Quantization of ecological interactions yields insights into community assembly and dynamics

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abstract goes here

Introduction

Amazing words. The best words.

Model Description

The ANIMe 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. Such 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 ANIMe model consists of four directed interactions: a: assimilate, 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 needed, assimilated, or ignored by the others. We also note that such objects are to be considered in the abstract, as they could represent actual molecules or tissues that a species makes (e.g. oxygen respired by plants), habitat a species provides (e.g. as an elephant clears savannas of trees, facilitating shrubs), or even an abiotic condition (e.g. example).

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 $a \leftrightarrow i$ interaction describes a typical predator-prey relationship, where species 1 assimilates species 2, and species 2 ignores species 1. Of course, a prey's abundance does not *ignore* 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. Both the $a \leftrightarrow n$ and $n \leftrightarrow n$ interactions describe service-resource and service-service mutualisms, respectively. In 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. Uniquely, the $m \leftrightarrow n$ interaction describes ecosystem engineering, where a species makes an object, while 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, 2) the rules for species assembly, and 3) the rules for species extinction.

Building the source pool The source pool is generated by first seeding an $S \times S$ interaction matrix with the directional interactions (a), need (n), make (m), and ignore (i) given the respective probabilities p_a, p_n, p_m, and
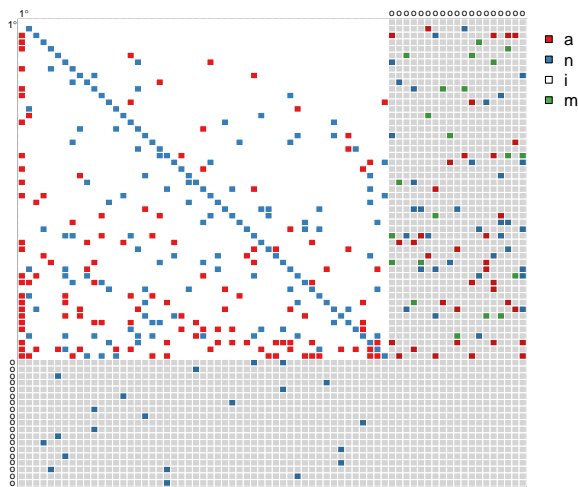

Figure 1: The number of species (closed circles; set to $\mathcal{S} = 400$) and objects (open circles) in the interaction matrix as a function of $\mathrm{pr}(m)$.

$p_i = 1 - p_a + p_n + p_m$. We can then calculate the probabilities of pairwise interactions between both species and objects as

$$p_{ai} = p_i(p_a/(p_a + p_n + p_i)) + p_a(p_i/(p_a + p_i + p_n)), \quad (1)$$

$$p_{an} = p_n(p_a/(p_a + p_n + p_i + p_m)) + p_a(p_n/(p_a + p_i + p_n)),$$

$$p_{aa} = p_a(p_a/(p_i + p_n + p_a)),$$

$$p_{nn} = p_n(p_n/(p_a + p_n + p_i + p_m)),$$

$$p_{ni} = p_n(p_i/(p_a + p_n + p_i + p_m)) + p_i(p_n/(p_a + p_n + p_i)),$$

$$p_{mn} = p_n(p_m/(p_a + p_n + p_i + p_m)) + p_m,$$

$$p_{ii} = p_i(p_i/(p_a + p_n + p_i)).$$

The directional interaction between species $i \rightarrow j$ is thus described by the element in the ith row and j^{th} column of the interaction matrix.

We build the interaction matrix for the source pool (figure 1) according to the following steps: 1) 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 assimilate interaction in column 1 means that the consumer is capable of primary production; conversely, it is assumed that the basal resource does not interact with any species/objects. Moreover, we assume that a fixed proportion of 'assimilate' interactions across agents that must be linked to the basal resource, such that a given proportion of agents are capable of primary production.

2) We next assume that – initially – all agents in the system are species, and assign trophic interactions based on an exponential degree distribution [?]. The degree distribution is based on the trophic connectance of the system, which in this case is calculated as

$$C_{\text{trophic}} = p_{ai} + p_{an} + p_{aa}. \quad (2)$$

For large communities, the number of trophic interactions for a given species i in the Niche Model (d_i) is proportional to the niche range r_i, where $d_i = r_i * \mathcal{N}$ given $r_i = X\eta_i$, where $X \sim \text{Beta}(1, 1/2C - 1)$ and $\eta_i \sim \text{Uniform}(0, 1)$. Importantly, because we do not stipulate which species are connected according to where the range falls within a niche axis (as in the Niche Model), we incorporate the trophic interaction degree distribution without imposing a structure of interactions. Accordingly, the only input to the interaction matrix of the source pool include the probabilities p_a, p_n, p_m, and the exponential nature of the trophic degree distribution. Given the drawn number of trophic interactions for each species, pairwise interactions $a \leftrightarrow i$, $a \leftrightarrow n$, and $a \leftrightarrow a$ are assigned randomly given p_{ai}, p_{an}, and p_{aa}, respectively. Non-trophic species interactions $n \leftrightarrow i$ and $n \leftrightarrow n$ interactions are also assigned randomly given the respective probabilites p_{ni} and p_{nn}, leaving only interactions involving species and objects to be determined.

3) Finally, we declare that species with 'make' interactions are engineers species that produce objects. Thus,
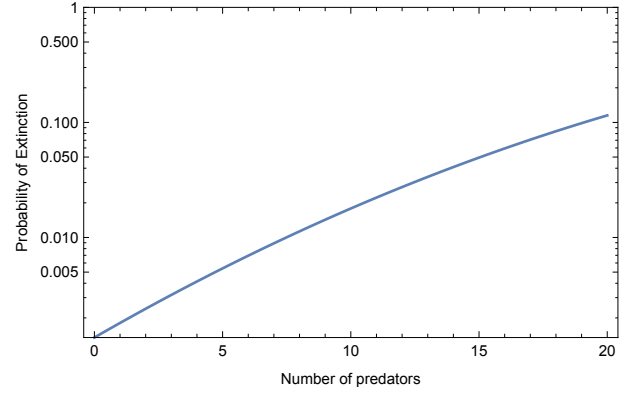

Figure 2: The number of species (closed circles; set to $\mathcal{S} = 400$) and objects (open circles) in the interaction matrix as a function of $\text{pr}(m)$.

a certain proportion of the agents in the system are declared species if there is a 'make' interaction connecting them to another agent; the receiving agent is declared an object. When an object is declared, it ignores all other agents in the pool except for those species that make it (which are set to 'need'). Objects are not allowed to 'make' other objects; if this occurs, the 'm' interaction will be randomly assigned to a declared species. Species can interact with objects (they may make, assimilate, or need them), however objects do not interact with anything except to 'need' the engineers that make them. Multiple species can make the same object: for example, most plant species engineer O_2, which is then used by other species. Because the number of 'make' interactions is stochastic, the number of objects $\mathcal{O}$ and by extenstion the size of the pool $\mathcal{N} = \mathcal{S} + \mathcal{O}$ is also stochastic. To obtain the desired $\mathcal{S}$, we use a simulated annealing algorithm to generate multiple interaction matrices of different sizes until the desired $\mathcal{S}$ is found.

Colonization and Extinction The interaction matrix for the source pool specifies how each species interacts with every other. Assembly of a species community is the result of both 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. However not all species can 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 assimilate at least one species/object, which may include the basal resource if that species is a primary producer, 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 (a higher proportion of need interactions must be satisfied). If the assimilate and need threshold conditions are both satisfied, colonization is permitted. At each time-step t, we determine which species in the source pool can

colonize the assembling community based on each meets the assimilate and need threshold conditions. If multiple species can colonize, we select one at random and add it (and the objects it makes) to the community. 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.

Although colonization depends only on satisfaction of assimilate/need interactions, persistence depends on 1) both assimilate and need thresholds remaining fulfilled, and 2) the pressure levied onto species by predation. Although the ANIMe framework does not track population densities, we integrate a central concept from population dynamics: that resource densities decline with increased predation pressure, and that this increases the risk of extinction. Assuming Lotka-Volterra predator-prey dynamics, a given resource has density R, growth rate α, and carrying capacity κ. The consumption of this resource by m non-specialist predators with equivalent steady state densities P^* and attack rates β results in the dimensionless steady state resource density $r^* = R^*/\kappa = 1 - m\epsilon$, where $\epsilon = \beta P^*/\alpha$. 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 m. 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 (defined as the probability that $r^* < 0$) has an exact solution of the form

$$\omega = \frac{1}{2}\text{Erfc}\left(\frac{1 - m\epsilon}{\sigma\sqrt{2}}\right). \tag{3}$$

The probability of extinction for a resource increases sigmoidally with the number of predators on that resource. At each time-step, we calculate ω for each species in the assembled community and determine whether each species becomes extinct by drawing from a binomial distribution $\sim \text{Bin}(\omega)$. 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 temporal bin.

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 cascade until the threshold conditions for every remaining species are satisfied. We differentiate between extinctions that are initiated as the result of predation pressure (primary extinctions) from those that result because assimilate or need interactions fall below their respective threshold conditions following one or more primary extinctions (secondary extinctions). Taken together, the community dynamics occur as the result of a minimal set of rules:

1. At time-step t, determine whether assimilate/need threshold conditions are met for species in the source pool

2. Select at random a colonizing species and its attendant objects from this subset

3. Assess the probability of extinction for all species in the assembling community

4. Independently draw extinction events from a binomial distribution that is parameterized from these extinction probabilities. Eliminate these species and any uniquely made objects from the community. These are *primary extinctions*.

5. Re-assess whether assimilate/need threshold conditions are satisfied in the post-extinction community. Eliminate these species and any uniquely made objects from the community. If further extinctions occur, continue to re-assess threshold conditions until all species meet their requirements. Combined, these are *secondary extinctions*.

6. t=t+1.

Results & Discussion

Parameter	Definition	Value/Range
$\overrightarrow{a}$	assimilate	
$\overrightarrow{n}$	need	
$\overrightarrow{i}$	ignore	
$\overrightarrow{m}$	make	
$a \leftrightarrow i$	Asymmetric Predation	
$a \leftrightarrow a$	Symmetric predation	
$n \leftrightarrow a$	Trophic mutualism	
$n \leftrightarrow n$	Non-trophic mutualism	
$n \leftrightarrow i$	Commensalism	
$i \leftrightarrow i$	Null	
$m \leftrightarrow n$	Engineering	
$\mathcal{N}$	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.