

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. While small numbers of engineers reduce stability by increasing the primary extinction frequency, larger numbers of engineers increase stability by both reducing the primary extinction frequency and the size 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.



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}. This perspective has also been used to shed light on the generative processes driving the assembly of complex ecological communities^{8,9}.

To what extent assembly leaves its fingerprint on the structure and function of ecological communities is a source of considerable debate^{10–12}. There is strong evidence that functional traits constrain assembly^{12–14}, while differences in species' trophic niche^{15,16}, coupled with early establishment of fast/slow energy channels¹⁷, appear to significantly impact long-term community dynamics. There has been growing interest in understanding the combined role of trophic and mutualistic interactions in driving assembly^{18,19}, where the establishment of species from a source pool^{19–21} and the plasticity of species interactions^{22–25} constrain colonization and extinction dynamics. Despite these advances, there is not yet a well-defined theory for the assembly of communities

43 that incorporates multiple interaction types and both biotic/abiotic components from which functioning ecosystems are composed (cf. Ref.²⁶).

44 Recent interest in 'multilayer networks' comprising
45 multiple interaction types (multitype interactions) may
46 provide additional insight into these processes^{27,28}. However,
47 interactions where species affect others by alter-
48 ing the abiotic environment in a lasting way have not
49 yet been incorporated into models of ecological networks.
50 These interactions, known as ecosystem engineering^{29,30}
51 or more generally niche construction^{12,31}, are quite com-
52 mon in nature and exist in almost every ecosystem.

53 Diverse interactions occur not only between species
54 but indirectly through the effects that species have
55 on their environment^{30,32,33}. Elephants root out large
56 saplings and small trees, enabling the formation and
57 maintenance of grasslands^{34,35} and creating habitat for
58 smaller vertebrates³⁶. Burrowing rodents such as go-
59 phers and African mole rats create shelter and promote
60 primary production by aerating the soil^{37,38}, salmon
61 and aquatic invertebrates create freshwater habitats by
62 changing stream morphology³⁹, and leaf-cutter ants al-
63 ter microclimates, influencing seedling survival and plant
64 growth⁴⁰. These examples illustrate ecosystem engineer-
65 ing, where the engineering organism alters the environ-
66 ment on timescales longer than its own⁴¹. Engineers are
67 widely acknowledged to have impacts on both small and
68 large spatial scales⁴², and likely serve as important key-



71 stone species in many habitats⁴³.

72 Ecosystem engineering not only impacts communities
73 on ecological timescales, but has profoundly shaped the
74 evolution of life on Earth⁴⁴. For example, the emergence
75 of multicellular cyanobacteria fundamentally altered the
76 atmosphere during the Great Oxidation Event of the
77 Proterozoic roughly 2.5 Byrs BP^{44,45}, paving the way
78 for the biological invasion of terrestrial habitats. In the
79 oceans it is thought that rRNA and protein biogenesis of
80 aquatic photoautotrophs drove the nitrogen:phosphorous
81 ratio (the Redfield Ratio) to ca. 16:1 matching that of
82 plankton⁴⁶, illustrating that engineering clades can have
83 much larger, sometimes global-scale effects.

84 The effect of abiotic environmental conditions on
85 species is commonly included in models of ecological
86 dynamics^{47–49} due to its acknowledged importance and
87 because it can – to first approximation – be easily sys-
88 tematized. By comparison the way in which species en-
89 gineer the environment defies easy systemization due to
90 the multitude of mechanisms by which engineering oc-
91 curs. While interactions between species and the abi-
92 otic environment have been conceptually described^{33,50},
93 the absence of engineered effects in network models was
94 addressed by Odling-Smee et al.³⁰, where they outlined
95 a conceptual framework that included both species and
96 abiotic compartments as nodes of a network, with links
97 denoting both biotic and abiotic interactions.

98 How does the assembly of species constrained by multi-
99 type interactions impact community structure and stabil-
100 ity? How are these processes altered when the presence of
101 engineers modifies species' dependencies within the com-
102 munity? Here we model the assembly of an ecological
103 network where nodes represent ecological entities, includ-
104 ing engineering species, non-engineering species, and the
105 effects of the former on the environment, which we call
106 abiotic *modifiers*. The links of the network that connect
107 both species and modifiers represent trophic (*eat* inter-
108 actions), service (*need* interactions), and engineering de-
109 pendencies, respectively (Fig. 1; see Methods for a full
110 description). Trophic interactions represent both preda-
111 tion as well as parasitism, whereas service interactions

112 account for non-trophic interactions associated with re-
113 productive facilitation such as pollination or seed disper-
114 sal. In our framework a traditional mutualism (such as a
115 plant-pollinator interaction) consists of a service (need)
116 interaction in one direction and a trophic (*eat*) inter-
117 action in the other. These multitype interactions be-
118 tween species and modifiers thus embed multiple depen-
119 dent ecological sub-systems into a single network (Fig. 1).
120 Modifiers in our framework overlap conceptually with the
121 'abiotic compartments' described in Odling-Smee et al.³⁰.
122 Following Pillai et al.⁵¹, we do not track the abundances
123 of biotic or abiotic entities but track only their presence
124 or absence. We use this framework to explore the dy-
125 namics of ecosystem assembly, where the colonization
126 and extinction of species within a community depends
127 on the constraints imposed by the trophic, service, and
128 engineering dependencies. We then show how observed

129 network structures emerge from the process of assembly,
130 compare their attributes with those of empirical systems,
131 and examine the effects of ecosystem engineers.

132 Our results offer four key insights into the roles of
133 multitype interactions and ecosystem engineering in
134 driving community assembly. First, we show that the
135 assembly of communities in the absence of engineering
136 reproduces many features observed in empirical systems.
137 These include changes in the proportion of generalists
138 over the course of assembly that accord with measured
139 data and trophic diversity similar to empirical observa-
140 tions. Second, we show that increasing the frequency
141 of mutualistic interactions leads to the assembly of
142 ecological networks that are more nested, a common
143 feature of diverse mutualistic systems⁵², but are also
144 prone to extinction cascades. Our third key result shows
145 that increasing the proportion of ecosystem engineers
146 within a community has nonlinear effects on observed
147 extinction rates. While we find that a low amount of
148 engineering increases extinction rates, a high amount of
149 engineering has the opposite effect. Finally we show that
150 redundancies in engineered effects promote community
151 diversity by lowering the barriers to colonization.

152 F Assembly without ecosystem engineering.

153 Our framework assumes that communities assemble by ran-
154 dom colonization from a source pool. A species from
155 the source pool can colonize if it finds at least one re-
156 source that it can consume (one *eat* interaction is satis-
157 fied; cf. Ref.⁵³) and all of its non-trophic needs are met
158 (all *need* interactions are satisfied; see Fig. 1). As such,
159 service interactions are assumed to be obligate, whereas
160 trophic interactions are flexible – except in the case of
161 a consumer with only a single resource. While a basal
162 resource is always assumed to be present (white node in
163 Fig. 1b), following the establishment of an autotrophic
164 base, the arrival of mixotrophs (i.e. mixing auto- and
165 heterotrophy) and lower trophic heterotrophs create op-
166 portunities for organisms occupying higher trophic levels
167 to invade. This expanding niche space initially serves as
168 an accelerator for community growth.

169 Following the initial colonization phase, extinctions be-
170 gin to slow the rate of community growth. Primary ex-
171 tinctions occur if a given species is not the strongest
172 competitor for at least one of its resources. A species'
173 competition strength is determined by its interactions:
174 competition strength is enhanced by the number of need
175 interactions and penalized by the number of its resources
176 (favoring trophic specialists) and consumers (favoring
177 species with fewer predators). This encodes three key as-
178 sumptions: that mutualisms provide a fitness benefit⁵⁴,
179 specialists are stronger competitors than generalists^{55–58},
180 and many predators entail an energetic cost⁵⁹. Secondary
181 extinctions occur when a species loses its last trophic
182 or any of its service requirements. See Fig. 1d,e for
183 an illustration of the assembly process. As the colo-
184 nization and extinction rates converge, the community
185 reaches a steady state around which it oscillates (Fig.

2a). See Methods and Supplementary Appendix 1 for 208 distributions of similar means but with reduced variance
 188 a complete description of the assembly process. Specific 209 (Supplementary Appendix 3).
 189 model parameterizations are described in Supplementary 210 Recent empirical work has suggested that general-
 190 Appendix 2. 211 ist species may dominate early in assembly, whereas
 212 specialists colonize after a diverse resource base has
 213 accumulated^{16,53}. Here the trophic generality of species
 214 i is defined as $G_i(t) = k_i^{in}(t)/(L^*/S^*)^{60}$, where $k_i^{in}(t)$ is
 215 the number of species consumed by species i at time t ,
 216 which is scaled by the steady state link density L^*/S^* , as
 217 is typically done in empirical investigations¹⁶. A species
 218 is classified as a generalist if $G_i > 1$ and a specialist
 219 if $G_i < 1$. If generality is evaluated with respect to
 220 the steady state link density, we find that species with
 221 many potential trophic interactions realize only a subset
 222 of them, thereby functioning as specialists early in the
 223 assembly process (Fig. 2b). As the community grows,
 224 more potential interactions become realized, and func-
 225 tional specialists become functional generalists. More-
 226 over, as species assemble the available niche space ex-
 227 pands, and the proportion of potential trophic specialists
 228 grows (Fig. 2b). This latter observation confirms expec-
 229 tations from the trophic theory of island biogeography⁵³,
 230 where communities with lower richness (i.e. early assem-
 231 bly) are less likely to support specialist consumers than
 232 species-rich communities (late assembly). At steady state
 233 the proportion of functional specialists is ca. 56%, which
 234 is similar to empirical observations of assembling food
 235 webs¹⁶.

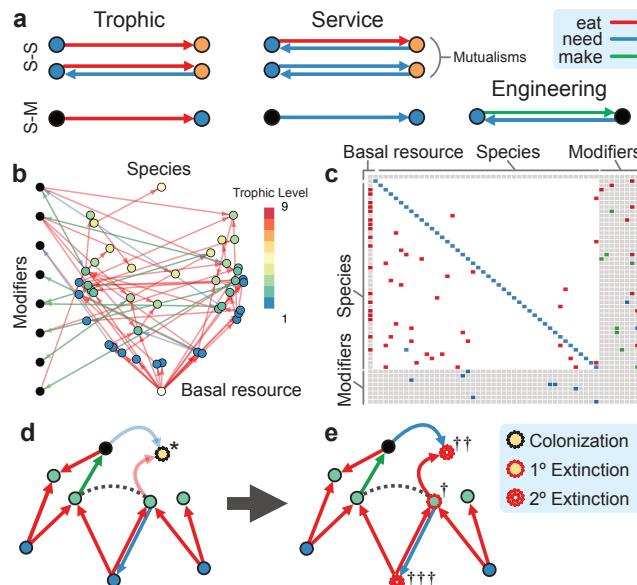


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mu-
 tualistic relationships define both species-species (S-S) and species-modifier (S-M) interactions; an engineering interaction is denoted by an engineer that makes a modifier, such that the modifier needs the engineer to persist. **b**, An assem-
 bling food web with species (color denotes trophic level) and modifiers. The basal resource is the white node at the bottom of the network. **c**, The corresponding adjacency matrix with colors denoting interactions between species and modifiers. **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 exclu-
 sion (competition denoted by dashed line) to species (†). The extinction of species (†) will cascade to affect those connected by trophic (††) and service (†††) dependencies.

191 Assembly of ecological communities in the absence of
 192 engineering results in interaction networks with struc-
 193 tures consistent with empirical observations. As the com-
 194 munity reaches steady state (Fig. 2a), we find that the
 195 connectance of trophic interactions ($C(t) = L(t)/S(t)^2$,
 196 where $S(t)$ is species richness and $L(t)$ is the number
 197 of links at time t) decays to a constant value (Fig. S1).
 198 Decaying connectance followed by stabilization around
 199 a constant value has been documented in the assem-
 200 bly of mangrove communities¹⁶ and experimental aquatic
 201 mesocosms¹⁷. The initial decay is likely inevitable in
 202 sparse webs as early in the assembly process the small set
 203 of tightly interacting species will have a high link density
 204 from which it will decline as the number of species in-
 205 creases. Compared to trophic networks constructed using
 206 the Niche model⁶⁰ given similar species richness and con-
 207 nection, our framework results in networks with degree

208 distributions of similar means but with reduced variance
 209 (Supplementary Appendix 3).
 210 Recent empirical work has suggested that general-
 211 ist species may dominate early in assembly, whereas
 212 specialists colonize after a diverse resource base has
 213 accumulated^{16,53}. Here the trophic generality of species
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 219 if $G_i < 1$. If generality is evaluated with respect to
 220 the steady state link density, we find that species with
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 222 of them, thereby functioning as specialists early in the
 223 assembly process (Fig. 2b). As the community grows,
 224 more potential interactions become realized, and func-
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 231 bly) are less likely to support specialist consumers than
 232 species-rich communities (late assembly). At steady state
 233 the proportion of functional specialists is ca. 56%, which
 234 is similar to empirical observations of assembling food
 235 webs¹⁶.

The dominance of functional specialists early in as-
 sembly is primarily due to the initial colonization by
 autotrophs. 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 typ-
 ically 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 ± 2.8 (Fig.
 2c). While the maximum trophic level is higher than
 that measured in most consumer-resource systems⁶¹, it
 is not unreasonable if parasitic interactions (which we do
 not differentiate from other consumers) are included⁶².
 Overall, the most common trophic level among species
 at steady state is ca. TL = 4.75.

The distribution of trophic levels changes shape over
 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 models⁶³.

Structure and dynamics of mutualisms. Nested
 interactions, where specialist interactions are subsets
 of generalist interactions, are a distinguishing feature

of mutualistic networks^{52,64–66}. Nestedness has been shown to maximize the structural stability of mutualistic networks⁶⁷, emerge naturally via adaptive foraging behaviors^{24,68} and neutral processes⁶⁹, and promote the influence of indirect effects in driving coevolutionary dynamics⁷⁰. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties^{71,72}, interaction asymmetry among species may promote nestedness in both trophic⁶⁶ and mutualistic systems⁷³. Processes that operate on different temporal and spatial scales may have a significant influence on these observations⁷⁴. For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity²⁵, and there is some evidence from Pleistocene food webs that geographic insularity may reinforce this process⁷⁵.

generalists are at a competitive disadvantage when they share the same resources with a specialist consumer. Yet we find that as we increase the frequency of service interactions (holding constant trophic interaction frequency; see Supplementary Appendix 2), the assembled community at steady state becomes more nested (Fig. 3a). More service interactions increase a species' competition strength, lowering its primary extinction risk. Participation in a mutualism thus delivers a fitness advantage to the species receiving the service, compensating for the lower competitive strength of generalists and allowing generalists to share subsets of resources with specialists, which promotes nestedness. However increases in mutualisms also increase inter-species dependencies, which raises the potential risk associated with losing mutualistic partners^{76,77}. While this shifting landscape of extinction risks lowers the steady state species richness of highly mutualistic communities, we do not observe a direct relationship between nestedness and richness (Fig. S4).

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 versus secondary extinction rates. Because service dependencies bolster the competitive strength of otherwise susceptible species such as trophic generalists and species with multiple predators, the rate of primary extinctions is lowered, though this effect is weak (Fig. 3b). However, because mutualisms build rigid dependencies between species, more service interactions result in higher frequencies of secondary extinctions (Fig. 3c). In communities with many mutualistic interactions, this combined influence yields extinctions that are less likely to occur, but lead to 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, or persistence. If we measure persistence in terms of the proportion of time species are established in the community, we find that higher frequencies of service interactions lower average persistence (increased species turnover; Fig. 3d). Analysis of species-specific interactions reveals that it is the species that require more services that have lower persistence (Fig. S5). 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 state⁷⁸.

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^{23,24,68,80,81}. 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.

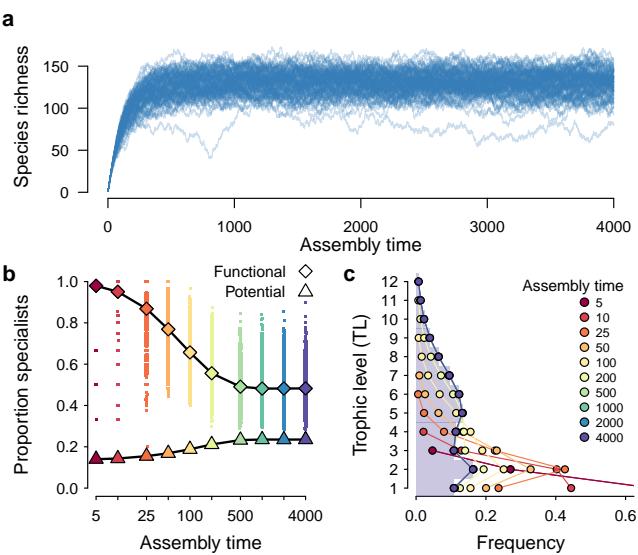


Figure 2. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index $G_i < 1$. All measures of G_i are scaled by the average number of links per species where L and S are measured at steady state. Diamonds denote expected values for functional (realized) trophic interactions at each point in time, and triangles denote expected values for potential trophic interactions (as if all trophic interactions with all species in the pool were realized), where the expectation is taken across replicates. Individual replicate results are shown for functional trophic interactions (small points). **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 Methods for parameter values.

Does the assembly of ecological networks favor nestedness when mutualistic interactions are frequent? In the absence of mutualisms, the trade-offs in our model preclude high levels of nestedness because we assume that

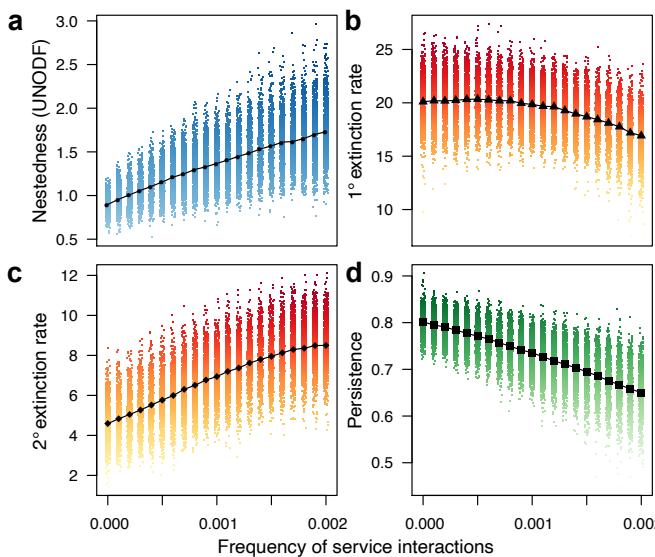


Figure 3. **a**, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)⁷⁹. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. **b**, Primary extinction rate and **c**, secondary extinction rate as a function of service interaction frequency. **d**, Species persistence as a function of service interaction frequency. Measures were evaluated for 10^4 replicates; see Methods and Supplementary Appendix 2 for parameter values.

344

Assembly with ecosystem engineering. The concept of ecosystem engineering, or more generally niche construction, has both encouraged an extended evolutionary synthesis⁸² while also garnering considerable controversy^{83,84}. Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground^{30,41}. For example, engineering has been shown to promote invasion⁸⁵, alter primary productivity⁸⁶, and change the selective environment over eco-evolutionary timescales^{87,88} which can lead to unexpected outcomes such as the fixation of deleterious alleles⁸⁹. On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities⁹⁰, the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems⁹¹. The soil is one place where these macro- and microbiotic systems intersect⁹². Many microbes and detritivores transform and deliver organic matter into the macrobiotic food web, themselves hosting a complex network of trophic and service dependencies between species and abiotic entities^{93,94}.

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 made per engineer 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 in the community.

While the inclusion of engineering does not significantly impact the structure of species-species interactions within assembling food webs (see Supplementary Appendix 4 and Fig. S6), it does have significant consequences for community stability. Importantly, these effects also are sensitive to the frequency of service interactions within the community, and we find that their combined influence can be complex.

As the number of engineers increases, 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). When engineered modifiers are rare ($0 < \eta \leq 0.5$), higher rates of primary extinction coupled with lower rates of secondary extinction 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. Assessment of species persistence as a function of trophic in-degree (number of resources) and out-degree (number of consumers) generally supports this proposed dynamic (Fig. S7).

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*)⁹⁵. 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 interdependencies between and among species. As trophic interactions are replaced by service interactions, previously vulnerable species gain a competitive foothold and persist, lowering rates of primary extinctions (Fig. 4a). The cost of these added services to the community is an increased rate of secondary extinctions (Fig. 4b) and higher species turnover (Fig. 4c), such that extinctions are less common but lead to larger cascades.

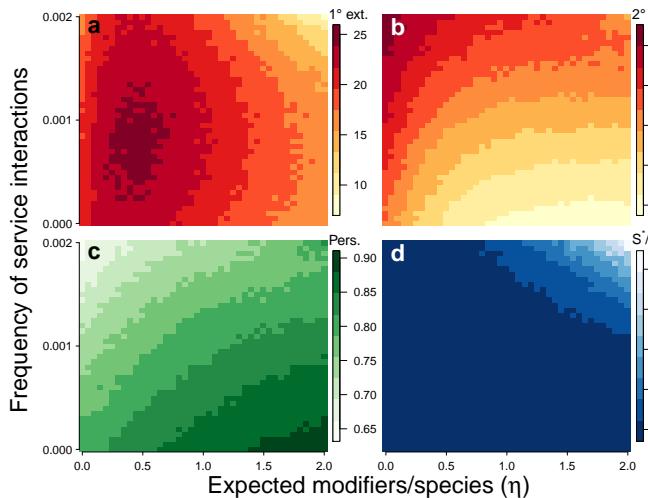


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence. **d**, The ratio S^*/S_u^* , 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. Higher values of S^*/S_u^* mean that systems with redundant engineers have higher richness at the steady state than those without redundancies. Primary and secondary extinction rates were evaluated at the community level, whereas persistence was determined for each species and averaged across the community. Each measure reports the expectation taken across 50 replicates. See Methods and Supplementary Appendix 2 for parameter values.

While the importance of engineering timescales has been emphasized previously⁴¹, redundant engineering has been assumed to be unimportant²⁹. We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when the effects of engineers increase their own fitness⁸⁵ as is generally assumed to be the case with niche construction⁸⁸. If ecosystem engineering also includes, for example, biogeochemical processes such as nitrogen-fixing among plants and mycorrhizal fungi, redundancy may be perceived as the rule rather than the exception. Moreover, the vast

majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant engineers appear rare²⁹. If we consider longer timescales, diversification of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification³¹. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic^{44,45} among other large-scale engineering events in the history of life⁴⁴. 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 descendants⁹⁶.

In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production⁹⁷. In these systems, redundancy in the production of shared metabolic resources may play a key role in community structure and dynamics^{90,91}.

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. S8), 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. S9). 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. S10a). In contrast, when redundant engineering is not allowed, steady state community richness S_u^* declines sharply (Figs. 4d, S10b).

Communities lacking redundant engineering have lower species richness because species' trophic and service dependencies are unlikely to be fulfilled within a given assemblage (Fig. S10c,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 order¹², precluding many species from colonizing. In contrast, redundant engineering increases the temporal stability of species' niches while minimizing priority effects by allowing multiple engineers to fulfill the dependencies of a particular species. Our results thus suggest that redundant engineers may play important roles in assembling ecosystems by lowering the barriers to colonization, promoting community diversity.

We have shown that simple process-based rules governing the assembly of species with multitype interactions can produce 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 – serves to promote colonization and by extension diversity. 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 with which humans are currently engineering environments⁹⁸, understanding the role of ecosystem engineers is thus tantamount to understanding our own effects on the assembly of natural communities.

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.⁵¹, we do not track the abundances of entities but track only their presence or absence (see also Refs.^{19,20}). 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 expected total number of entities (before considering engineering redundancies) and η is the expected number of modifiers made per species in the community, where the expectation is taken across independent replicates. 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 species x eats modifier m and a probability q_n that species x needs modifier m. Throughout we assume that $p_e = q_e$ and $p_n = q_n$ for simplicity. Each species i makes a number of modifiers $M_i \sim \text{Poiss}(\eta)$. If engineering redundancies are allowed, once the number of modifiers per species is determined each modifier is assigned to a species independently to match its assigned number of modifiers. This means that multiple species may make the same modifier, and that there may be some modifiers that are not assigned to any species, which are eliminated from the pool. Accounting for engineering redundancies, the number of modifiers in the pool becomes $M' = \eta S(e-1)/e$ where e is Euler's number. If engineering redundancies are not allowed, each modifier is made by a single engineer and $M' = M$.

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.

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 benefit⁵⁴, specialists are stronger competitors than generalists⁵⁷, and many predators entail an energetic cost⁵⁹. The coefficients c_n , c_e , c_v describe the relative effects of these contributions to competition strength. In the following, we use the relationship $c_n > c_e > c_v$, such that the competitive benefit of adding an additional mutualism is greater than the detriment incurred by adding another resource or predator. A species at risk of extinction leaves the community stochastically in time at rate r_e .

A modifier is present in the community whenever at least one species that makes the modifier is present. If a species that makes a modifier colonizes a community, the modifier is introduced as well, however modifiers may persist for some time after the last species that makes the modifier goes extinct. Any modifier that has lost all of its makers disappears stochastically in time at rate r_m .

The model described here can be simulated efficiently with an 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 $r_a / \sum_j r_j$. The effect of the event is then 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 efficiency⁹⁹. Simulations described in the main text have default parameterizations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$, $c_v = 1$, and 4000 iterations. Replicates are defined as the independent assembly of independently drawn source pools with a given parameterization.

Data availability

The study is theoretical; no new empirical data were generated.



Code availability

The simulation code supporting this work is available for download from <https://github.com/jdyeakel/Lego>.

221

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920 Acknowledgements

921 We would like to thank Uttam Bhat, Irina Birskis Barros, Emmet
 922 Brickowski, Jennifer A. Dunne, Ashkaan Fahimipour, Marilia
 923 P. Gaiarsa, Jean Philippe Gibert, Christopher P Kempes, Eric
 924 Libby, Lauren C. Ponisio, Taran Rallings, Samuel V. Scarpino,
 925 Megha Suswaram, Ritwika VPS, and two anonymous reviewers
 926 for insightful discussions and comments throughout the lengthy
 927 gestation of this manuscript. The original idea was conceived at
 928 the Networks on Networks Working Group in Göttingen, Germany
 929 (2014) and the Santa Fe Institute (2015). This work was formerly
 930 prepared as a part of the Ecological Network Dynamics Working
 931 Group at the National Institute for Mathematical and Biolog-
 932 ical Synthesis (2015–2019), sponsored by the National Science
 933 Foundation through NSF Award DBI-1300426, with additional
 934 support from The University of Tennessee, Knoxville. Infinite
 935 revisions were conducted at the Santa Fe Institute made possible
 936 by travel awards to JDY and TG. Additional support came
 937 from UC Merced startup funds to JDY, the International Centre
 938 for Theoretical Physics ICTP-SAIFR, FAPESP (2016/01343-7)
 939 and CNPq (302049/2015-0) to MAMA, CNPq and FAPESP
 940 (2018/14809-0) to PRG, and DFG research unit 1748 and EPSRC
 941 (EP/N034384/1) to TG.

942

943

944 Author contributions

945 JDY and TG conceived of the model framework. JDY, MMP,
 946 MAMA, and TG designed the analyses. JDY, MMP, MAMA,
 947 JLOD, PRG, DG, and TG analyzed the results and contributed
 948 to multiple versions of the manuscript.

949

950 Competing interests

951 The authors declare no competing interests.



952

SUPPLEMENTARY METHODS

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Appendix 1: Building the source pool

954 Here and henceforth, we refer to the assembly model presented in the main text as the ENIGMa model (E:eat, N:need, Ig:ignore, Ma:make). To initiate the ENIGMa assembly model, we must first construct the source pool, where each ecological entity (species + modifiers) is defined by their potential interactions. The model is initialized by creating S species and $M = \eta S$ modifiers, such that $N = S + M$ is the expected total number of entities (prior to considering engineering redundancies) and η is the expected number of modifiers made per species in the community. The 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 species x eats modifier m and a probability q_n that species x needs modifier m . For simplicity we assume throughout that $p_e = q_e$ and that $p_n = q_n$, such that the probability of drawing a species-modifier interaction is taken across replicates. 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 species x eats modifier m and a probability q_n that species x needs modifier m . For simplicity we assume throughout that $p_e = q_e$ and that $p_n = q_n$, such that the probability of drawing a species-modifier interaction is the same.

955 Without engineering redundancies (i.e. each modifier that a species makes is unique), the expected number of modifiers is $M = \eta S$ where η is the mean number of modifiers made per species. If we allow for engineering redundancies, the realized number of modifiers $M' < M$. To determine the number of modifiers in the pool, for each species a set number of modifiers is drawn, where $M_i \sim \text{Poiss}(\eta)$. The expected proportion of species that are engineers (species that make modifiers) is thus $1 - e^{-\eta}$, where e is Euler's number. If a particular modifier is randomly and independently drawn for a given engineer from a complete list of all possible

956 modifiers, such that multiple species – with some probability – can make the same modifier, the expected number of modifiers becomes

$$M' = \eta S \left(1 - \frac{1}{e}\right).$$

957 The frequencies of eat and need interactions, p_e and p_n respectively, are assigned a priori (see Supplementary Appendix 2 for different model parameterizations). The frequency of engineering (make) interactions can be calculated as

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

958 The frequency of the null interaction is then calculated by $p_\emptyset = 1 - (p_e + p_n + p_m)$

959 species-modifier interactions, respectively. Pairwise interactions are established randomly, such that the source pool matrix has no imbuited structure apart from the number of species, the number of modifiers, and the frequency of each directional interaction

960 type. Each source pool is provided a *basal resource* (the first row/column). A species with a trophic interaction to this resource is identified as an autotroph (or mixotroph depending on its other trophic interactions). If they do not have service dependencies with other species/modifiers, it is these species that are uniquely able to initiate assembly.

961 When engineering redundancies are allowed, the expected number of unique versus redundant modifiers in the source pool can be determined analytically. The total number of modifiers is $M' = \eta S(1 - e^{-1})$, and can be subdivided into modifiers that have a unique engineer and those that have multiple engineers. The number of modifiers with a single engineer is $M'_{\text{unique}} = \eta S e^{-1}$.

962 The number of modifiers made by multiple engineers is calculated as $M' - M'_{\text{unique}}$, such that

$$M'_{\text{redundant}} = M' - M'_{\text{unique}} = \eta S \frac{e - 2}{e},$$

963 such that the proportion of redundant modifiers ϕ is

$$\phi = \frac{M' - M'_{\text{unique}}}{M'} = \frac{e - 2}{e - 1} \approx 0.418.$$

964 Accordingly, we find that the number of redundant modifiers increases linearly with η , while the proportion of modifiers that are redundant is fixed. Figure S8a,b shows both analytical expectations and numerically-derived measures for $M'_{\text{redundant}}$ and ϕ , respectively.

965 As described in Methods, the assembly process can be simulated efficiently with an event-driven simulation utilizing a Gillespie algorithm. Generally, one computes the rates r_j of all possible events 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 $r_a / \sum_j r_j$. The effect of the event is then realized and the list of possible events is updated for the next step. In our framework, at the beginning of each simulation step we compute: 1) all species in the pool and absent from the community that have trophic and service dependencies met by those species in the community: these species are subject to colonization; 2) all species x needs modifier m . For simplicity we assume throughout that $p_e = q_e$ and that $p_n = q_n$, such that the probability of drawing a species-modifier interaction is highest for at least one of their resources: these species are subject to primary extinction; 3) all species in the community that do not meet their eat and/or need dependencies: these species are subject to secondary extinction; 4) all modifiers in the community that no longer have an engineer: these modifiers are subject to elimination. We then select one of the four events with a probability proportional to the number of entities that satisfy the criteria for each modifier $M' < M$. To determine the number of modifiers in the pool, for each species a set number of modifiers is drawn, where $M_i \sim \text{Poiss}(\eta)$. The expected proportion of species that are engineers is thus $1 - e^{-\eta}$, where e is Euler's number. If a particular modifier is randomly and independently drawn for a given engineer from a complete list of all possible

966 modifiers, such that multiple species – with some probability – can make the same modifier, the expected number of modifiers becomes

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1070 there are many similarities, there are also some important differ- 1114 **Appendix 4: The structure of engineered food webs**
 1071 ences, some of which are highlighted in the main text. While we
 1072 consider a comparison of our framework with other food web mod-
 1073 els such as the Niche Model relevant, we emphasize that the mo-
 1074 tivations underlying both are distinct. Our approach is intended
 1075 to provide a deeper understanding into how multitype dependen-
 1076 cies between species and the environment impact the dynamics of
 1077 community assembly. While capturing general qualitative features
 1078 of empirical systems demonstrates that the dynamics we consider
 1079 are ecologically relevant, the goal of our approach is distinct from
 1080 that of static food web models, which aim to maximize structural
 1081 similarities between model and empirical systems^{2,3}.

1115 We examined whether and to what extent the structure of food
 1116 webs was altered when engineers are introduced into the commu-
 1117 nity. Because trophic links can now exist between species-modifiers
 1118 as well as species-species, there are different ways of accounting
 1119 for structure, making direct comparisons with non-engineered food
 1120 webs somewhat difficult. We note that we exclude service interac-
 1121 tions in this case to best match the structural analysis described in
 1122 the main text and shown in Fig. 2. While the inclusion of engineers
 1123 ($\eta = 2$) does have an impact on stability in terms of primary versus
 1124 secondary extinction rates, there is not a strong effect of engineer-
 1125 ing on steady state species richness (Fig. S6a; species richness is
 1126 shown in blue, modifier richness is shown in red).

1127 The role of specialists *does* and *does not* change with the intro-
 1128 duction of engineering, depending on how specialization is defined.
 1129 As in the main text, a specialist is defined when its generality
 1130 index $G_i < 1$ relative to the steady state link density. When engi-
 1131 neered modifiers are included, we account for a trophic interaction
 1132 between a species and another's modifier as an interaction that
 1133 occurs between those two species indirectly through the modifier
 1134 intermediary. So if a species B makes a modifier M , and A eats
 1135 M , then we set A to (indirectly) eat B . This accounting of both
 1136 direct and indirect trophic interactions between species can then be
 1137 compared to *i*) the direct trophic link density of the community,
 1138 or *ii*) the direct + indirect trophic link density of the community,
 1139 and some insights can be gained from both approaches.

1082 We compared steady state ecological networks that emerge from
 1083 ENIgMa (described in Methods, main text) with food webs con-
 1084 structed from the Niche Model² with similar species richness and
 1085 connectance. Because species richness and connectance of the
 1086 Niche Model are often altered by eliminating disconnected species,
 1087 we compared *i*) species richness, *ii*) connectance, *iii*) mean species
 1088 degree, *iv*) standard deviation of out-degree distributions, and *v*)
 1089 standard deviation of in-degree distributions averaged across 1000
 1090 replicates for each model.

1129 We found that all measures resulted in fairly similar values be- 1141 In the first case, where G_i is determined relative to L_{direct}^*/S^* ,
 1142 tween ENIgMa and the Niche Model food webs with a some im- 1143 we find that there are no potential specialists that colonize the
 1144 portant differences (Figs. S2,S3). While similar, ENIgMa pro- 1145 community, and (as in the main text) functional specialists colonize
 1146 duces consistently lower values of connectance, mean species de- 1147 at steady state (mean proportion specialists at steady state is 0.04;
 1147 gree, as well as standard deviations of the in- and out-degree dis- 1148 Fig. S6b). This means that the indirect links that define trophic in-
 1149 tributions. This means that the food webs produced by ENIgMa 1149 teractions between species and modifiers increase the link-density of
 1150 are more sparsely connected with less variance between species. 1150 the network relative to that defined only by direct trophic inter-
 1151 These results were expected, as the Niche Model assumes system- 1151 actions. In words, modifiers serve to connect otherwise disconnected
 1152 atically increasing dietary ranges with higher niche values, whereas 1152 species, formalizing the otherwise indirect relationships that struc-
 1153 the trophic interactions assigned to species in the source pool of 1153 ture the role of engineers in the community. In the second case,
 1154 ENIgMa are drawn independently. An important difference be- 1154 where G_i is determined relative to $L_{\text{indirect}}^*/S^*$, we find that the
 1155 tween the Niche Model and ENIgMa is that we do not distinguish 1155 changes in both functional and potential specialists over the course
 1156 between traditional consumers and parasites. A different frame- 1156 of assembly (Fig. S6c) follow those observed for non-engineered
 1157 work known as the Inverse Niche Model⁴ has been proposed to ad- 1157 food webs (Fig. 2b).

1158 dress parasitic interactions. The Inverse Niche Model assumes in- 1158 Finally, we observe that while the number of trophic levels in-
 1159 creasing specialization with feeding hierarchies, which would serve 1159 crease in the presence of species-modifier interactions, the overall
 1160 to lower the average generality of species (lower degree). In ad- 1160 structure of the community advances over the course of as-
 1161 dition, the Inverse Niche model outputs lower standard deviations 1161 sembly in much the same way as it does without engineers (Fig.
 1162 of in- and out-degree distributions. Together these trends suggest 1162 S6d). Trophic levels are calculated with respect to indirect species
 1163 that the qualitative structural differences that we observe for the 1163 interactions through modifier intermediaries. Because species at
 1164 assembly and Niche model may reflect an important structural dis- 1164 any trophic level can engineer modifiers used as resources by other
 1165 tinction between food webs that do and do not include parasitic 1165 species, the mean trophic level of the community is systematically
 1166 species.

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 1166 [2] Williams, R. J. & Martinez, N. D. Simple rules yield 1172 The inverse niche model for food webs with parasites.
 1167 complex food webs. *Nature* **404**, 180–183 (2000). 1173 *Theor. Ecol.* **3**, 285–294 (2010).
 1168 [3] Williams, R. J. & Purves, D. W. The probabilistic niche 1174
 1169 model reveals substantial variation in the niche structure

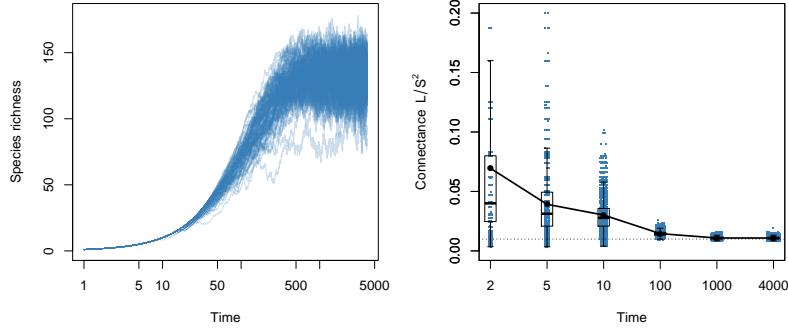


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because a small number of species interact with each other such that the proportion of realized interactions (out of all possible interactions) is closer to unity. Over time, connectance decays as species richness increases, and the density of trophic interactions declines.

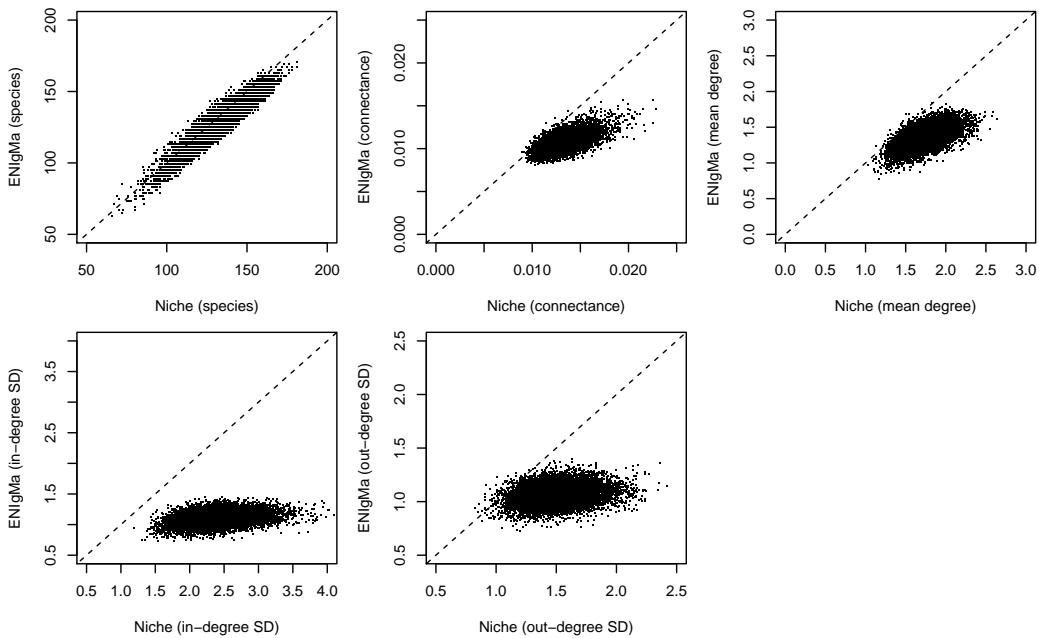


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in-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

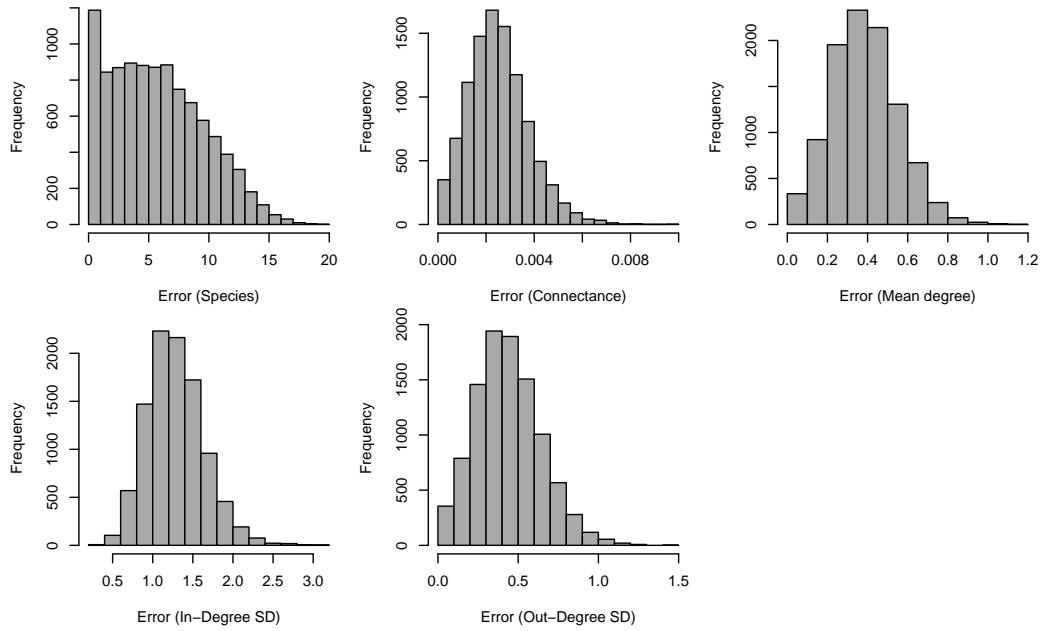


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as $\sqrt{(m_i - m_j)^2}$, where m_i and m_j are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model was used to assess metrics.

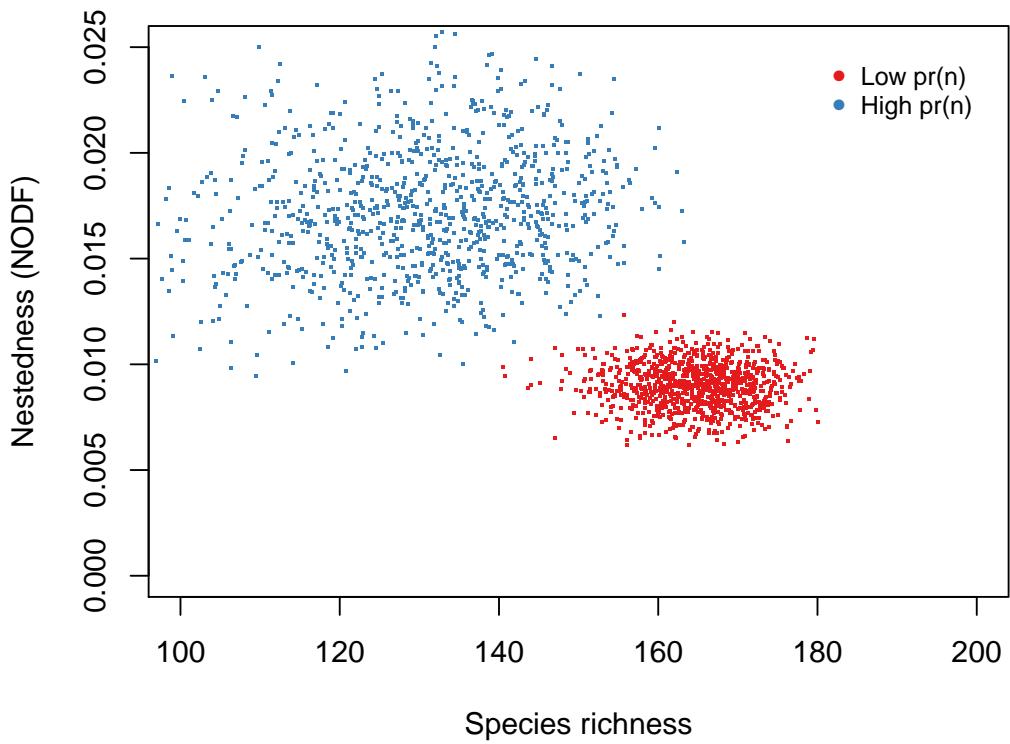


Figure S4. Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities without service interactions ($p_n = 0$) compared to those with a high frequency of service interactions ($p_n = 0.002$). While higher frequencies of service interactions do lower steady state species richness (due to increasing secondary extinction rates), there is not a relationship between nestedness and species richness across replicates for a given service interaction frequency.

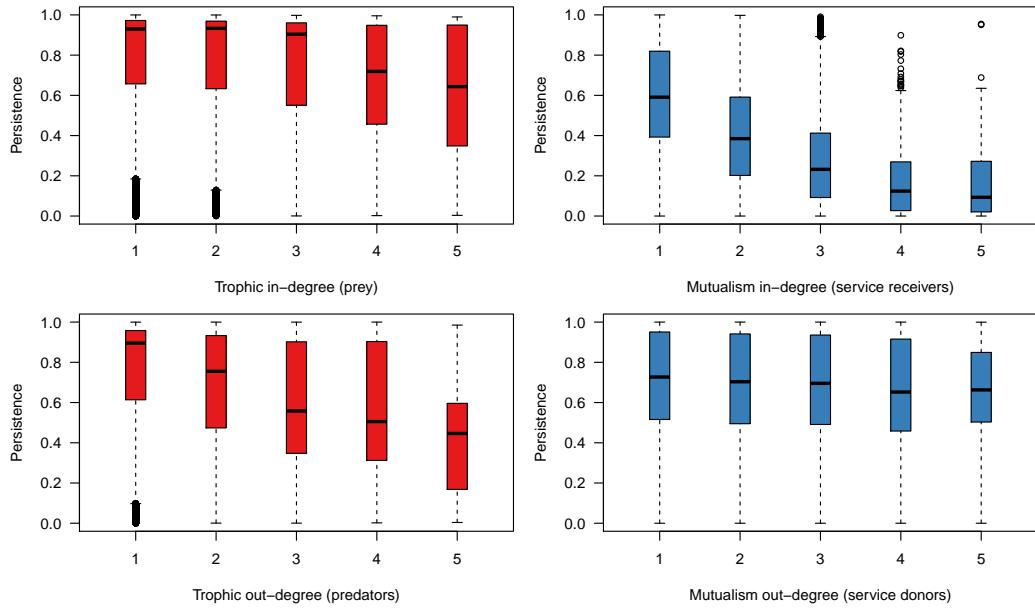


Figure S5. Persistence as a function of trophic and service in/out-degree for communities with higher densities of service interactions ($p_e = 0.01$; $p_n = 0.002$). Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top) and out-degree (the number of predators a species has; bottom). Right column: species-specific persistence as a function of the mutualism in-degree (the number of service receivers a species has; top) and out-degree (the number of service providers a species has; bottom). As the trophic in- and out-degree of species increases, competition strength is lowered and persistence decreases. As the mutualism in-degree increases, so does the number of service donors that are needed for the receiving species to remain in the community. This introduces structural constraints that lowers persistence.

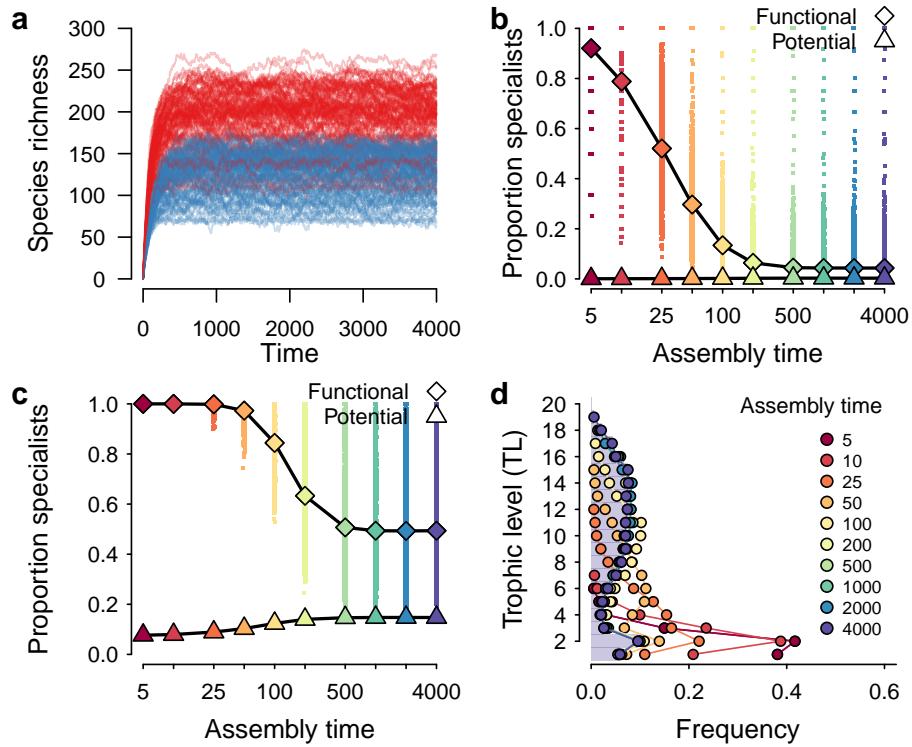


Figure S6. **a**, Assembling communities over time from a pool of 200 non-engineering species. Species richness is blue; modifier richness is red. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$ relative to the steady state link density. G_i is scaled to the steady state link density where links are direct trophic interactions between species. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **c**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$. Here G_i is scaled to the steady state link density where links are composed of *both* direct trophic interactions between species and indirect trophic interactions between consumers and those species that produce modifiers as resources. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **d**, 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 Methods for parameter values.

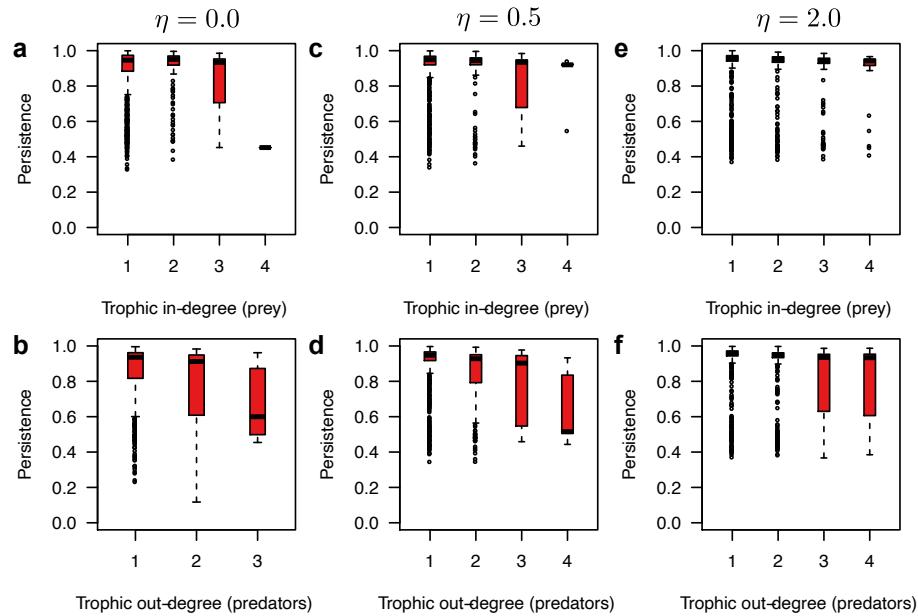


Figure S7. Species-specific persistence as a function of **a**, trophic in-degree (number of resources a species has; top) and **b**, out-degree (number of consumers that eat the species; bottom) when there are no engineers in the community. Species-specific persistence as a function of **c**, trophic in-degree (number of resources a species has; top) and **d**, out-degree (number of consumers that eat the species; bottom) when engineers are rare ($\eta = 0.5$). The notion that having a small number of engineers and modifiers in the community increases rates of primary extinction (Fig. 4a) by stabilizing consumers at the expense of their prey is supported by *i*) increased persistence of generalist consumers, and *ii*) the presence of species with larger number of predators. Species-specific persistence as a function of **e**, trophic in-degree (number of resources a species has; top) and **f**, out-degree (number of consumers that eat the species; bottom) when engineers are common ($\eta = 2.0$). The notion that a large number of engineers and modifiers in the community decrease rates of primary extinction (Fig. 4a) due to expanding niche space (diffusing the effects of competitive exclusion) is supported by the lack of correlation between trophic in/out-degree and persistence.

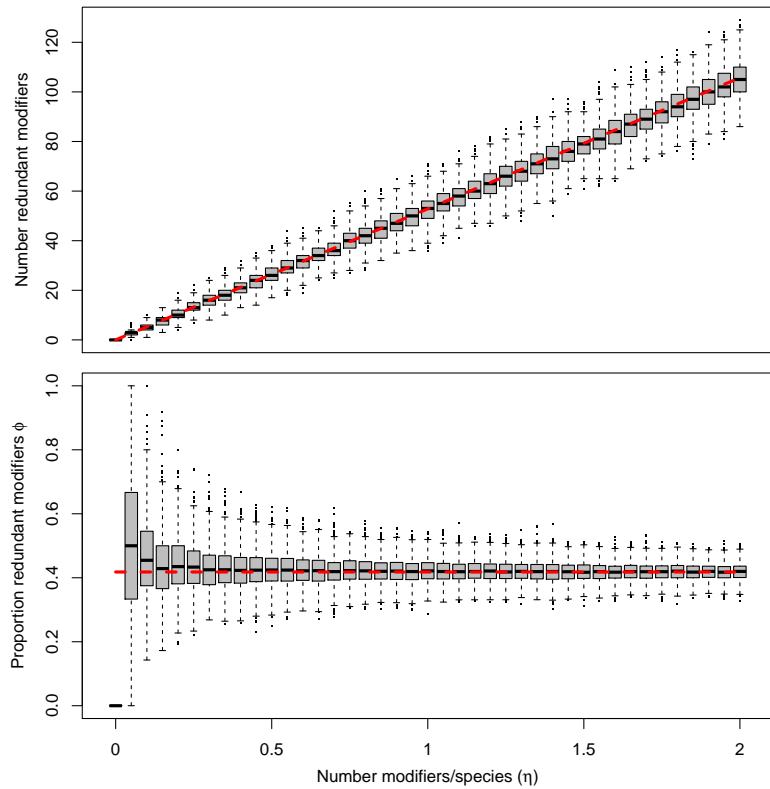


Figure S8. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the source pool as 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).

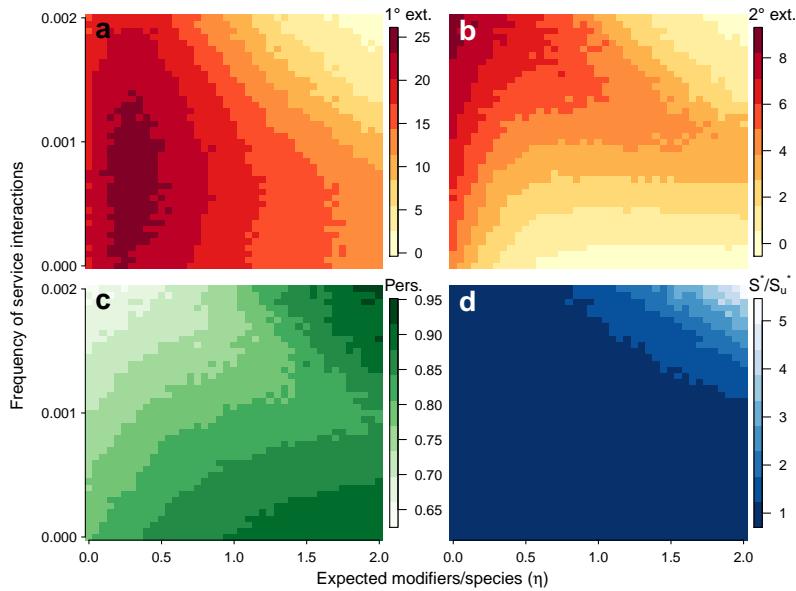


Figure S9. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers 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 Methods for default parameter values.

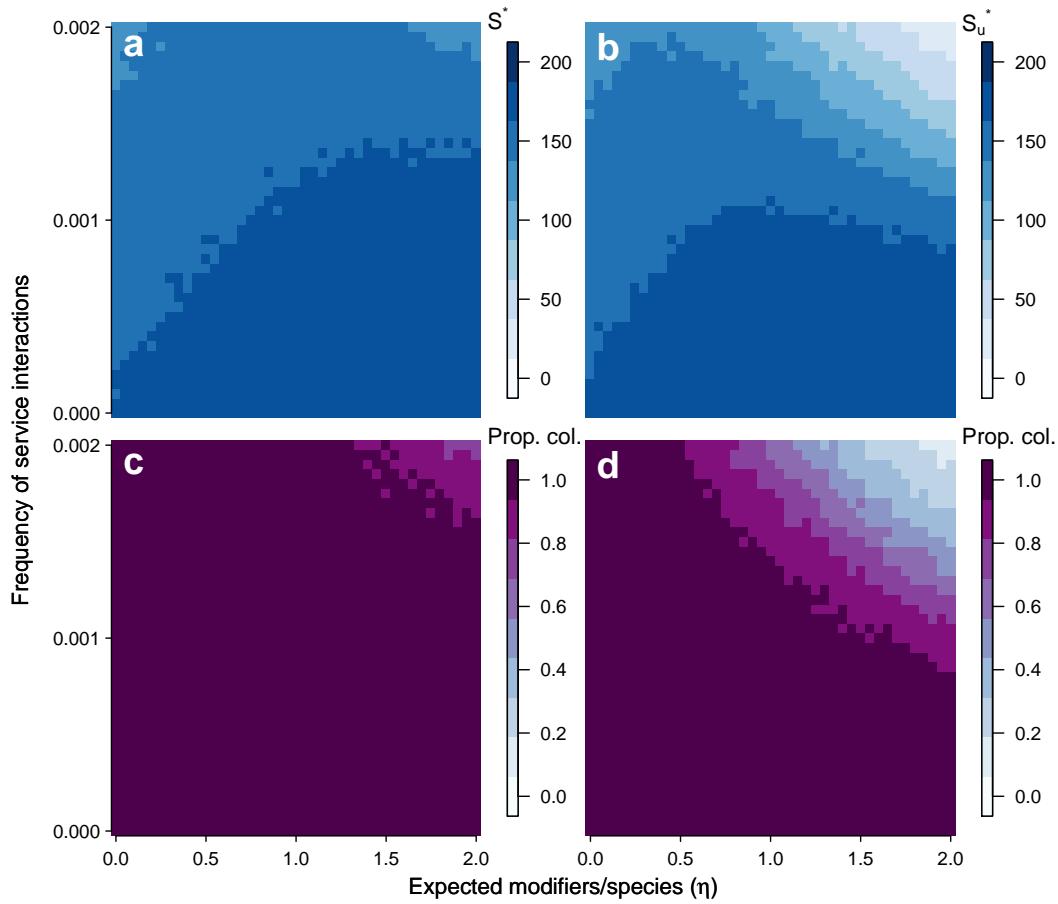


Figure S10. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (without redundant engineering).