}$ is the asymmetrical adjacency matrix of eat and need interactions with rows corresponding to species and columns corresponding to both species *and* objects. The number of users (eaters or needers) of each species/object is given by summing across columns resulting in the vector $\boldsymbol{x}$, and the number of species or objects eaten or consumed by each species is given by summing across rows resulting in the vector $\boldsymbol{y}$.

We calculate the number of species consuming or needing each of a species' possible resources (i.e. the number of species sharing a species' resources), not including itself by $\boldsymbol{z} = (\boldsymbol{A} \cdot \boldsymbol{x}) - \boldsymbol{y}$. Thus the average number of species sharing each species' resources is $\boldsymbol{ro} = \boldsymbol{z}/\boldsymbol{y}$ (where division is element-by-element), and the average *proportion* of species sharing each species' resources is given by $\boldsymbol{RO} = \boldsymbol{ro}/(S-1)$ where $S-1$ is the number of potential competitors in the community.

Thus, a species consuming/needing resources that have no other consumers/needers will have an $\boldsymbol{RO} = 0$. In contrast, if all of a species' resources are shared by every other species in the community, $\boldsymbol{RO} = 1$. Partial overlap of resource use by other species ranges of course between 0 and 1.

The probability of extinction is assumed to be logistic as a function of $\boldsymbol{RO}$, where a value close to one will result in a probability of extinction close to one (and zero in the opposing case). Where the probability of extinction increases, and the slope of the increase are inputs of the model and largely set the steady state of the assembly process.

Extinction via Predator Load Assuming Lotka-Volterra predator-prey dynamics, a given resource i has density R_i, growth rate α_i, and carrying capacity κ_i. The

Parameter	Definition	Value/Range
$\vec{a}$	assimilate	
$\vec{n}$	need	
$\vec{i}$	ignore	
$\vec{m}$	make	
$e \leftrightarrow i$	Asymmetric Predation	$p_{ei} = p_i(p_e/(p_e + p_n + p_i)) + p_e(p_i/(p_a + p_i + p_n))$
$e \leftrightarrow e$	Symmetric predation	$p_{ee} = p_e(p_e/(p_i + p_n + p_e))$
$e \leftrightarrow n$	Trophic mutualism	$p_{en} = p_n(p_e/(p_e + p_n + p_i + p_m)) + p_e(p_n/(p_a + p_i + p_n))$
$n \leftrightarrow n$	Non-trophic mutualism	$p_{nn} = p_n(p_n/(p_e + p_n + p_i + p_m))$
$n \leftrightarrow i$	Commensalism	$p_{ni} = p_n(p_i/(p_e + p_n + p_i + p_m)) + p_i(p_n/(p_e + p_n + p_i))$
$m \leftrightarrow n$	Engineering	$p_{mn} = p_n(p_m/(p_e + p_n + p_i + p_m)) + p_m$
$i \leftrightarrow i$	Null	$p_{ii} = p_i(p_i/(p_e + p_n + p_i))$
$\mathcal{N}$	Number of species + objects	dyn.
$\mathcal{S}$	Number of species	dyn.
$\mathcal{O}$	Number of objects	dyn.
a_t	Assimilate threshold	0.0
n_t	Need threshold	0.2
k	Number of consumers interacting with species i	dyn.
ω_{b}	Background probability of extinction at time t	
$\omega(t)$	Cumulative probability of extinction at time t	$\frac{\omega_{\mathrm{b}} + \epsilon n}{1 + \epsilon n}$
$1/\epsilon$	Number of consumers of resource i at which $\omega_i(t) = \frac{1}{2}$	1000

Table I: Table of parameters, definitions, and assigned values or ranges.

consumption of this resource by q non-specialist predators with equivalent steady state densities P^* and attack rates β results in the dimensionless steady state resource density $r_i^* = R_i^*/\kappa_i = 1 - q\epsilon_i$, where $\epsilon_i = \beta P^*/\alpha_i$ (see figure 2 for an exemplary motif illustrating the described interactions). Thus, ϵ describes the relative impact of a single predator on the resource steady state, which decreases linearly with an increase in the number of predators q. Although our framework does not track changes in population densities, if we assume that the true resource density is normally distributed around r^* with variance σ^2, the probability of extinction ω_i (defined as the probability that $r^* < 0$) has an exact solution of the form

$$\omega_i(q) = \frac{1}{2}\mathrm{Erfc}\left(\frac{1 - q\epsilon_i}{\sigma\sqrt{2}}\right). \tag{3}$$

The probability of extinction for a resource increases sigmoidally with the number of predators on that resource, and the number of predators where the probability of extinction is $\omega = 0.5$ is given by $q(\omega = 0.5) = 1/\epsilon$. At each time-step, we calculate ω_i for each species in the assembled community and determine extinction by drawing from a binomial distribution where there is a single trial with success probability ω_i.