

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

Justin D. Yeakel,¹ Mathias Pires, James O'Donnell, Marcus de Aguiar, Paulo Guimarães Jr, Dominique Gravel, and Thilo Gross

¹*School of Natural Sciences, University of California, Merced, Merced, CA 95340, USA*

The dynamics of community assembly has a rich history in ecological theory. Recently, there has been much interest in assessing how changes in diversity within assembling communities impact the structure of interactions and vice versa. Here we examine a novel theoretical framework that seeks to generate communities by distilling many types of ecological interactions into a small number of unique pairwise directed links between species, including, but not limited to, ‘assimilate’ interactions (e.g. resource dependencies) and ‘need’ interactions (e.g. reproductive or habitat dependencies). Different pairwise combinations of directed link types between species give rise to the larger diversity of species interactions observed in nature, such as consumer-resource, and both service-resource and service-service mutualisms. Moreover, our framework permits the explicit inclusion of interactions that create or modify abiotic elements, which other species may depend on for survival, such as nutrients or habitat. Inclusion of both biotic and abiotic agents permits more complex and indirect interdependencies between species, effectively incorporating the concept of ecosystem engineering into interaction networks, where the environment can be altered by a species or groups of species, thereby facilitating or inhibiting the colonization of others. Our framework makes specific predictions that are borne out by observations in the field. First, we find that communities initially exhibit higher connectance (link density), which is quickly eroded to empirically observed values as competition for resources increases exclusion. Niche overlap among species follows similar trends: there is initially a greater degree of overlap between species, and as the system settles to a steady state, this overlap becomes minimized, mirroring observations of assembly in natural grasslands. Importantly, we find that an increase in the number of engineering species, by creating a greater number of direct and indirect interdependencies, constrains the assembly of communities initially, yet promotes assembly as the system matures. This leads to communities that exhibit greater diversity, however the increased species richness facilitated by engineers comes at a cost: as the number of engineers grows early in the assembly process, extinction cascades become larger. Our framework shows that despite the complexity of real communities, some of the most remarkable processes and patterns such as competitive exclusion, resource complementarity and extinction cascades, can be generated by simple interaction rules. Moreover our findings indicate that ecosystem engineering might be an important component that is overlooked in ecological network theory.

Introduction

Model Description

The ENIgMa Model We seek to understand the compound nature of species interactions by disentangling their often complex forms into a limited set of elementary, directional relationships. We aim to examine how these 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 multiple types of directional interactions between species, which, when paired represent specific ecological relationships including trophic interactions, service-resource and service-service mutualisms, and commensalisms. We also introduce two types of nodes in our depiction of ecological networks: species and objects. Objects are made by species (here and henceforth referred to as engineers) and represent a modification to the available niche-space for other species in the community, including but not limited to: an introduced compound, metabolite, or alteration to the environment.

The ENIgMa model consists of four directed interactions: *e*: eat, which specifies a dependency involving the exchange of biomass, *n*: need, which specifies a dependency (e.g. reproductive) 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. 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).

The $e \leftrightarrow i$ 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 co-occur, they have positive population densities, such that the prey’s state (presence/absence) ignores the predator. A second type of trophic interaction is described by $e \leftrightarrow e$, where consumption is symmetric, and The $e \leftrightarrow n$ and $n \leftrightarrow n$ interactions describe service-

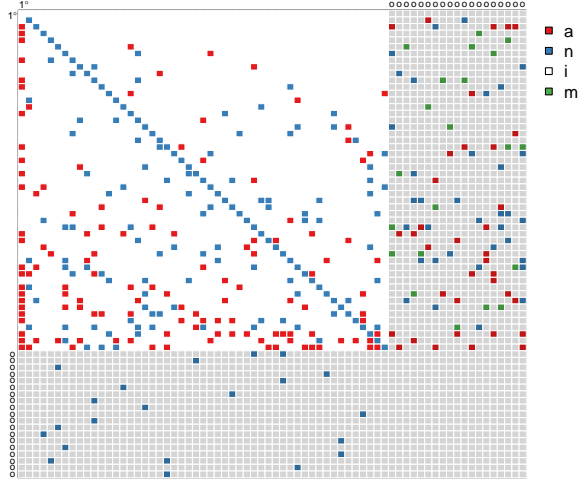


Figure 1: An example of the source pool interaction matrix where $\mathcal{S} = 50$. Species and objects are aligned across the rows and columns; objects are shaded and labeled by ‘o’ to distinguish them from species. The interaction recorded in row i and column j describes the directed interaction from 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.

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. 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 make the same object) and/or used by multiple species (many species eat or need the same object).

We explore the assembly of a novel community that emerges from a species source pool, which is represented by a source pool interaction matrix where all eat, need, ignore, make interactions are established between all species and objects. As such, a species’ set of interactions defines how it interacts with any other *a priori*, thereby establishing its potential interaction niche space. The source pool is used to seed a novel community, which arises as the result of colonization and extinction rules operating on the interactions established in the source pool matrix, the details of which we describe below.

Building the source pool The source pool interaction matrix \mathbf{P} is generated by first setting the number of species \mathcal{S} and determining the number of objects \mathcal{O} that are made by ecosystem engineers. The resulting matrix

is $\mathcal{N} \times \mathcal{N}$ where $\mathcal{N} = \mathcal{S} + \mathcal{O}$, and is subdivided into four quadrants, only two of which play a role here: species-species interactions and species-object interactions (see Fig. 1). In each quadrant, the frequency of eat interactions $E\{p_e\}$ and the frequency of need interactions $E\{p_n\}$ are free parameters, as is the expected number of objects made per species $E\{\mathcal{O}_i\} = \eta$. For each species, a set number of objects is drawn from $\text{Poiss}(\eta)$, such that the expected proportion of species that are engineers (species that make objects) is $1 - e^{-\eta}$. If a particular object is drawn for a given engineer from a complete list of all possible objects (assuming each engineer created unique objects), the expected number of objects is

$$E\{\mathcal{O}\} = \mathcal{S}\eta \left(1 - \frac{1}{e}\right), \quad (1)$$

thus permitting multiple species can make a single object, where e is Euler’s number. The frequency of $m \leftrightarrow n$ interactions is then calculated as

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

Finally the frequency of the ignore interaction is calculated as $p_i = 1 - p_e + p_n + p_m$. Pairwise interaction probabilities between both species and objects are then calculated as shown in Table I. These pairwise interactions are assigned randomly between species and objects independently in both quadrant, such that the source pool matrix has no imbued structure apart from the number of species, the number of objects, and the frequency of each directional interaction type. Each source pool is provided a *basal resource* (the first row/column). A single trophic interaction between a species and this resource is identified as a primary producer (Fig. 1), however the basal resource does not have eat, need, or make interactions itself.

Colonization and Extinction 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 \mathbf{C} are thus a subset of the potential interactions observed if every species were present (as recorded in the source pool \mathbf{P}), 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 conditions: 1) the colonizing species must eat *at least one* species/object including the basal resource, and 2) the colonizing species must satisfy all of its need interactions. If these conditions are both satisfied, colonization is possible. At each time-step, one potential colonizer is selected at random and added to the community, as well as the objects that it makes if it is an engineer. 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.

Extinction occurs directly via competitive exclusion, or indirectly via the subsequent loss of a consumer’s sin-

gle resource or any of the species/objects it needs. Extinction due to competitive exclusion is determined by violation of a single condition: a species must be the strongest competitor for at least one of its food resources. In a given community, each species i has a competition strength σ_i that is compared to that for every species j that shares its resources. If σ_i is not the highest σ for at least one of its resources, then species i is competitively excluded from the community along with all unique objects that it makes. Competition strength is a function of the number of a species' mutualisms, to what extent it is a generalist or specialist consumer, and its vulnerability to predation. Although mutualisms serve to tie the existence of one species to another, which increases its risk exposure, we assume that this dependency evolved as the consequence of a fitness advantage inherent in the interaction, providing a competitive edge. Conversely, we assume that specialists (species with fewer trophic interactions) are competitively superior to generalists (ref), and that as a species spends more energy avoiding predation, it spends less energy competing. Importantly, the role of mutualisms and trophic interactions in determining a species' competition strength is with respect to its *potential* interaction niche, and thus calculated from the source pool matrix \mathbf{P} , whereas its vulnerability to predation is determined by a species' predators within the assembled community \mathbf{C} . Taken together, competition strength for species i , σ_i , increases as the sum of a species' potential need interactions, and decreases as both the sum of its potential eat interactions and the sum of its realized predators, such that

$$\sigma_i = \pi \sum_{j=1}^{\mathcal{N}} n_{\mathbf{P}(i,j)} - \sqrt{2} \sum_{j=1}^{\mathcal{N}} e_{\mathbf{P}(i,j)} - \sum_{j=1}^{\mathcal{R}} e_{\mathbf{C}(j,i)}, \quad (3)$$

where the summations describe the number of need interactions, eat interactions, and predators, respectively, and \mathcal{R} is the species richness of the assembled community \mathbf{C} . The coefficients serve only to prevent the substitution of different interaction types. We note that due to the threshold conditions for colonization, $\sum_{j=1}^{\mathcal{N}} n_{\mathbf{P}(i,j)} = \sum_{j=1}^{\mathcal{N}} n_{\mathbf{C}(i,j)}$.

We integrate these colonization and extinction conditions to simulate community assembly over time using a Gillespie algorithm. At each time-step a single event is chosen at random to iterate the simulation forward,

where possible events include: 1) species colonization, 2) species extinction, and 3) object extinction. The likelihood of drawing each event increases with the number of potential colonizers or species/objects that meet the conditions required for extinction. The change in time dt at each point in the simulation is therefore dynamic, where $dt = 1/k(t)$ where $k(t)$ is the number of possible events at time t . Because each event is selected at random, this means that when a species is competitively excluded, it may remain in the system for some time before it is chosen for removal. Similarly, objects can remain in the system long after the engineers that made them were excluded. As we will discuss, this is an important attribute of ecosystem engineering that this particular framework allows us to explore.

Results & Discussion

Simulation of the assembly process in the absence of engineers ($\eta = 0$) reveals the emergence of food web and mutualistic web properties consistent with observations of empirical systems. Because only primary producers that do not have service-side mutualisms (outgoing need interactions) can colonize initially, a diverse base of these autotrophs typically constitutes the early assembly process. We do not consider the competitive dynamics of this autotrophic base such that we assume that the area containing the community is large enough to sustain all pure autotrophs from the source pool. Following the establishment of this first trophic level, both mixotrophs and low trophic-level heterotrophs begin to colonize, and it is with the establishment of higher trophic levels that

First we find that the connectance of trophic interactions ($C = \sum_{i,j} e_{i,j} / (\mathcal{S} - 1)^2$) follows a decay-like trajectory to values within the observed range and consistently greater than the connectance of the source pool matrix \mathbf{P} . Decaying connectance has been documented in the assembly of a wild community (Peitchnik) and is likely a combination of both increasing species richness as well as

Appendices

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	$\frac{\omega_b + \epsilon n}{1 + \epsilon n}$
$1/\epsilon$	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.