

1 Diverse interactions and ecosystem engineering stabilize community assembly

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The complexity of an ecological community can be distilled into a network, where diverse interactions connect species in a web of dependencies. Species interact not only with each other but indirectly through environmental effects, however the role of these ecosystem engineers has not yet been considered in models of ecological networks. Here we explore the dynamics of ecosystem assembly, where the colonization and extinction of species within a community depends on the constraints imposed by trophic, service, and engineering dependencies. We show that our assembly model reproduces many key features of ecological systems, such as the role of generalists during assembly, realistic maximum trophic levels, and increased nestedness with higher frequencies of mutualisms. We find that ecosystem engineering has large and nonlinear effects on extinction rates, facilitating stability by creating niche space, but at the same time increasing the magnitude of extinction cascades. We emphasize the importance of redundancies in engineered effects and show that such redundancy lowers the barriers to colonization, promoting community diversity. Together, our results suggest that ecological engineers may enhance community diversity while increasing persistence by facilitating colonization and limiting competitive exclusion.

11 To unravel nature's secrets we must simplify its abundant complexities and idiosyncrasies. 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. Networks are generally constructed for one type of interaction, such as food webs capturing predation^{1–3} or pollination networks capturing a specific mutualistic interaction⁴, and continues to lead to significant breakthroughs in our understanding of the dynamical consequences of community structure^{5–7}, assembly⁸, and coevolution⁹.

23 Paragraph on the importance of assembly and models of assembly on structure/dynamics. The structure evolves from a feedback between different types of interactions between species and their environment, which leads into the next section.

28 Recent interest in ‘multilayer networks’ comprising multiple interaction types (multitype interactions) may provide additional insight into these processes^{10,11}. However, interactions where species affect others by altering the environment in a lasting way have not yet been incorporated into models of ecological networks. These interactions, known as ecosystem engineering^{12,13} or more generally niche construction^{14,15}, are quite common in nature and exist in almost every ecosystem.

37 Diverse interactions occur not only between species but indirectly through the effects that species have on their environment^{13,16,17}. Elephants root out large saplings and small trees, enabling the formation and maintenance of grasslands¹⁸ and creating habitat for smaller vertebrates¹⁹. Burrowing rodents create shelter and pro-

43 mote primary production by aerating the soil²⁰, salmon
44 and aquatic invertebrates create freshwater habitats by
45 changing stream morphology²¹, and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth²². These examples illustrate ecosystem engineering, where the engineering organism alters the environment on timescales longer than its own²³. Engineers are widely acknowledged to have impacts on both small and large spatial scales⁷, and may serve as important keystone species in many habitats⁷.

53 Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth²⁴. For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the Proterozoic roughly 2.5 Byrs BP^{24,25}, paving the way for the biological 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 plankton²⁶, illustrating that engineering clades can have much larger, sometimes global-scale effects.

65 The effect of the environment on species is commonly included in models of ecological dynamics^{27–29} 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^{17,30}, the absence of engineered effects in network models was addressed by Odling-Smee et

75 al.¹³, where they outlined a conceptual framework that 133 pool. A species from the source pool can colonize if it
 76 included both species and abiotic compartments as nodes 134 finds at least one resource that it can consume (one *eat*
 77 of a network, with links denoting both biotic and abiotic 135 interaction is satisfied; cf. Ref. 33) and all of its non-
 78 interactions. 136 trophic needs are met (all *need* interactions are satisfied;
 137 see Fig. 1). As such, the service interactions are as-
 138 sumed to be obligate, whereas trophic interactions are
 139 flexible. While a basal resource is always assumed to be
 140 present, (white node in Fig. 1b) following the establish-
 141 ment of an autotrophic base, the arrival of mixotrophs
 142 (i.e. mixing auto- and heterotrophy) and lower trophic
 143 heterotrophs create opportunities for organisms occupy-
 144 ing higher trophic levels to invade. This expanding niche
 145 space initially serves as an accelerator for community
 146 growth.

79 Here we model the assembly of an ecological network 147 Following the initial colonization phase, extinctions be-
 80 where nodes represent ecological entities, including en- 148 gin to slow the rate of community growth. Primary ex-
 81 gineering species, non-engineering species, and the ef- 149 tions occur if a given species is not the strongest com-
 82 fects of the former on the environment, which we call 150 petitor for at least one of its resources (see Methods). A
 83 abiotic *modifiers*. The links of the network that con- 151 species' competition strength is determined by its inter-
 84 nect both species and modifiers represent trophic (*eat* 152 actions: competition strength is enhanced by the number
 85 interactions), service (*need* interactions), and engineer- 153 of need interactions and penalized by the number of its
 86 ing dependencies, respectively (Fig. 1; see Materials and 154 prey (favoring trophic specialists) and predators (favor-
 87 Methods for a full description). Trophic interactions rep- 155 ing species with fewer predators). Secondary extinctions
 88 resent both predation as well as parasitism, whereas ser- 156 occur when species lose its last trophic or any of its ser-
 89 vice interactions account for non-trophic interactions as- 157 vice requirements. See Fig. 1D, E for an illustration
 90 sociated with reproductive facilitation such as pollination 158 of the assembly process. As the colonization and ex-
 91 or seed dispersal. In our framework a traditional mutual- 159 tinction rates converge, the community reaches a steady
 92 ism (such as a plant-pollinator interaction) consists of a 160 state around which it oscillates (Fig. 2A). See Methods
 93 service (need) interaction in one direction and a trophic 161 and Supplementary Appendix 1 for a complete descrip-
 94 (eat) interaction in the other. These multitype interac- 162 tion of the assembly process. Specific model parameter-
 95 tions between species and modifiers thus embed multiple 163izations for each section are described in Supplementary
 96 dependent ecological sub-systems into a single network 164 Appendix 2.
 97 (Fig. 1). Modifiers in our framework overlap conceptu-
 98 ally with the 'abiotic compartments' described in Odling-
 99 Smeel et al.¹³. Following Pillai et al.³¹, we do not track 165 Assembly of ecological communities in the absence of
 100 the abundances of biotic or abiotic entities but only track 166 engineering results in interaction networks with struc-
 101 their presence or absence. We use this framework to ex- 167 tures consistent with empirical observations. As the com-
 102 plore the dynamics of ecosystem assembly, where the col- 168 munity reaches steady state, we find that the connectance
 103 onization and extinction of species within a community 169 of trophic interactions ($C = L/S^2$, where S is species
 104 depends on the constraints imposed by the trophic, ser- 170 richness and L is the number of links) decays to a value
 105 vice, and engineering dependencies. We then show how 171 similar to that of the source pool (Fig. S1). Decay-
 106 observed network structures emerge from the process of 172 ing connectance has been documented in the assembly of
 107 assembly, compare their attributes with those from em- 173 mangrove communities³⁴, however this decay is a statis-
 108 pirical systems, and examine the effects of ecosystem en- 174 tical inevitability, as early in the assembly process small
 109 gineers. 175 food webs will have high link density, from which it can
 110 Our results offer four key insights into the roles of 176 only decline. Compared to trophic networks constructed
 111 multitype interactions and ecosystem engineering in 177 using the Niche model³⁵ given similar species richness
 112 driving community assembly. First, we show that the 178 and connectance, our framework results in networks with
 113 assembly of communities in the absence of engineering 179 degree distributions of similar means but with reduced
 114 reproduces many features observed in empirical systems. 180 variance (Supplementary Appendix 3).
 115 These include changes in the proportion of generalists 181 Recent empirical work has suggested that general-
 116 over the course of assembly that accord with measured 182 ist species may predominate early in assembly, whereas
 117 data and trophic diversity similar to empirical observa- 183 specialists colonize after a diverse resource base has
 118 tions. Second, we show that increasing the frequency 184 accumulated^{33,34}. Here the trophic generality of species
 119 of mutualistic interactions leads to the assembly of 185 i is defined $G_i = k_i^{\text{in}}/(L/S)$ where k_i^{in} is the in-degree, or
 120 ecological networks that are more nested, a common 186 number of resources consumed, by species i ³⁵. A species
 121 feature of diverse mutualistic systems³², but are also less 187 is classified as a generalist if $G_i > 1$ and a specialist if
 122 stable. Our third key result shows that increasing the 188 $G_i < 1$. If generalism is scaled to the steady state link
 123 proportion of ecosystem engineers within a community 189 density (see Supplementary Appendix, section 4), we ob-
 124 has nonlinear effects on observed extinction rates. While 190 serve that generalists dominate early in assembly, with an
 125 we find that a low amount of engineering increases
 126 extinction rates, a high amount of engineering has the
 127 opposite effect. Finally we show that redundancies
 128 in engineered effects promote community diversity by
 129 lowering the barriers to colonization.

130
 131 **Assembly without ecosystem engineering.** Com-
 132 munities assemble by random colonization from a source

133 pool. A species from the source pool can colonize if it
 134 finds at least one resource that it can consume (one *eat*
 135 interaction is satisfied; cf. Ref. 33) and all of its non-
 136 trophic needs are met (all *need* interactions are satisfied;
 137 see Fig. 1). As such, the service interactions are as-
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 156 occur when species lose its last trophic or any of its ser-
 157 vice requirements. See Fig. 1D, E for an illustration
 158 of the assembly process. As the colonization and ex-
 159 tinction rates converge, the community reaches a steady
 160 state around which it oscillates (Fig. 2A). See Methods
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165 Assembly of ecological communities in the absence of
 166 engineering results in interaction networks with struc-
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 178 and connectance, our framework results in networks with
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 182 ist species may predominate early in assembly, whereas
 183 specialists colonize after a diverse resource base has
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 186 number of resources consumed, by species i ³⁵. A species
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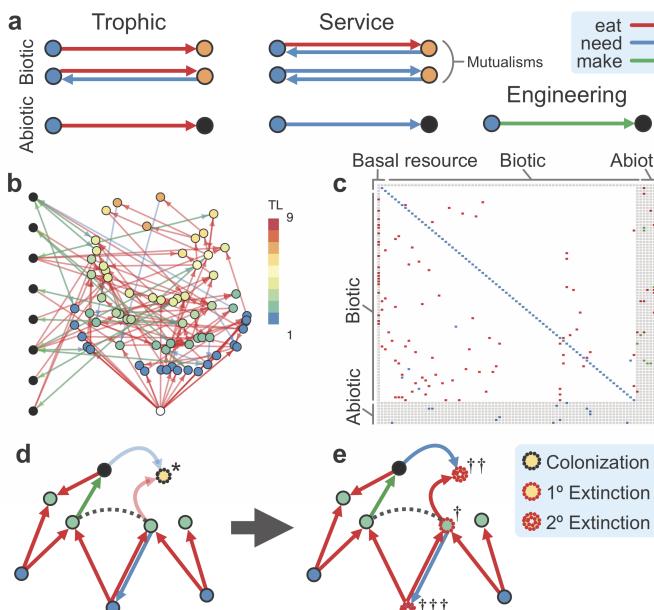


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). **b**, An assembling food web with species (colored nodes; color denotes trophic level, TL) and modifiers (black nodes). The basal resource is the white node rooted at the bottom of the network. **c**, The corresponding adjacency matrix with colors denoting interactions between biotic (species) and abiotic (modifiers) entities. **d**, A species (*) can colonize a community when a single trophic and all service requirements are met. **e**, Greater vulnerability increases the risk of primary extinction via competitive exclusion (competition denoted by dashed line) to species (†). The extinction of species (†) will cascade to affect those connected by trophic (††) and service (†††) dependencies.

the course of assembly. Early in assembly, we observe a skewed pyramidal structure, where most species feed from the base of the food web. At steady state, we observe that intermediate trophic levels dominate, with frequencies taking on an hourglass structure (purple bars, Fig. 2C). 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 models³⁸.

Structure and dynamics of mutualisms. Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks³² and defined by asymmetric interactions between species^{32? ?}. A nested structure has been shown to maximize the structural stability of mutualistic networks³⁹, emerge naturally via adaptive foraging behaviors^{40,41} and neutral processes⁴², and promote the influence of indirect effects in driving coevolutionary dynamics⁹. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties^{43,44}, interaction asymmetry among species may promote nestedness in both trophic⁴⁵ and mutualistic systems⁴⁶. Processes that operate on different temporal and spatial scales may have a significant influence on these observations⁴⁷. For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity⁴⁸, and there is some evidence from Pleistocene food webs that geographic insularity may reinforce this process⁴⁹.

Does the assembly of ecological networks favor nestedness when mutualistic interactions are frequent? Increasing the number of need interactions (Fig. 1) increases the number of both service-resource and service-service dependencies. Consider how species with more service interactions compare to those with fewer. More service interactions *i*) increase a species' competition strength, (lowering its primary extinction risk) while also *ii*) increasing inter-species dependencies. While the occurrence of a mutualism assumes a fitness advantage for the species receiving the service, the latter highlights the potential risk associated with losing mutualistic partners^{50,51}. Indeed, the balance that mutualists must maintain with their partners may have large implications for the future of global biodiversity⁵².

We find that as we increase the frequency of service interactions (holding constant the frequency of trophic interactions; see Appendix 2), the assembled community at steady state becomes more nested (Fig. 3). In this case, nestedness emerges from the assembly process itself. Increasing nestedness with the frequency of service interactions can be understood by examining the different extinction risks among species within a simple nested motif (Fig. 3, inset). In the trophic motif, species with high vulnerability (multiple predators) are at greater risk of primary extinction via competitive exclusion. This will result in the secondary extinction of the special-

increase in specialists as assembly progresses (Fig. 2B). This confirms expectations from the trophic theory of island biogeography³³, where early communities with lower richness are less likely to support specialist consumers than late, species-rich communities. At steady state the proportion of specialists is ca. 56%, similar to empirical observations of assembling food webs³⁴.

The role of specialists early in assembly is primarily due to the accumulation of autotrophic specialists. This is evident when we observe that the trophic level (TL) distribution early in assembly ($t = 5$) has an average

$TL = 1.6$. Four trophic levels are typically established by $t = 50$, where colonization is still dominant, and by the time communities reach steady state the interaction networks are characterized by an average $TL_{max} (\pm standard deviation) = 11 \pm 2.8$ (Fig. 2c). While the maximum trophic level is higher than that measured in most predator-prey systems³⁶, it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers) are included³⁷. Overall, the most common trophic level among species at steady state is ca. $TL = 4.75$.

The distribution of trophic levels changes shape over

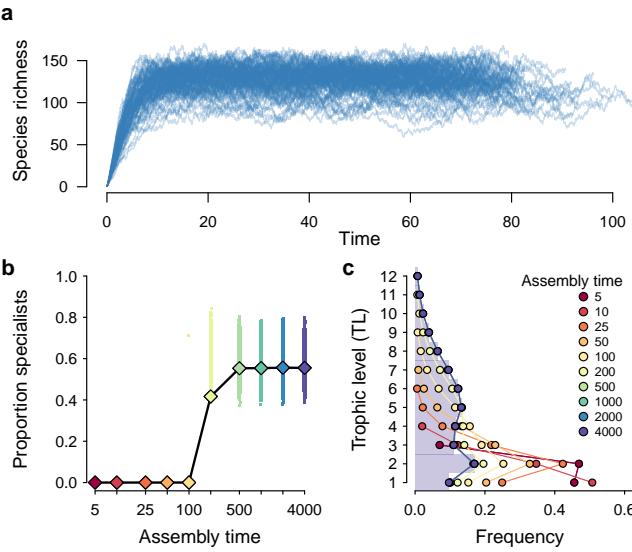


Figure 2. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index $G_i < 1$. All measures of G_i are scaled by the average number of links per species where L and S are measured at steady state. **c**, The frequency distribution of trophic levels as a function of assembly time (iterations). Autotrophs occupy $TL = 1$. Measures were evaluated across 10^4 replicates; see Materials and Methods for parameter values.

ist consumer, eliminating the interaction asymmetry. In our framework mutualistic networks are more commonly formed by composite interactions, where the consumer species is engaged in a trophic interaction while the resource species is engaged in a service interaction. As such, the consumer species becomes a trophic partner and the resource species gains the competitive advantages of the service. If the competitive advantages of services are greater than the costs of vulnerability (see Materials and Methods), it is the low vulnerability species with fewer trophic partners that is at greater risk of exclusion (Fig. 3, inset). As such, interaction asymmetry is conserved when interactions are mutualistic, but is prone to decay when interactions are purely trophic. As increased nestedness requires conservation of interaction asymmetry, we observe it to emerge in systems with higher frequencies of mutualistic interactions.

The relative stability conferred by services to interaction asymmetries should not be confused with stability of the network as a whole. When we examine the dynamics of the community as a function of service interaction frequency, we observe that mutualistic interactions have different effects on primary vs. secondary extinction rates. Because service dependencies bolster the competitive strength of otherwise susceptible species such as trophic generalists and those with multiple predators, the

rate of primary extinctions is lowered, though this effect is weak (). However, because mutualisms build rigid dependencies between species, more service dependencies result in higher frequencies of secondary extinctions (Fig. S5). In communities with many mutualistic interactions, this combined influence yields extinctions that are less likely to occur, but that promote larger cascades when they do.

An increased rate of secondary extinctions means that the network is less robust to perturbation, which may impact community turnover. If we measure persistence in terms of the proportion of time species are established in the network, we find that higher frequencies of service interactions lower average persistence, i.e. increased species turnover (Fig. 3a). Observations of empirical systems appear to support model predictions. For example, assembling plant-pollinator systems have demonstrated high rates of species and interaction turnover, both during the assembly process and at the steady state⁸.

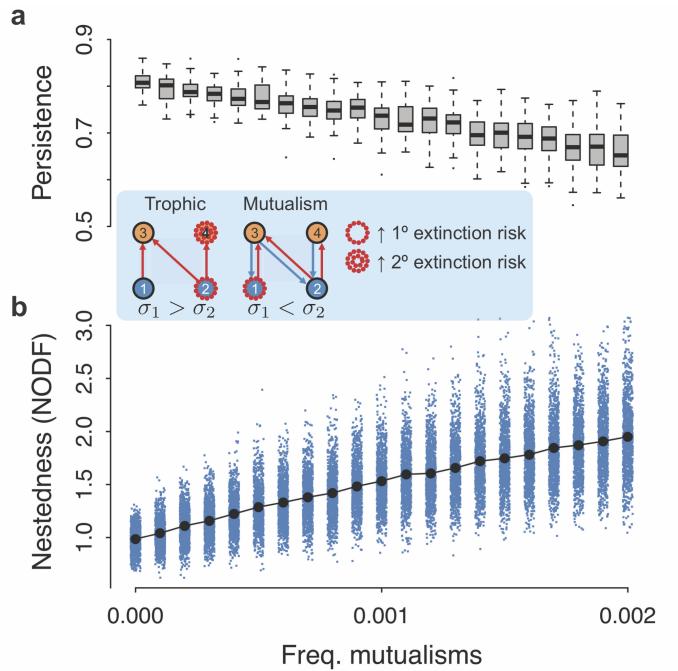


Figure 3. **a**, Species persistence with increasing frequencies of mutualistic (service) interactions without ecosystem engineers. **b**, Structural nestedness of communities, measured as NODF (Nestedness based on Overlap and Decreasing Fill)⁵³. Measures were evaluated across 10^4 replicates; see Materials and Methods for parameter values. Inset: A trophic and mutualistic nested motif for resource species 1, 2 and consumer species 3, 4. Trophic motif: the vulnerable species 2 is subject to primary extinction because it has a lower competition strength σ , resulting in an extinction cascade of species 4. Mutualistic motif: the least vulnerable species 1 with fewer mutualistic partners is subject to primary extinction without cascading effects.

We emphasize that we have restricted ourselves to

examining the effects of obligate mutualisms, although the importance of non-obligate mutualisms has long been recognized^{8,40,41,54,55}. We expect that the increased rate of secondary extinctions attributable to the loss of obligate mutualistic partners to have greater impact on system stability than the potential loss of non-obligate mutualistic partners. As such, we do not expect inclusion of non-obligate mutualisms to alter the qualitative nature of our findings.

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Assembly with ecosystem engineering. The concept of ecosystem engineering, or more generally niche construction, has both encouraged an extended evolutionary synthesis⁵⁶ while also garnering considerable controversy^{57,58}. Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground^{13,23}. For example, engineering has been shown to promote invasion⁵⁹, alter primary productivity⁶⁰, and change the selective environment over eco-evolutionary timescales^{61,62} which can lead to unexpected outcomes such as the fixation of deleterious alleles⁶³. On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities⁶⁴, the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems⁶⁵.

We next explore the effects of ecosystem engineering by allowing species to produce abiotic modifiers as additional nodes in the ecological network (Fig. 1). These modifier nodes produced by engineers can serve to fulfill resource or service requirements for other species. The parameter η defines the mean number of modifiers produced per species in the pool, drawn from a Poisson distribution (see Methods and Supplementary Appendix 1 for details). If a species makes ≤ 1 modifier, we label it an engineer. As the mean number of modifiers/species η increases, both the number of engineers in the pool as well as the number of modifiers each engineer makes increases. As detailed in Supplementary Appendix 1, multiple engineers can make the same modifier, such that engineering redundancies are introduced when η is large. When an engineer colonizes the community, so do its modifiers, which other species in the system may interact with. When engineers are lost, their modifiers will also be lost, though can linger in the community for a period of time inversely proportional to the density of disconnected modifiers (modifiers without a maker) in the community.

The inclusion of engineers does not have a significant impact on the species-species interactions within assembling food webs. See Supplementary Appendix XX for details. Transition from structure to dynamics. However, increasing engineering does have significant consequences for community stability, but these effects also are sensitive to the frequency of service interactions within the community. We measure community stability by *i*) rates of primary versus secondary extinctions, *ii*) species persistence, and *iii*) steady state community diversity. 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). At the same time, the mean rates of secondary extinction systematically decline and persistence systematically increases (Fig. 4b-c). Higher rates of primary extinction coupled with lower rates of secondary extinction that occur when modifiers are rare ($0 < \eta \leq 0.5$) mean that extinctions are common, but of limited magnitude such that disturbances are compartmentalized. As modifiers become more common both primary and secondary extinction rates decline, which corresponds to increased persistence. We suggest two mechanisms that may produce the observed results. First, when engineers and modifiers are present but rare, they provide additional resources for consumers. This stabilization of consumers ultimately results in increased vulnerability of prey, such that the cumulative effect is increased competitive exclusion of prey and higher rates of primary extinction (Fig. 4a). Second, when engineers and their modifiers are common ($\eta > 0.5$) the available niche space expands, lowering competitive overlap and suppressing both primary and secondary extinctions. Notably the presence of even a small number of engineers serves to limit the magnitude of secondary extinction cascades.

Increasing the frequency of service interactions promotes service interactions between species and engineered modifiers (Fig. 1). A topical example of the latter is the habitat provided to invertebrates by the recently discovered rock-boring teredinid shipworm (*Lithoredo abatanica*)⁶⁶. Here, freshwater invertebrates are serviced by the habitat modifications engineered by the shipworm, linking species indirectly via an abiotic effect (in our framework via a modifier node). As the frequency of service interactions increases, the negative effects associated with rare engineers is diminished (Fig. 4A). Increasing service interactions both elevates the competitive strength of species receiving services (from species and/or modifiers), while creating more interdependences between and among species. As trophic interactions are replaced by service interactions, previously vulnerable species gain a competitive foothold and persist (Fig. 4B, inset), lowering rates of primary extinctions (Fig. 4A). The costs of these added services to the community are an increased rate of secondary extinctions (Fig. 4B) and higher 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.

While the importance of engineering timescales has been emphasized previously²³, redundant engineering has been assumed to be unimportant¹². We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when the effects of engineers increase their own fitness⁵⁹ as is generally assumed to be the case with niche construction⁶². The vast majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant

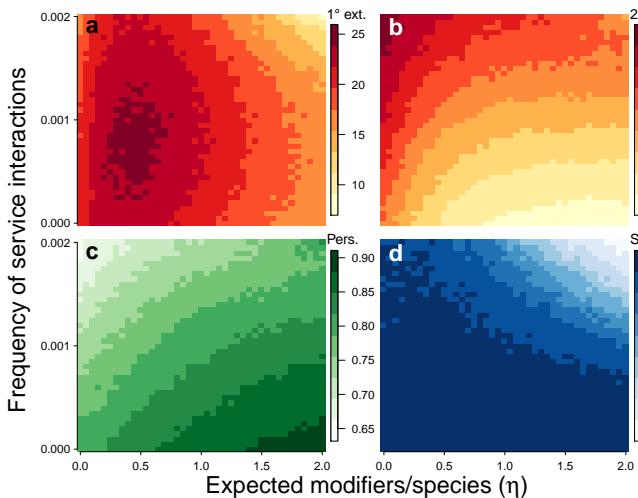


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence. **d**, The ratio S_u^*/S^* , where S_u^* denotes steady states for systems where all engineered modifiers are unique to each engineer, and S^* denote steady states for systems with redundant engineering. Lower values of S_u^*/S^* mean that systems with redundant engineers have higher richness at the steady state than those without redundancies. Measures were evaluated across 50 replicates; see Materials and Methods for parameter values.

engineers appear rare¹². However if we consider longer timescales, increasing diversity of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification¹⁴. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic^{24,25} among other large-scale engineering events in the history of life²⁴. 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 of their ancestors, such that the engineered effects of the clade determine the future fitness of descendants⁶⁷. In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production⁶⁸. In these systems, redundancy in the production of shared metabolic resources may play a key role in community structure and dynamics^{64,65}.

When there are few engineers, each modifier in the community tends to be unique to a particular engineering species. Engineering redundancies increase linearly with η (Supplementary Appendix 1; Fig. S6), such that the loss of an engineer will not necessarily lead to the loss of engineered modifiers. We examine the effects of this redundancy by comparing our results to those produced by the same model, but where each modifier is

uniquely produced by a single species. Surprisingly, the lack of engineering redundancies does not alter the general relationship between engineering and measures of community stability (Fig. S7). However we find that redundancies play 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 (Fig. S8A). In contrast, when redundant engineering is not allowed, steady state community richness S_u^* declines sharply (Figs. 4D, S8B).

Communities lacking redundancy have lower species richness because species' trophic and service dependencies are unlikely to be fulfilled, precluding colonization (Fig. S8C,D). Colonization occurs only when trophic and service dependencies are fulfilled. A species requiring multiple engineered modifiers, each uniquely produced, means that each required entity must precede colonization. This magnifies the role of priority effects in constraining assembly order¹⁵, precluding many species from colonizing. In contrast, redundancy increases the temporal stability of species' niches while minimizing priority effects by allowing multiple engineers to fulfill dependencies. Our results thus suggest that redundant engineers may play important roles in assembling ecosystems by lowering the barriers to colonization thereby promoting community diversity.

We have shown that the dynamics of assembly driven by multitype interactions can produce model communities with realistic structures and dynamics. Moreover, the inclusion of ecosystem engineering by way of modifier nodes reveals that low levels of engineering may be expected to produce higher rates of extinction while limiting the size of extinction cascades, and that engineering redundancy – whether it is common or rare – may have considerable dynamical implications. 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 engineering today. Given the rate and magnitude that humans are currently engineering environments⁶⁹, understanding the role of ecosystem engineers is tantamount to understanding our own.

Methods

We model an ecological system with a network where nodes represent *ecological entities* such as populations of species and/or the presence of abiotic modifiers affecting species. Following Pilai et al.³¹, 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 modifier y .

The assembly process entails two steps: first a source pool of species is created, followed by colonization/extinction into/from a local community. The model is initialized by creating S species and $M = \eta S$ modifiers, such that $N = S + M$ is the average total number of entities and η is the average number of modifiers per

522 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 modifier m , there is a probability q_e that x eats m and a probability q_n that species x needs modifier m . Additionally, each species makes a number of modifiers that is drawn from a Poisson distribution with mean $\mu = \eta e / (e - 1)$ where e is Euler's number. Once the number of modifiers per species is determined, each modifier is assigned to a species independently. This means that multiple species may make the same modifier, and that there may be some modifiers that are not made by any species, which are eliminated from the pool.

523 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. See Supplementary Appendix 1 for additional details on defining the source pool.

524 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 .

525 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

$$\sigma_i = c_n n_i - c_e e_i - c_v v_i, \quad (1)$$

526 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

527 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 $c_n > c_e > c_v$, 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 .

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- [16] Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
- [17] Olff, H. *et al.* Parallel ecological networks in ecosystems. *Philos T Roy Soc B* **364**, 1755 (2009).
- [18] Haynes, G. Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology* **157**, 99 – 107 (2012).
- [19] Pringle, R. M. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* **89**, 26–33 (2008).
- [20] Reichman, O. & Seabloom, E. W. The role of pocket gophers as subterranean ecosystem engineers. *Trends Ecol Evol* **17**, 44 – 49 (2002).
- [21] Moore, J. W. Animal Ecosystem Engineers in Streams. *BioScience* **56**, 237–246 (2006). arXiv:<http://oup.prod.sis.lan/bioscience/article-pdf/56/3/237/26897844/56-3-237.pdf>.
- [22] Meyer, S. T., Leal, I. R., Tabarelli, M. & Wirth, R. Ecosystem engineering by leaf-cutting ants: nests of atta cephalotes drastically alter forest structure and microclimate. *Ecol Entomol* **36**, 14–24 (2011).
- [23] Hastings, A. *et al.* Ecosystem engineering in space and time. *Ecol Lett* **10**, 153–164 (2007).
- [24] Erwin, D. H. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends Ecol Evol* **23**, 304 – 310 (2008).
- [25] Schirrmeyer, B. E., de Vos, J. M., Antonelli, A. & Bagheri, H. C. Evolution of multicellularity coincided with increased diversification of cyanobacteria and the great oxidation event. *Proc Natl Acad Sci USA* **110**, 1791–1796 (2013). arXiv:<https://www.pnas.org/content/110/5/1791.full.pdf>
- [26] Loladze, I. & Elser, J. J. The origins of the Red-field nitrogen-to-phosphorus ratio are in a homoeostatic protein-to-rRNA ratio. *Ecol Lett* **14**, 244–250 (2011).
- [27] Woodward, G., Perkins, D. M. & Brown, L. E. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philos T Roy Soc B* **365**, 2093–2106 (2010).
- [28] Brose, U. *et al.* Climate change in size-structured ecosystems. *Philos T Roy Soc B* **367**, 2903–2912 (2012).
- [29] Gibert, J. P. Temperature directly and indirectly influences food web structure. *Sci Rep-UK* **9**, 5312 (2019).
- [30] Getz, W. M. Biomass transformation webs provide a unified approach to consumer-resource modelling. *Ecol Lett* **14**, 113–124 (2011).
- [31] Pillai, P., Gonzalez, A. & Loreau, M. Metacommunity theory explains the emergence of food web complexity. *Proc Natl Acad Sci USA* **108**, 19293–19298 (2011).
- [32] Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. The nested assembly of plant-animal mutualistic networks. *Proc Natl Acad Sci USA* **100**, 9383–9387 (2003).
- [33] Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. Trophic theory of island biogeography. *Ecol Lett* **14**, 1010–1016 (2011).
- [34] Piechnik, D. A., Lawler, S. P. & Martinez, N. D. Food-web assembly during a classic biogeographic study: species “trophic breadth” corresponds to colonization order. *Oikos* **117** (2008).
- [35] Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* **404**, 180–183 (2000).
- [36] Williams, R. & Martinez, N. Limits to trophic levels and omnivory in complex food webs: The
- [37] Lafferty, K. D., Dobson, A. P. & Kuris, A. M. Parasites dominate food web links. *Proc Natl Acad Sci USA* **103**, 11211–11216 (2006).
- [38] Turnley, S. & Buddle, C. M. Pyramids of species richness: the determinants and distribution of species diversity across trophic levels. *Oikos* **125**, 1224–1232 (2016).
- [39] Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497–1253497 (2014).
- [40] Valdovinos, F. S. *et al.* Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecol Lett* **19**, 1277–1286 (2016).
- [41] Valdovinos, F. S. Mutualistic networks: moving closer to a predictive theory. *Ecol Lett* **0** (2019).
- [42] Krishna, A., Guimarães Jr, P. R., Jordano, P. & Bascompte, J. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* **117**, 1609–1618 (2008).
- [43] Stouffer, D. B. Compartmentalization increases food-web persistence. *Proc Natl Acad Sci USA* **108**, 3648–3652 (2011).
- [44] Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J. & Gonzalez, A. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science* **357**, 199–201 (2017).
- [45] Araújo, M. S. *et al.* Nested diets: a novel pattern of individual-level resource use. *Oikos* **119**, 81–88 (2010).
- [46] Pires, M. M., Prado, P. I. & Guimarães Jr, P. R. Do food web models reproduce the structure of mutualistic networks? *PLoS ONE* **6**, e27280 (2011).
- [47] Massol, F. *et al.* Linking community and ecosystem dynamics through spatial ecology. *Ecol Lett* **14**, 313–323 (2011).
- [48] Ponisio, L. C. *et al.* A network perspective for community assembly. *Front Ecol Evol* **7**, 103 (2019).
- [49] Yeakel, J. D., Guimarães Jr, P. R., Bocherens, H. & Koch, P. L. The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. *Proc Roy Soc B* **280**, 20130239–20130239 (2013).
- [50] Bond, W. J., Lawton, J. H. & May, R. M. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Phil Trans Roy Soc B* **344**, 83–90 (1994).
- [51] Colwell, R. K., Dunn, R. R. & Harris, N. C. Coextinction and persistence of dependent species in a changing world. *Ann Rev Ecol Evol Sys* **43**, 183–203 (2012).
- [52] Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P. & Sodhi, N. S. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc Roy Soc B* **276**, 3037–3045 (2009).
- [53] Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D. & Ulrich, W. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239 (2008).
- [54] Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de Españo's, P. & Flores, J. D. Topological plasticity increases robustness of mutualistic networks. *J Anim Ecol* **81**, 896–904 (2012).
- [55] Vieira, M. C. & Almeida Neto, M. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecol Lett* **18**, 144–152 (2015).

- 771 [56] Laland, K. N. *et al.* The extended evolutionary synthesis: 836 the International Centre for Theoretical Physics ICTP-SAIFR,
 772 its structure, assumptions and predictions. *Proc Roy Soc 837 FAPESP (2016/01343-7) and CNPq (302049/2015-0) to MAMA,*
 773 *B* **282**, 20150109 (2015). 838 CNPq and FAPESP (2018/14809-0) to PRG, and DFG research
 774 [57] Gupta, M., Prasad, N., Dey, S., Joshi, A. & Vidya, T. 839 unit 1748 and EPSRC (EP/N034384/1) to TG.
 775 Niche construction in evolutionary theory: the construc- 840
 776 tion of an academic niche? *J Gen* **96**, 491–504 (2017). 841
 777 [58] Feldman, M. W., Odling-Smee, J. & Laland, K. N. Why 842 **Author contributions**
 778 Gupta et al.'s critique of niche construction theory is 843 JDY and TG conceived of the model framework. JDY, MMP,
 779 off target. *J Gen* **96**, 505–508 (2017). 844 MAMA, and TG designed the analyses. JDY, MMP, MAMA,
 780 [59] Cuddington, K. Invasive engineers. *Ecol Model* **178**, 845 JLOD, PRG, DG, and TG analyzed the results and contributed
 781 335–347 (2004). 846 to multiple versions of the manuscript.
 782 [60] Wright, J. P. & Jones, C. G. Predicting effects of ecosys- 847
 783 tem engineers on patch-scale species richness from pri- 848 **Competing interests**
 784 mary productivity. *Ecology* **85**, 2071–2081 (2004). 849 The authors declare no competing interests.
 785 [61] Kyklafis, G. & Loreau, M. Ecological and evolutionary 849
 786 consequences of niche construction for its agent. *Ecol 849*
 787 *Lett* **11**, 1072–1081 (2008).
 788 [62] Krakauer, D. C., Page, K. M. & Erwin, D. H. Diversity, 849
 789 dilemmas, and monopolies of niche construction. *Am Nat* 849
 790 **173**, 26–40 (2009).
 791 [63] Laland, K. N., Odling-Smee, F. J. & Feldman, M. W. 849
 792 Evolutionary consequences of niche construction and 849
 793 their implications for ecology. *Proc Natl Acad Sci USA* 849
 794 **96**, 10242–10247 (1999).
 795 [64] Kallus, Y., Miller, J. H. & Libby, E. Paradoxes in leaky 849
 796 microbial trade. *Nat Commun* **8**, 1361 (2017).
 797 [65] Muscarella, M. E. & O'Dwyer, J. P. Ecological insights 849
 798 from the evolutionary history of microbial innovations. 849
 799 *bioRxiv* 220939 (2017).
 800 [66] Shipway, J. R. *et al.* A rock-boring and rock-ingesting 849
 801 freshwater bivalve (shipworm) from the Philippines. *Proc 849*
 802 *Roy Soc B* **286**, 20190434 (2019).
 803 [67] Kidwell, S. M. Taphonomic feedback in Miocene assem- 849
 804 blages: testing the role of dead hardparts in benthic com- 849
 805 munities. *Palaeos* **1**, 239–255 (1986).
 806 [68] Polz, M. F., Alm, E. J. & Hanage, W. P. Horizontal 849
 807 gene transfer and the evolution of bacterial and archaeal 849
 808 population structure. *Trends Genet* **29**, 170–175 (2013).
 809 [69] Corlett, R. T. The anthropocene concept in ecology and 849
 810 conservation. *Trends in Ecology & Evolution* **30**, 36–41 849
 811 (2015).
 812 [70] Gillespie, D. T. Exact stochastic simulation of coupled 849
 813 chemical reactions. *J Phys Chem* **81**, 2340–2361 (1977).
 814 [71] Williams, R. J. & Purves, D. W. The probabilistic niche 849
 815 model reveals substantial variation in the niche structure 849
 816 of empirical food webs. *Ecology* **92**, 1849–1857 (2011).
 817 [72] Warren, C. P., Pascual, M., Lafferty, K. D. & Kuris, 849
 818 A. M. The inverse niche model for food webs with para- 849
 819 sites. *Theor Ecol* **3**, 285–294 (2010).

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850

SUPPLEMENTARY METHODS

904

Appendix 2: Model parameterizations

851

Appendix 1: Building the source pool

852 Here and henceforth, we refer to the assembly model presented
 853 in the main text as the ENIgMa model (E:eat, N:need, Ig:ignore,
 854 Ma:make). To initiate the ENIgMa assembly model, we must first
 855 construct the source pool, where each ecological entity (species and
 856 modifiers) is defined by its potential interactions with each other.
 857 The source pool interaction matrix \mathbf{P} is generated by first setting
 858 the number of species in the pool S_P and determining the number
 859 of modifiers M_P that are made by ecosystem engineers. The result-
 860 ing matrix is $N_P \times N_P$ where $N_P = S_P + M_P$, and is subdivided
 861 into four quadrants, only two of which play a role here: species-
 862 species interactions and species-modifier interactions (see Fig. 1).

863 In these two quadrants, the expected frequency of eat interactions
 864 $E\{p_e\}$ and the expected frequency of need interactions $E\{p_n\}$ are
 865 free parameters, as is the expected number of modifiers made per
 866 species $E\{M_i\} = \eta$. Here and throughout, we simplify this pa-
 867 rameter space by assuming that the frequency of eat and need in-
 868 teractions for species-species (SS) interactions and species-modifier
 869 (SM) interactions are equivalent, such that $E_{SS}\{p_e\} = E_{SM}\{p_e\}$
 870 and $E_{SS}\{p_n\} = E_{SM}\{p_n\}$. For each species, a set number of modi-
 871 fiers is drawn from Poiss(η), such that the expected proportion of
 872 species that are engineers (species that make modifiers) is $1 - e^{-\eta}$.
 873 If a particular modifier is randomly and independently drawn for
 874 a given engineer from a complete list of all possible modifiers, such
 875 that multiple species – with some probability – can make the same
 876 modifier, the expected number of modifiers is

$$E\{M_P\} = S_P \eta \left(1 - \frac{1}{e}\right), \quad (S1)$$

877 where e is Euler's number. The frequency of engineering (make)
 878 interactions is then calculated as

$$E\{p_m\} = \frac{\eta}{S_P \left(1 + \eta - \frac{\eta}{e}\right)^2}. \quad (S2)$$

879 Finally the frequency of the non-interaction is calculated as
 880 $E_{SS}\{p_\emptyset\} = 1 - E_{SS}\{p_e\} + E_{SS}\{p_n\}$ and $E_{SM}\{p_\emptyset\} = 1 - E_{SM}\{p_e\} +$
 881 $E_{SM}\{p_n\} + E_{SM}\{p_m\}$ for species-species and species-modifier in-
 882 teractions, respectively. Pairwise interactions are assigned ran-
 883 domly from these probabilities between species-species and species-
 884 modifiers independently in both quadrants, such that the source
 885 pool matrix has no imbued structure apart from the number of
 886 species, the number of modifiers, and the frequency of each direc-
 887 tional interaction type. Each source pool is provided a *basal re-*
 888 *source* (the first row/column). A species with a trophic interaction
 889 to this resource is identified as an autotroph (or mixotroph depend-
 890 ing on its other trophic interactions). If they do not have service
 891 dependencies with other species/modifiers, it is these species that
 892 are uniquely able to initiate assembly.

893 We can determine analytically the expected number of unique
 894 versus redundant modifiers in the source pool. As the total number
 895 of modifiers is given in Eq. S1, the number of unique modifiers is
 896 given by $E\{M_P\}_{\text{unique}} = S_P \eta e^{-1}$. The number of redundant
 897 modifiers is then given as

$$E\{M_P\}_{\text{redundant}} = \eta S_P \frac{e - 2}{e}, \quad (S3)$$

898 such that the proportion of redundant modifiers ϕ is

$$\phi = \frac{e - 2}{e - 1} \approx 0.418. \quad (S4)$$

899 Accordingly, we find that the number of redundant modifiers in-
 900 creases linearly with η , while the proportion of modifiers that are
 901 redundant is fixed. Figure S6A,B shows both analytical expecta-
 902 tions and numerically-derived measures for $E\{M_P\}_{\text{redundant}}$ and
 903 ϕ , respectively.

905 Simulations described in the main text have default parameter-
 906 izations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$, $c_v = 1$, and 4000
 907 iterations (time-steps).

908 **Assembly without ecosystem engineering** Here we set the
 909 average number of modifiers made per species $\eta = 0$ and the prob-
 910 ability of need interactions in the species pool $p_n = 0.002$.

911 **Structure and dynamics of mutualisms** Again we used the de-
 912 fault parameterizations but set $\eta = 0$, while varying $p_n \in [0, 0.002]$.

913 **Assembly with ecosystem engineering** Here we used the de-
 914 fault parameterizations but varied $\eta \in [0, 2]$ and $p_n \in [0, 0.002]$.

915 Appendix 3: Comparison to Niche Model

916 We compared certain structural features of ENIgMa at steady
 917 state to those of the Niche Model³⁵. Comparisons were restricted
 918 to networks constructed in the absence of engineering because engi-
 919 neers introduce indirect effects that are not considered in static food
 920 web models, and may make such comparisons irrelevant. While
 921 there are many similarities, there are also some important differ-
 922 ences, some of which are highlighted in the main text. While we
 923 consider a comparison of our framework with other food web mod-
 924 els such as the Niche Model relevant, we emphasize that the mo-
 925 tivations underlying both are distinct. Our approach is intended
 926 to provide a deeper understanding into how multitype dependen-
 927 cies between species and the environment impact the dynamics of
 928 community assembly. While capturing general qualitative features
 929 of empirical systems demonstrates that the dynamics we consider
 930 are ecologically relevant, the goal of our approach is distinct from
 931 that of static food web models, which aim to maximize structural
 932 similarities between model and empirical systems^{35,71}.

933 We compared steady state ecological networks that emerge
 934 from ENIgMa (described in Materials and Methods, main text)
 935 with food webs constructed from the Niche Model³⁵ with simi-
 936 lar species richness and connectance. Because species richness and
 937 connectance of the Niche Model are often altered by eliminating dis-
 938 connected species, we compared *i*) species richness, *ii*) connectance,
 939 *iii*) mean species degree, *iv*) standard deviation of out-degree dis-
 940 tributions, and *v*) standard deviation of in-degree distributions av-
 941 eraged across 1000 replicates for each model.

942 We found that all measures resulted in fairly similar values be-
 943 tween ENIgMa and the Niche Model food webs with a some im-
 944 portant differences (Figs. S2,S3). While similar, ENIgMa pro-
 945 duces consistently lower values of connectance, mean species de-
 946 gree, as well as standard deviations of the in- and out-degree dis-
 947 tributions. This means that the food webs produced by ENIgMa
 948 are more sparsely connected with less variance between species.
 949 These results were expected, as the Niche Model assumes system-
 950 atically increasing dietary ranges with higher niche values, whereas
 951 the trophic interactions assigned to species in the source pool of
 952 ENIgMa are drawn independently. An important difference be-
 953 tween the Niche Model and ENIgMa is that we do not distinguish
 954 between predators and parasites. A different framework known
 955 as the Inverse Niche Model⁷² has been proposed to address par-
 956 asitic interactions. The Inverse Niche Model assumes increasing
 957 specialization with feeding hierarchies, which would serve to lower
 958 the average generality of species (lower degree). In addition, the

959 Inverse Niche model outputs lower standard deviations of in- and
 960 out-degree distributions. Together these trends suggest that the
 961 qualitative structural differences that we observe for the assembly
 962 and Niche model may reflect an important structural distinction
 963 between food webs that do and do not include parasitic species.

964

Appendix 4: Measures of generality

965 The trophic breadth of potential colonizers is thought to play an
 966 important role in community assembly. The definition of a special-
 967 ist or generalist to some degree depends on the size and connectance
 968 of the larger food web. Trophic generality for a species i is defined
 969 $G_i = k_i^{\text{in}}/(L/S)$, where k_i^{in} is the in-degree, or number of resources
 970 consumed by species i^{35} . A species is classified as a generalist if
 971 the number of its trophic interactions is greater than the average
 972 number of links per species, or $G_i > 1$, and a specialist if $G_i < 1$,
 973 where a community can be described by the proportion of special-
 974 ists found therein. For interaction networks that are assembling
 975 over time, generality can be scaled by a number of different mea-
 976 sures of L/S , and this has a large effect on our interpretation of the
 977 role of generality in community assembly. For instance, L/S may
 978 be quantified by either including all autotrophic species or only au-
 979 totrophic functional groups. Furthermore, the scaling of generality 980 may be made with respect to the current state of the community 981 at each point in time, or with respect to the community at steady 982 state. For instance, in their investigation of assembling mangrove 983 food webs, Piechnik et al.³⁴ scaled trophic breadth to a standard 984 steady state value of $L^*/S^* = 0.2$ averaged across 102 food webs.

985 To examine how our assessment of the role of generalism over 986 the course of assembly changes based on the application of differ- 987 ent scalings, we employ three different measures of L/S to calculate 988 G_i : 1) G_i^{all} , where L accounts for all links in the food web and S 989 accounts for all species relative to each time interval in the assem- 990 bly process (circles; Fig. S4b); 2) G_i^{hetero} , where we consider only 991 the links and species richness of heterotrophs, excluding autotrophs 992 to multiple interpretations.

992 (points; Fig. S4b); 3) G_i^* , where L and S are measured with re-
 993 spect to the communities at steady state, which is most similar to
 994 the measure used to evaluate assembling mangrove food webs (dia-
 995 monds; Fig. S4b). Whether trophic breadth is scaled to the current
 996 state of L/S or the steady state value of L^*/S^* has a large influence
 997 on the estimated proportion of generalists in the community, par-
 998 ticularly when the size of the system is small. We observe that for
 999 G_i^{all} , the system is initially assembled by specialist species, though
 1000 over the course of assembly the proportion of specialists relative
 1001 to generalists declines to intermediate values (circles represent-
 1002 ing the average over replicates in Fig. S4). If only the trophic links
 1003 between non-autotrophs are considered as in G_i^{hetero} , specialists
 1004 still dominate early in assembly, but there is a greater range, such
 1005 that some systems can be described by a mixed proportion of spe-
 1006 cialists and generalists (individual points representing independent
 1007 replicates in Fig. S4).

1008 The different normalizations by which generality is measured
 1009 will impact the interpretation of both empirical and model systems
 1010 alike. In our framework, species colonizing early in the assem-
 1011 bly process are generalists compared to how the term is defined
 1012 at the steady state, but they are functionally specialists with re-
 1013 spect to the assembling community. For example, a species that is
 1014 trophically connected to 10 resource species in the source pool may
 1015 colonize a community where it is consuming a small subset of its
 1016 potential range. As the community grows, that species may real-
 1017 ize more of its trophic niche if those resource species subsequently
 1018 colonize the system. To what end we label this species a generalist
 1019 or specialist relative to the assembling community is thus subject
 1020 to multiple interpretations.

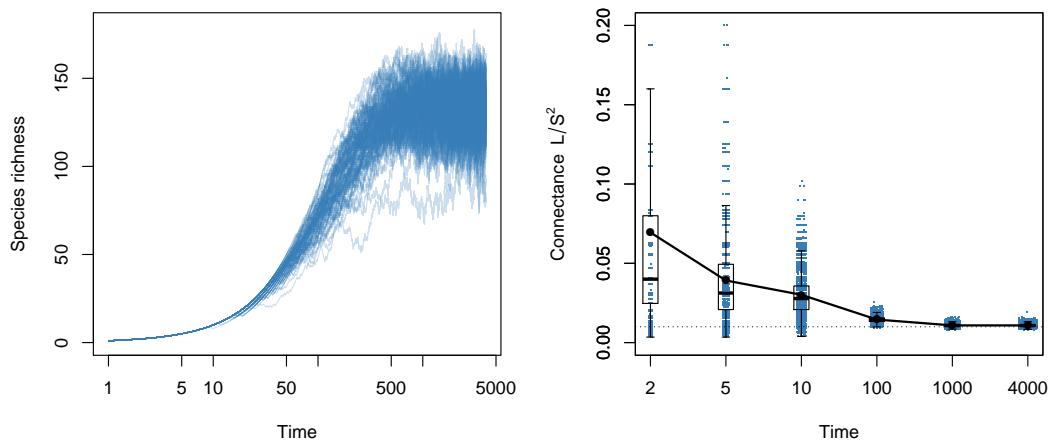


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because few species are tightly connected. Over time, connectance decays as species richness increases, and the density of trophic interactions declines.

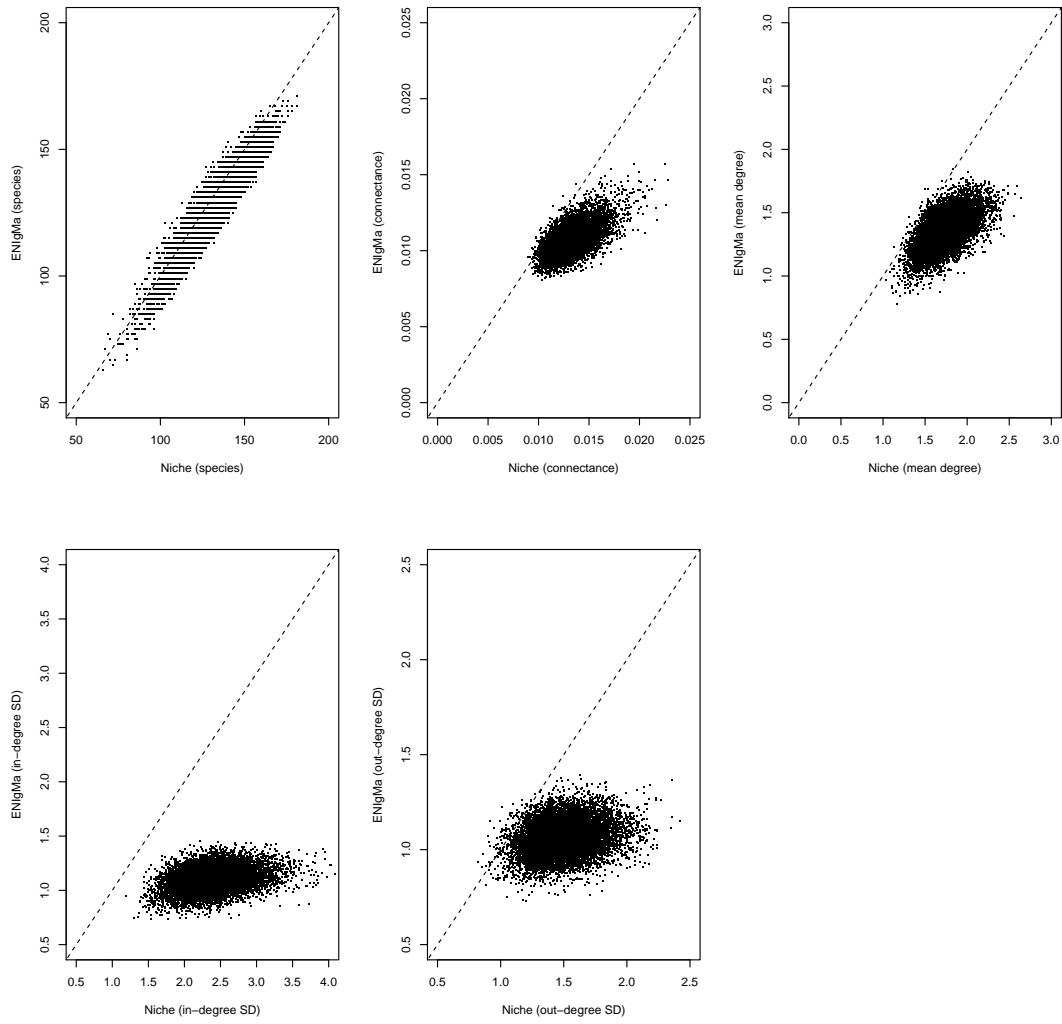


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in- and out-degree are all lower for the assembly model relative to those measures for the Niche model.

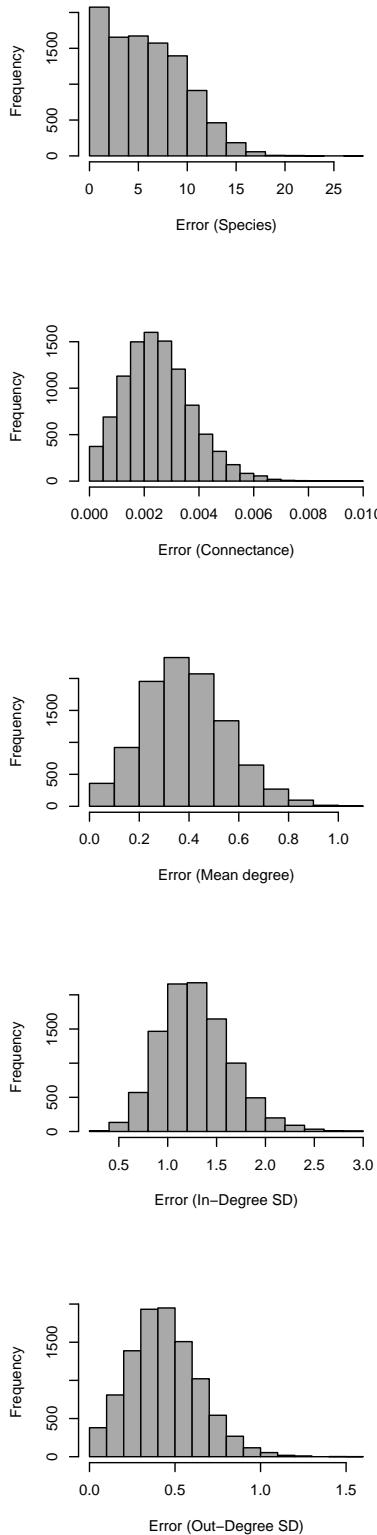


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as $\sqrt{(m_i - m_j)^2}$, where m_i and m_j are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model used to assess metrics.

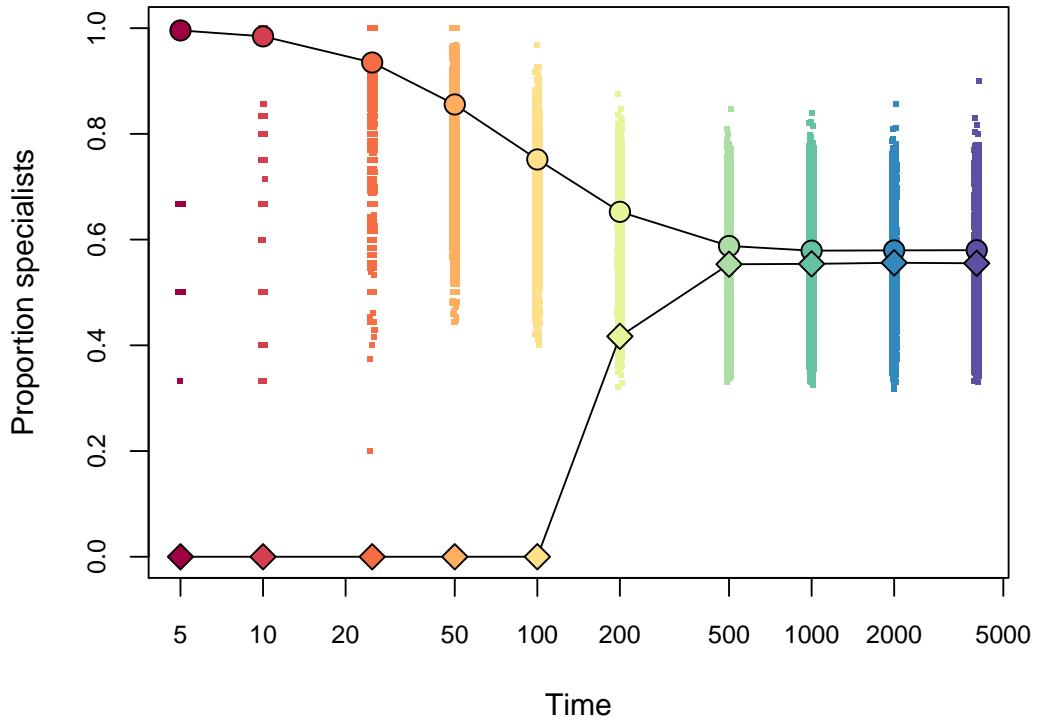


Figure S4. The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$. Measures of G_i are shown normalized to different measures of link-density. Circles: G_i^{all} where L accounts for all links in the food web and S accounts for all species relative to each time interval in the assembly process (averaged across replicates). Points: G_i^{hetero} , where we consider only the links and species richness of heterotrophs, excluding autotrophs (each point shows an individual replicate). Diamonds: G_i^* , where L and S are measured with respect to the communities at steady state (averaged across replicates). This measure is the one presented in the main text and most similar to that used to evaluate assembling mangrove food webs³⁴.

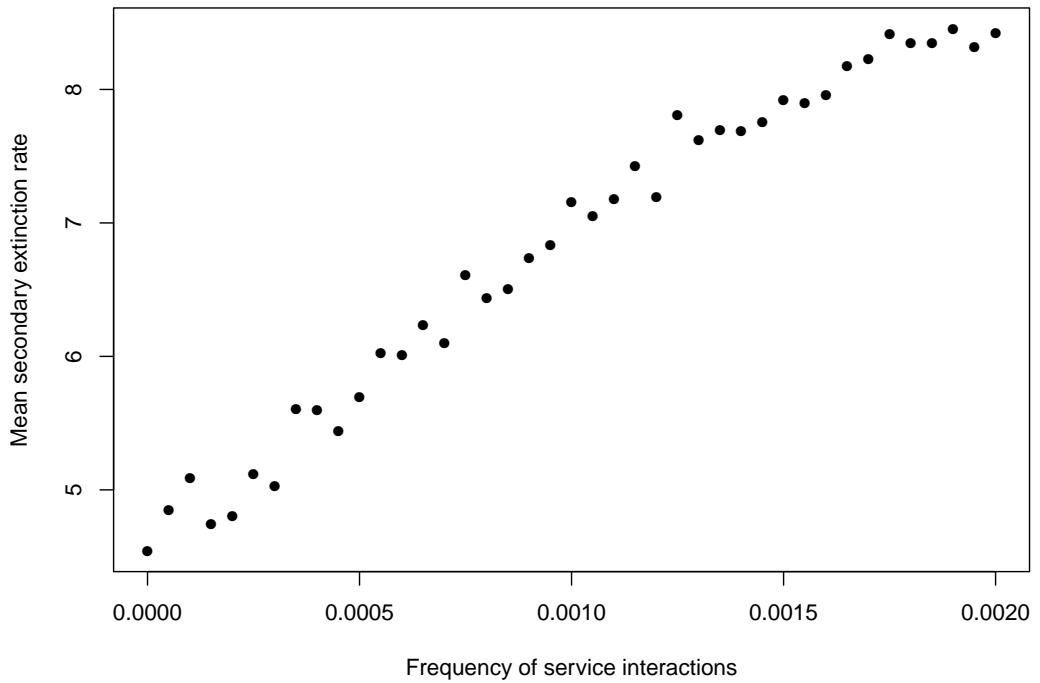


Figure S5. Mean rates of secondary extinction with increasing service interactions.

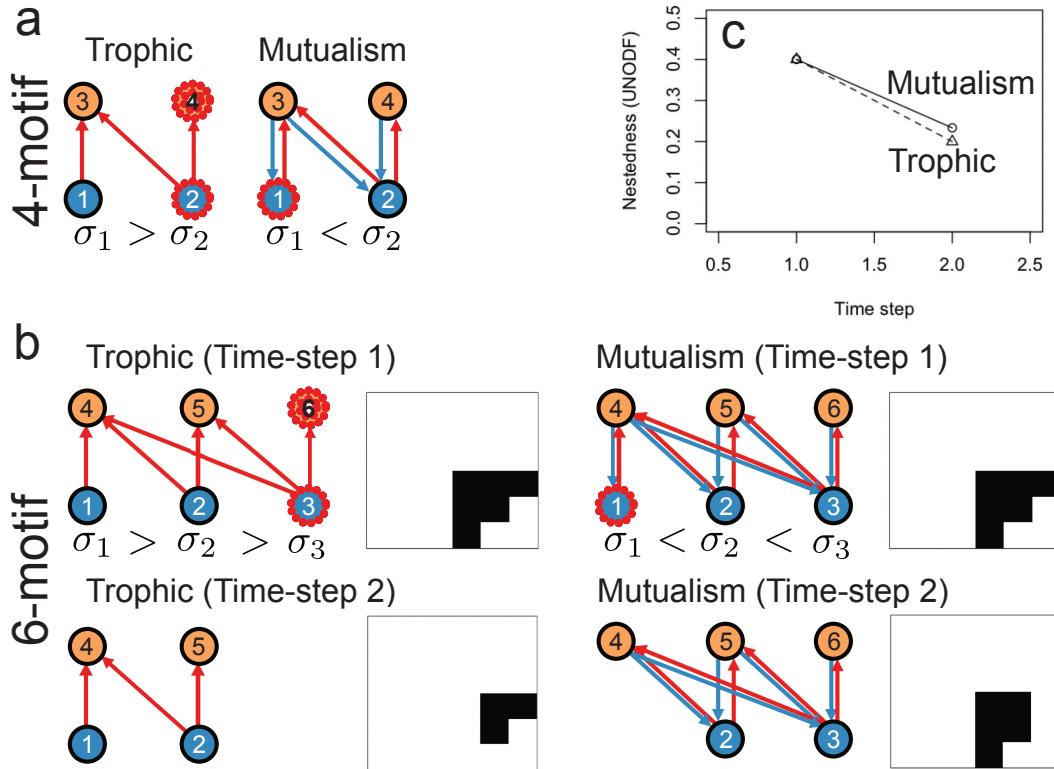


Figure S6. Motif.

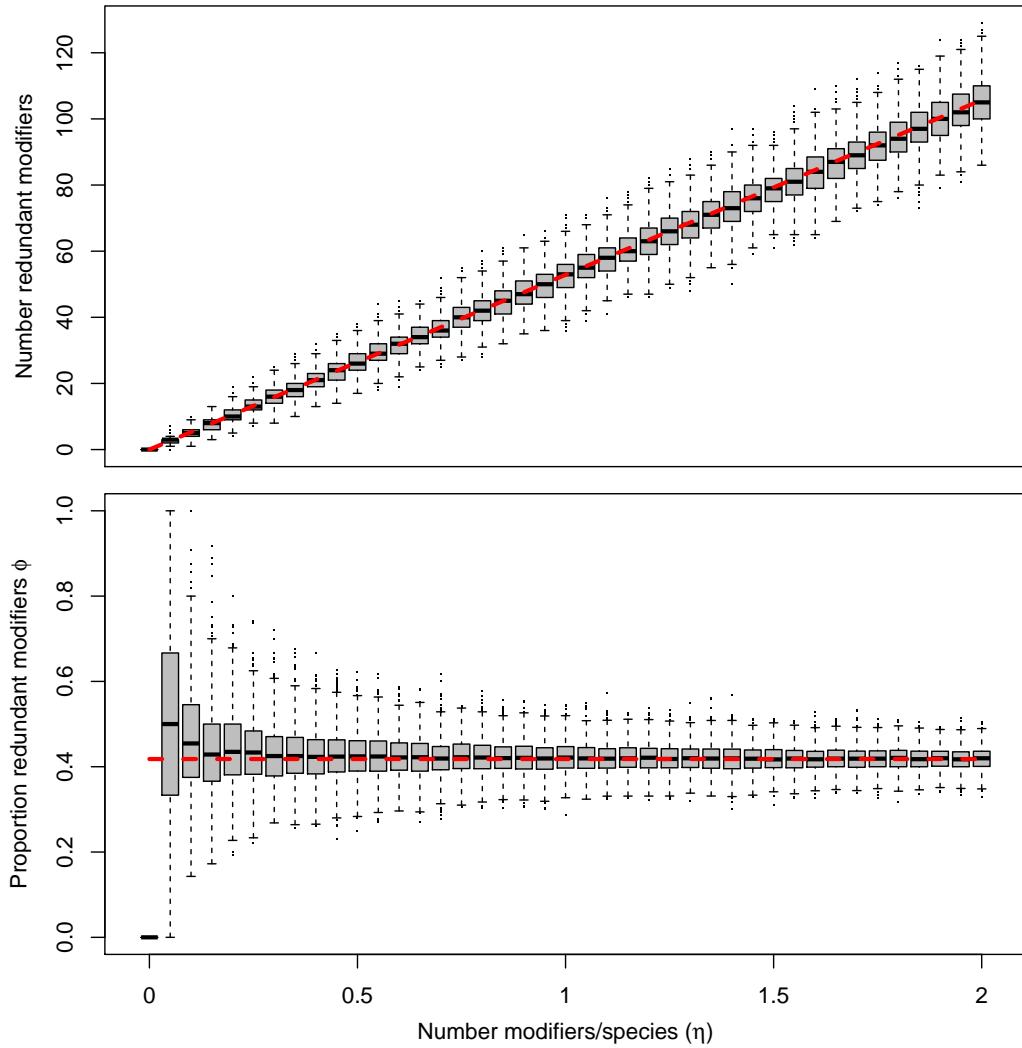


Figure S7. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation of $\phi \approx 0.418$ (Eq. S4).

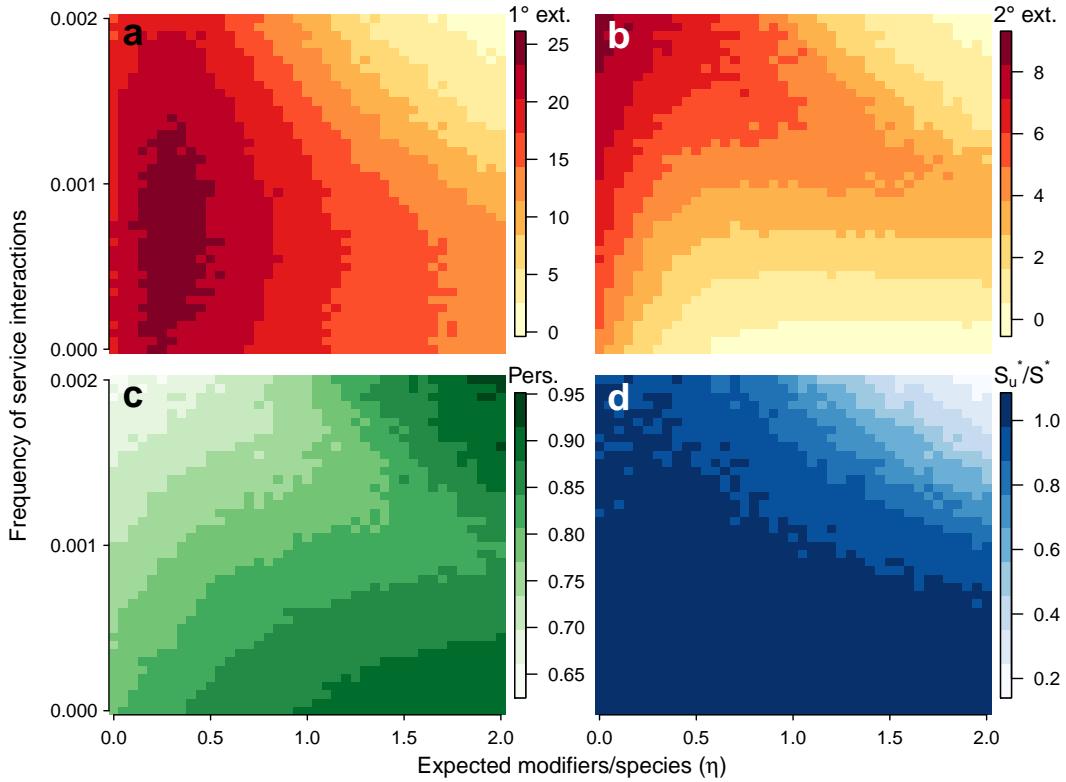


Figure S8. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence, defined as the percent simulation time the community is occupied by a given species, averaged across all species that successfully colonize. **d**, The ratio S_u^*/S^* , where S_u^* denotes steady states for systems where all engineered modifiers are unique to each engineer, and S^* denote steady states for systems with redundant engineering. Lower values of S_u^*/S^* mean that systems with redundant engineers have higher steady states than those without redundancies. Values are averaged over 50 replicates for each parameterization. See Materials and Methods for default parameter values.

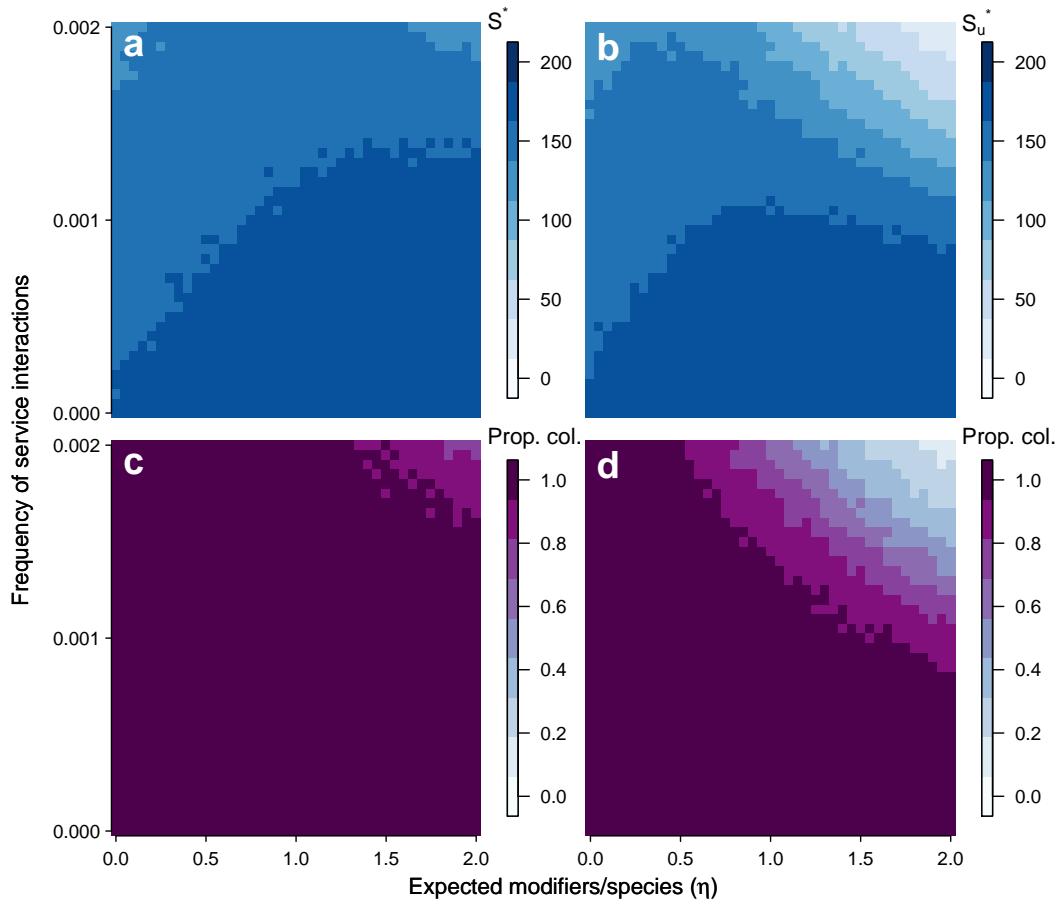


Figure S9. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (without redundant engineering).