

Diverse interactions and ecosystem engineering stabilize assembly of ecological networks

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Some cool shit.

Ecosystem assembly | Ecological networks | Colonization | Extinction | Ecosystem engineering

To unravel nature's secrets we must simplify its abundant complexities and eccentricities. The layers of natural history giving rise to an ecological community can be distilled – among many forms – into a network, where nodes represent species and links represent interactions between them. In the past the necessary simplifications meant that networks were typically constructed for one type of interaction, such as food webs, capturing predation (1–3), or pollination networks capturing a specific mutualistic interaction (4). While this has led to significant breakthroughs (5–7), recent interest in ‘multilayer networks’, comprising multiple interaction types has been gaining momentum (8, 9). However, still difficult to accommodate are interactions where species affect others by altering the environment in a lasting way. These interactions, labeled ecosystem engineering (10, 11), are quite common in nature and exist in almost every ecosystem.

Diverse interactions occur not only between species, but indirectly through the effects that species have on their environment (11–13). An organism that alters the environment on timescales longer than its lifetime is known as an ecosystem engineer (14). In contemporary systems, ecosystem engineers are relatively common and can alter the landscape on which ecological interactions occur (15). Thereby elephants root out large saplings and small trees, enabling the formation and maintenance of grasslands (16) and creating habitat for smaller vertebrates (17). Burrowing rodents create shelter and promote primary production by aerating the soil (18), salmon and aquatic invertebrates create freshwater habitats by changing stream morphology (19), and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth (20).

Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth. For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the Proterozoic roughly 2.5 Byrs BP (21), paving the way for the invasion of terrestrial habitats. In the oceans, it is

thought that rRNA and protein biogenesis of aquatic photoautotrophs drove the nitrogen:phosphorous ratio (the Redfield Ratio) to ca. 16:1, matching that of plankton (22). While engineering species such as elephants can have considerable impact on local environments, engineering clades can have much larger, sometimes global-scale, effects.

The effect of the abiotic environment on species is commonly included in models of ecological dynamics (23–25) both due to its acknowledged importance and because it can – to first approximation – be easily systematized. By comparison the way in which species engineer the environment defies easy systematization due to the multitude of mechanisms by which engineering occurs. While interactions between species and the abiotic environment have been conceptually described (13, 26), the absence of engineered effects in ecological networks was addressed by Odling-Smee et al. (11), where they outlined a conceptual framework including both species and abiotic compartments as nodes of a network, with links denoting both biotic and abiotic interactions.

Here we model an ecological system as a network where nodes represent ecological entities, including engineering species, non-engineering species, and the effects of the former on the environment, which we call *objects*. The links of the network that connect both species and objects represent trophic (eat interactions), service (need interactions), and engineering dependencies, respectively (Fig. 1; see Materials and Methods for a full description). Objects in our framework overlap conceptually with the ‘abiotic compartments’ described in Odling-Smee et al. (11). Following Pillai et al. (27), we do not track the abundances of entities but only track their presence or absence. We use this framework to explore the dynamics of ecosystem

Significance Statement

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Please provide details of author contributions here.

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assembly, where the colonization and extinction of species within a community depends on the constraints imposed by the trophic, service, and engineering dependencies. Because ecological assembly is not a memory-less process, it is likely that engineers can have considerable impact on the emergence of community structure and dynamics.

Our results offer four key insights into the roles of diverse interactions and ecosystem engineering in driving community assembly. First, we show that the assembly of species networks in the absence of engineering reproduces many features observed in empirical systems. These include changes in the proportion of generalists over the course of assembly that accord with measured values, and trophic diversity similar to empirical observations. Second, we show that increasing the frequency of mutualistic interactions leads to the assembly of ecological networks that are more nested, a hallmark feature of mutualistic systems (28). However, we also observe that increased mutualistic dependencies in the assembled communities lower species' persistence. This suggests that while nested mutualistic networks appear to be dynamically favored (cf. Ref. 29), our model predicts that the additional inter-dependencies associated mutualisms should will lead to greater species turnover and changes in community composition.

We next explore the effects of ecosystem engineering on the dynamics of community assembly. Our third key result shows that increasing both the number of ecosystem engineers and engineering interactions within a community has nonlinear effects on observed extinction rates. While we find that a low amount of engineering increases extinction rates, a high amount of engineering serves to reduce extinction rates by increasing engineering redundancies. Finally, we show that the inclusion of engineering modifies the effects of mutualistic interactions, and can reduce the negative effects that mutualisms have on species' persistence.

Trophic assembly without engineering

Communities assemble by colonization from a source pool, and extinction due to competitive exclusion. Colonization is possible if a species can fulfill ≥ 1 trophic requirement and all of its service requirements. Following the establishment of an autotrophic base, mixotrophs and lower trophic heterotrophs comprise the initial colonizers, succeeded by higher trophic consumers. Primary extinctions occur by the competitive exclusion of species sharing similar resources. A species' competition strength is determined by its interactions: competition strength is enhanced by the number of its mutualistic partners and penalized by its trophic generality (number of prey) and vulnerability (number of predators). Secondary extinctions occur when species lose their trophic or service requirements. As the colonization and extinction rates converge, the community reaches a steady state around which it oscillates stochastically. see Materials and Methods for a complete description of the assembly process.

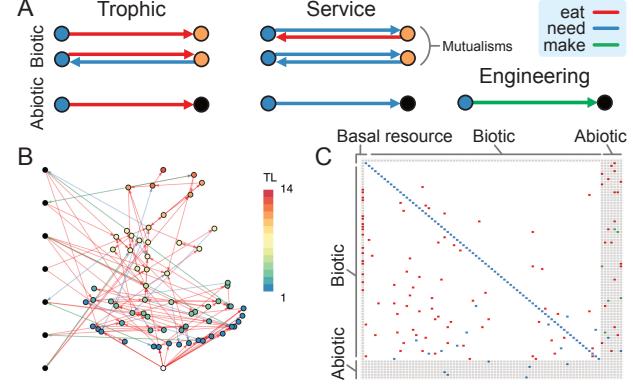


Fig. 1. A. Diverse interactions between species (colored nodes) and abiotic objects (black nodes) B. An assembling food web with species (colored nodes) and objects (black nodes). The basal resource is the white node rooted at the bottom of the network. C. The corresponding adjacency matrix with colors denoting interactions between biotic (species) and abiotic (objects) entities. The basal resource is denoted in row/column 1.

Assembly of ecological communities in the absence of engineering results in interaction networks with structures consistent with observations of empirical systems. As the community reaches steady state, we find that the connectance of trophic interactions ($C = L/S^2$, where S is species richness and L is the number of links in the community) begins high and then decays to a value similar to that of the source pool. Decaying connectance has been documented in the assembly of mangrove communities (30), however this decay is a statistical inevitability, as a growing food web early in the assembly process must have high link density (few species that are fully connected) from which it can only decline. Compared to trophic networks constructed using the Niche model (31) given equal species richness and connectance, our framework results in networks with degree distributions of similar means but with reduced variance (Supplementary Information: Appendix I).

Recent empirical work has suggested that generalist species may play an important role early in community assembly, whereas specialists tend to colonize after a diverse resource base has accumulated (30). Here, the trophic generality for a species i is defined as $G_i = \sum_j A_{i,j} (L/S)^{-1}$, where A is the adjacency matrix of trophic interactions such that the summation is the number of resources consumed by species i (31). A species is classified as a generalist if the number of its trophic interactions is greater than the average number of links per species, L/S , such that $G_i > 1$ and a specialist if $G_i < 1$. Following Piechnick et al. (30), if generalism is scaled to the steady state link density, we observe that generalists dominate early in assembly, with an increase in specialists as assembly progresses (Fig. 2A). At steady state the proportion of specialists levels out at ca. 60%, similar to empirical observations of assembling mangrove communities.

The role of specialists early in assembly is primarily

due to the accumulation of autotrophs specializing on the basal resource. This is evident when we observe that the trophic level (TL) distribution early in assembly ($t = 5$) has an average $\text{TL} = 1.6$. Four trophic levels are typically established by $t = 50$, where colonization is still the dominant dynamic, and by the time communities reach steady state the interaction networks are characterized by an average $\text{TL}_{\max} (\pm \text{standard deviation}) = 11 \pm 2.8$ (Fig. 2B). While the maximum trophic level is higher than that measured in most predator-prey systems (ref), it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers in our framework) are included (32). Overall, the most common trophic level among species at steady state is ca. $\text{TL} = 4.75$.

The distribution of trophic levels changes shape over the course of assembly. Early in assembly, we observe that the community exhibits a skewed pyramidal structure, where most species richness feeds from the base of the food web. At steady state, we observe that intermediate trophic levels dominate, with frequencies taking on an hour-glass structure. Compellingly, the trophic richness pyramids that we observe at steady state follow closely the hourglass distribution observed for empirical food webs and are less top-heavy than those produced by static food web models (33).

Structure and dynamics of mutualisms

Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks (28). Moreover, nested interactions have been shown to maximize the structural stability of mutualistic networks (29), emerge naturally via adaptive foraging behaviors (34, 35), and promote the influence of indirect effects in driving coevolutionary dynamics (36). While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties (37, 38), interaction asymmetry among individuals may promote nestedness in both trophic (39) and mutualistic systems (40). Processes that operate on different temporal and spatial scales may have a significant influence on these observations (41). For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity (42), and there is some evidence from Pleistocene food webs that geographical insularity may reinforce this process (43).

Does the assembly of ecological networks favor nested structures in systems where there are more mutualistic interactions between species? Increasing service dependencies (need interactions; see Fig. 1) leads to a higher frequency of both service-resource and service-service dependencies. These interactions alter two key dynamics in our model: more service interactions *i*) increases a species' competition strength, which will lower its probability of primary extinction, while also *ii*) increasing inter-species dependencies, potentially increasing the likelihood of secondary extinctions. While mutualisms must carry with them fitness advantages in order to evolve, the latter

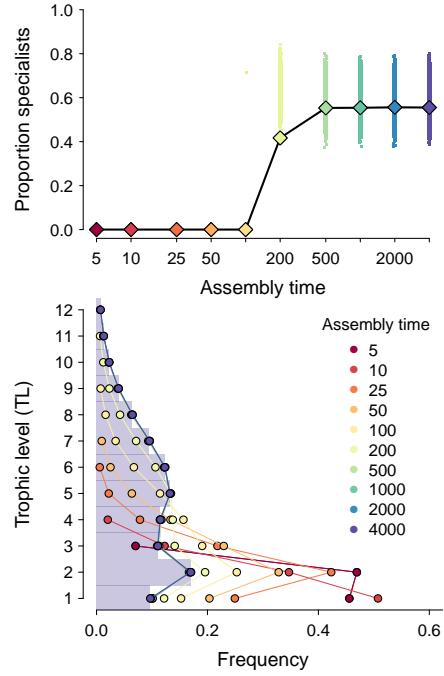


Fig. 2. A. The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$. All measures of G_i are scaled by the average number of links per species where L and S are measured with respect to the communities at steady state. B. The frequency distribution of trophic levels over the course of assembly taken across 10^4 replicates. Autotrophs occupy trophic level 1. We set $S = 200$, $p_e = 0.01$, $p_n = 0.002$, and $t = 4000$ (see Materials and Methods).

dynamic highlights the potential risk associated with losing mutualistic partners (44, 45). Indeed, the precarious balance that mutualists must maintain by way of their dependencies may have large implications for the future of global biodiversity (46).

We find that as we increase the frequency of mutualistic interactions, the assembled community at steady state becomes more nested (Fig. 3). In this case, nestedness is both the outcome of the assembly process as well as a stabilizing structure. We observe this by examining the differences in competition strength between species in mutualistic versus trophic networks in a simple nested motif (Fig. 3, inset). In trophic networks, species with many predators (high vulnerability) are at greater risk of competitive exclusion. Their elimination will have a larger effect on multiple consumers internal to the nested structure, rendering it prone to disturbance. In mutualistic networks, species with many predators gain the competitive advantages of services. If the benefit of mutualisms to competition strength is greater than the cost of vulnerability (as described in Materials and Methods), it is the low vulnerability species consumed by fewer predators that are at greater risk of competitive exclusion. Their elimination will affect fewer consumers external to the nested

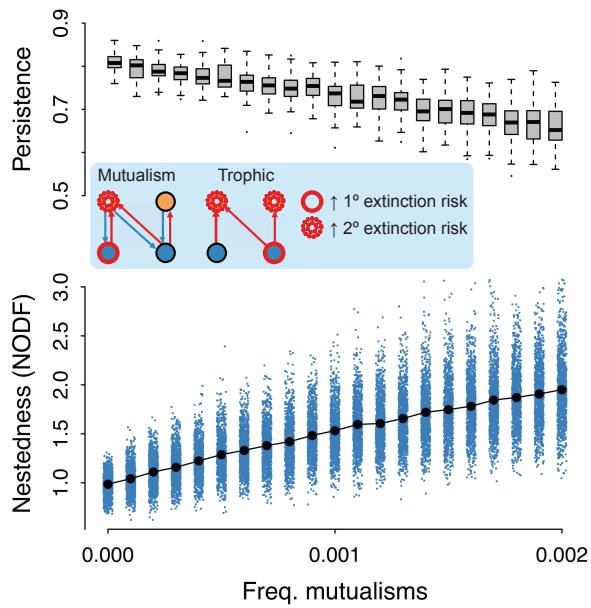


Fig. 3. A. Species persistence and B. Nestedness (measured as NODF) for communities with increasing frequencies of mutualistic (service) interactions.

structure, rendering it more resistant to disturbance.

Our results also suggest that the addition of mutualistic interactions comes at a cost. Because mutualisms increase dependencies between species, and by extension the frequency of secondary extinctions, we observe that these networks have lower species' persistence (Fig. 3). Persistence is defined by the percent simulation time a given species is present in the community, such that lower persistence means greater species turnover. In fact, assembling plant-pollinator systems have demonstrated high rates of species and interaction turnover, seemingly independent of whether the system was actively assembling or had reached a steady state (47). An important limitation of our framework is that we do not allow for flexible mutualistic interactions; a species must satisfy all of its service requirements to remain in the community. Relaxing these assumptions permits mutualism plasticity, long considered to be an important component driving the structure of mutualistic interactions (34, 35, 47, 48), which may be a fruitful perspective for future investigation.

Community assembly with ecosystem engineers

Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground (11, 14). Initial work focused on understanding how habitat modification might impact the persistence of engineering species (49), while more recent efforts have shown that engineering can promote invasion (50) and impact primary productivity (51). On eco-evolutionary timescales, ecosystem engineering can alter the selective environment

(11, 52) and ultimately lead to unexpected outcomes such as the fixation of deleterious alleles (53). On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities (54), the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems (55).

We next explore the effects of ecosystem engineering by allowing species to produce abiotic objects as additional nodes in the ecological network (Fig. 1). These object nodes produced by engineers can serve to fulfill resource or service requirements for other species. The parameter η defines the mean number of objects produced by each species, drawn from a Poisson distribution (see Materials and Methods for details). Increasing the frequency of engineering interactions both increases the number of engineering species (those species that make ≥ 1 object) and the number of objects made per species. There are two characteristics of engineering that have particular relevance for community assembly: objects can linger in the community even after the species that produce them have been excluded, and more than one engineer can produce the same object such that engineering redundancies increase with η .

Increasing engineering has significant consequences on community stability, but these effects also are sensitive to the frequency of service interactions within the community. We measure community stability from *i*) rates of primary versus secondary extinctions, *ii*) species persistence, and *iii*) steady state community diversity. Primary extinctions result from the competitive exclusion of species, whereas secondary extinctions are those that occur as a direct result of the former. All measures were averaged over each species within the community across assembly time.

As the number of engineers increase, mean rates of primary extinction are first elevated and then decline (Fig. 4A). This nonlinear effect of engineering on rates of primary extinction results from two competing forces. Increased production of abiotic objects supplies consumers with additional resources, limiting secondary extinctions and promoting persistence (Fig. 4B). However, the stabilization of consumers ultimately results in increased vulnerability of prey species. The cumulative effect is increased competitive exclusion of prey and higher rates of primary extinction, particularly when engineers are rare (Fig. 4A). The presence of abiotic objects limits the magnitude of extinction cascades. Higher rates of primary extinction coupled with lower rates of secondary extinction mean that extinctions are common, but do not result in large cascades, such that disturbances are compartmentalized. As engineering becomes more common (higher η) available niche space expands, diluting competition and leading to lower rates of primary extinction. Together, these results suggest that ecological networks are least stable when engineers are rare, and most stable when engineers are common.

Increasing the frequency of service interactions pro-

motes both mutualisms as well as service interactions between species and engineered objects (Fig. 1). A topical example of the latter is the habitat provided to invertebrates by the recently discovered rock-boring teredinid shipworm (*Lithoredo abatanica*) (56). Here, freshwater invertebrates are serviced by the habitat modifications engineered by the shipworm, linking species indirectly via an abiotic effect (object). As the frequency of service interactions increases, the negative effects associated with few engineers is diminished (Fig. 4A). Increasing service interactions both elevates the competitive strength of species receiving services (from species and/or objects), while creating more interdependencies between and among species. As trophic interactions are replaced by resource-service and/or service-service interactions, previously vulnerable species gain a competitive foothold and stabilize within the community. Increased frequencies of service interactions thus lower rates of primary extinctions, particularly in systems where consumers are facilitated by a small number of engineers (Fig. 4A). The cost of these added services comes with increased rates of secondary extinction (Fig. 4B) and greater species turnover (Fig. 4C). Low rates of primary extinction coupled with high rates of secondary extinction mean that extinctions are less common but lead to larger cascades.

When there are few engineers, each object in the community tends to be unique to a particular engineering species. Engineering redundancies increase monotonically with η (Fig. Supp), such that the loss of an engineer will not necessarily lead to the loss of engineered objects. We examine the effects of this redundancy by comparing our results to those produced by the same model, but where each object is uniquely produced by a single species. We find that while engineering redundancies do not alter the general relationship between engineering and measures of community stability (Fig. Supp), it plays a central role in maintaining species diversity. When engineering redundancies are allowed, steady state community richness S^* does not vary considerably with increasing service interactions and engineering. In contrast, when redundant engineering is not allowed, steady state community richness S_u^* declines sharply with increasing service interactions and engineering.

While the importance of engineering timescales has been emphasized previously (14), redundancy in the effects of engineers has not (10). We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when there exists a positive feedback between the effects of engineers on their fitness (50). For example, over evolutionary time adaptive radiation of successful engineering clades may lead to increased redundancy, and this may feed back to positively influence the radiation. The vast majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant engineers appear rare (10). However if we consider longer timescales, it is this type of dynamic that likely facilitated the global changes in-

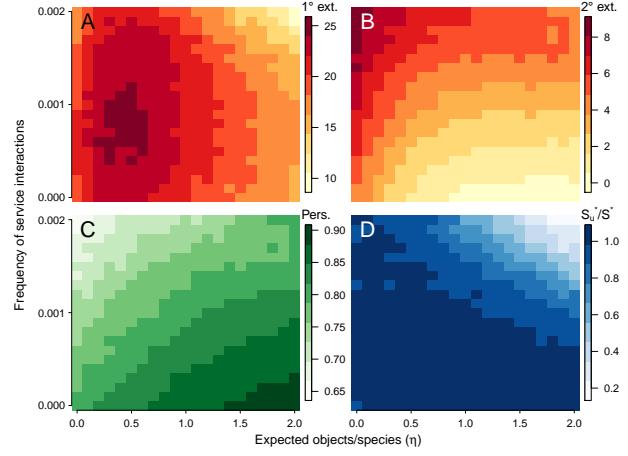


Fig. 4. A. Extinction rate and B. species persistence for communities with increasing frequencies of service interactions and average number of objects made per species η

duced by cyanobacteria in the Proterozoic (21) among other large-scale engineering events in the history of life. Engineering redundancies are likely important on shorter timescales as well. For example, diverse sessile epifauna on shelled gravels in shallow marine environments are facilitated by the engineering efforts of their ancestors, such that the engineered effects of the clade determine the future fitness of descendants (57). In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolic production (58). In these systems, redundancy in producing shared metabolic resources may play a key role in community structure and dynamics (54, 55).

Together, the results of our model point to the importance of considering diverse interactions both between species and as mediated through changes to the environment via engineering. We suggest that including the effects of engineers, either explicitly as we have done here, or otherwise, is vital for understanding the inter-dependencies that define ecological systems. As past ecosystems have fundamentally altered the landscape on which contemporary communities interact, future ecosystems will be defined by the influence of ecosystem engineers today. Understanding their role is thus tantamount to understanding our own.

Materials and Methods

We model an ecological system with a network where nodes represent *ecological entities* such as populations of species and/or the presence of inanimate objects affecting species such as (examples). Following Pilai et al. (27), we do not track the abundances of entities but only track their presence or absence. The links of the network represent interactions between pairs of entities (x,y) . We distinguish three types of such interactions: x eats y , x needs y to be present, x makes object y .

The model is initialized by creating S species and $O = \eta S$ objects, such that $N = S + O$ is the total number of entities and

η is the number of objects per species in the system. For each pair of species (x,y) there is a probability p_e that x eats y and probability p_n that x needs y . For each pair of species x and object o , there is a probability q_e that x eats o and a probability q_n that species x needs object o . Additionally, each species makes a number of objects that is drawn from a Poisson distribution with mean $\mu = \eta(e-1)^{-1}$ where e is Euler's number. Once the number of objects per species is determined, each object is assigned to a species independently. This means that there multiple species may make the same object, and that may be some objects that are not made by any species.

In addition to interactions with ecosystem entities, there can be interactions with a basal resource, which is always present. The first species always eats this resource, such that there is always a primary producer in the pool. Other species eat the basal resource with probability p_e . Species with zero assigned trophic interactions are assumed to be primary producers.

We then consider the assembly of a community which at any time will contain a subset of entities in the pool and always the basal resource. In time, the entities in the community are updated following a set of rules. A species from the pool can colonize the community if the following conditions are met: 1) all entities that a species needs are present in the community, and 2) at least one entity that a species eats is present in the community. If a colonization event is possible, it occurs stochastically in time with rate r_c .

An established species is at risk of extinction if it is not the strongest competitor at least one of its resources that it eats. We compute the competitive strength of species i as

$$\sigma_i = c_n n_i - c_e e_i - c_v v_i, \quad [1]$$

where n_i is the number of entities that species i needs, e_i is the number of entities from the pool that species i can eat, and v_i is the number of species in the community that eat species i . This captures the ecological intuition that mutualisms provide a fitness benefit, specialists are stronger competitors than generalists, and many predators entail an energetic cost. The coefficients c_n , c_e , c_v describe the relative effects of these contributions to competitive strength. In the following, we use the values $c_n = \pi$, $c_e = \sqrt{2}$, $c_v = 1$, such that the competitive benefit of adding an additional mutualism is greater than the detriment incurred by adding another prey or predator. A species at risk of extinction leaves the community stochastically in time at rate r_e .

An object is present in the community whenever at least one species that makes the object is present. If a species that makes an object colonizes a community, the object is created immediately, however objects may persist for some time after the last species that makes the object goes extinct. Any object that has lost all of its makers disappears stochastically in time at rate r_o .

The model described here can be simulated efficiently with a event-driven simulation utilizing a Gillespie algorithm. In these types of simulations, one computes the rates r_j of all possible events j in a given step. One then selects the time at which the next event happens by drawing a random number from an exponential distribution with mean $1/\sum_j r_j$. At this time, an event occurs that is randomly selected from the set of possible events such that the probability of event a is $r_a/\sum_j r_j$. Then the effect of the event is realized and the list of possible events is updated for the next step. This algorithm is known to offer a much better approximation to the true stochastic continuous time process than a simulation in discrete time steps, while providing a much higher numerical efficiency (59).

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