

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

Recent interest in ‘multilayer networks’ comprising multiple interaction types (multitype interactions) may provide additional insight into these processes^{27,28}. However, interactions where species affect others by altering the abiotic environment in a lasting way have not yet been incorporated into models of ecological networks. These interactions, known as ecosystem engineering^{29,30} or more generally niche construction^{12,31}, are quite common in nature and exist in almost every ecosystem.

Diverse interactions occur not only between species but indirectly through the effects that species have on their environment^{30,32,33}. Elephants root out large saplings and small trees, enabling the formation and maintenance of grasslands^{34,35} and creating habitat for smaller vertebrates³⁶. Burrowing rodents such as gophers and African mole rats create shelter and promote primary production by aerating the soil^{37,38}, salmon and aquatic invertebrates create freshwater habitats by changing stream morphology³⁹, and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth⁴⁰. These examples illustrate ecosystem engineering, where the engineering organism alters the environment on timescales longer than its own⁴¹. Engineers are widely acknowledged to have impacts on both small and large spatial scales⁴², and likely serve as important key-stone species in many habitats⁴³.

Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth⁴⁴. For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the

73 Proterozoic roughly 2.5 Byrs BP^{44,45}, paving the way 131 driving community assembly. First, we show that the
 74 for the biological invasion of terrestrial habitats. In the 132 assembly of communities in the absence of engineering
 75 oceans it is thought that rRNA and protein biogenesis of 133 reproduces many features observed in empirical systems.
 76 aquatic photoautotrophs drove the nitrogen:phosphorous 134 These include changes in the proportion of generalists
 77 ratio (the Redfield Ratio) to ca. 16:1 matching that of 135 over the course of assembly that accord with measured
 78 plankton⁴⁶, illustrating that engineering clades can have 136 data and trophic diversity similar to empirical observa-
 79 much larger, sometimes global-scale effects. 137 tions. Second, we show that increasing the frequency
 80 The effect of abiotic environmental conditions on 138 of mutualistic interactions leads to the assembly of
 81 species is commonly included in models of ecological 139 ecological networks that are more nested, a common
 82 dynamics^{47–49} due to its acknowledged importance and 140 feature of diverse mutualistic systems⁵², but are also
 83 because it can – to first approximation – be easily sys- 141 prone to extinction cascades. Our third key result shows
 84 tematized. By comparison the way in which species en- 142 that increasing the proportion of ecosystem engineers
 85 gineer the environment defies easy systematization due to 143 within a community has nonlinear effects on observed
 86 the multitude of mechanisms by which engineering oc- 144 extinction rates. While we find that a low amount of
 87 curs. While interactions between species and the abi- 145 engineering increases extinction rates, a high amount of
 88 otic environment have been conceptually described^{33,50}, 146 engineering has the opposite effect. Finally we show that
 89 the absence of engineered effects in network models was 147 redundancies in engineered effects promote community
 90 addressed by Odling-Smee et al.³⁰, where they outlined 148 diversity by lowering the barriers to colonization.
 91 a conceptual framework that included both species and
 92 abiotic compartments as nodes of a network, with links
 93 denoting both biotic and abiotic interactions.

94 How does the assembly dynamics of species constrained
 95 by multitype interactions impact community structure
 96 and stability? How are these processes altered when
 97 the presence of engineers modifies species' dependencies
 98 within the community? Here we model the assembly of
 99 an ecological network where nodes represent ecological
 100 entities, including engineering species, non-engineering
 101 species, and the effects of the former on the environment,
 102 which we call abiotic *modifiers*. The links of the network
 103 that connect both species and modifiers represent trophic
 104 (eat interactions), service (need interactions), and en-
 105 gineering dependencies, respectively (Fig. 1; see Meth-
 106 ods for a full description). Trophic interactions repre-
 107 sent both predation as well as parasitism, whereas service
 108 interactions account for non-trophic interactions associ-
 109 ated with reproductive facilitation such as pollination or
 110 seed dispersal. In our framework a traditional mutual-
 111 ism (such as a plant-pollinator interaction) consists of a
 112 service (need) interaction in one direction and a trophic
 113 (eat) interaction in the other. These multitype interac-
 114 tions between species and modifiers thus embed multiple
 115 dependent ecological sub-systems into a single network
 116 (Fig. 1). Modifiers in our framework overlap conceptu-
 117 ally with the ‘abiotic compartments’ described in Odling-
 118 Smee et al.³⁰. Following Pillai et al.⁵¹, we do not track
 119 the abundances of biotic or abiotic entities but track only
 120 their presence or absence. We use this framework to ex-
 121 plore the dynamics of ecosystem assembly, where the col-
 122 onization and extinction of species within a community
 123 depends on the constraints imposed by the trophic, ser-
 124 vice, and engineering dependencies. We then show how
 125 observed network structures emerge from the process of
 126 assembly, compare their attributes with those of empir-
 127 ical systems, and examine the effects of ecosystem engi-
 128 neers.

129 Our results offer four key insights into the roles of
 130 multitype interactions and ecosystem engineering in

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

150 **Assembly without ecosystem engineering.** Com-
 151 munities assemble by random colonization from a source
 152 pool. A species from the source pool can colonize if it
 153 finds at least one resource that it can consume (one eat
 154 interaction is satisfied; cf. Ref. 53) and all of its non-
 155 trophic needs are met (all need interactions are satisfied;
 156 see Fig. 1). As such, service interactions are assumed
 157 to be obligate, whereas trophic interactions are flexible –
 158 except in the case of a consumer with only a single re-
 159 source. While a basal resource is always assumed to be
 160 present (white node in Fig. 1b), following the establish-
 161 ment of an autotrophic base, the arrival of mixotrophs
 162 (i.e. mixing auto- and heterotrophy) and lower trophic
 163 heterotrophs create opportunities for organisms occupy-
 164 ing higher trophic levels to invade. This expanding niche
 165 space initially serves as an accelerator for community
 166 growth.

167 Following the initial colonization phase, extinctions be-
 168 gin to slow the rate of community growth. Primary ex-
 169 tinctions occur if a given species is not the strongest
 170 competitor for at least one of its resources. A species'
 171 competition strength is determined by its interactions:
 172 competition strength is enhanced by the number of need
 173 interactions and penalized by the number of its resources
 174 (favoring trophic specialists) and consumers (favoring
 175 species with fewer predators). This encodes three key as-
 176 sumptions: that mutualisms provide a fitness benefit⁵⁴,
 177 specialists are stronger competitors than generalists^{55–58},
 178 and many predators entail an energetic cost⁵⁹. Secondary
 179 extinctions occur when species lose its last trophic or any
 180 of its service requirements. See Fig. 1d,e for an illus-
 181 tration of the assembly process. As the colonization and ex-
 182 tinction rates converge, the community reaches a steady
 183 state around which it oscillates (Fig. 2a). See Methods
 184 and Supplementary Appendix 1 for a complete descrip-
 185 tion of the assembly process. Specific model parameteri-
 186 zations are described in Supplementary Appendix 2.

187 Assembly of ecological communities in the absence of
 188 engineering results in interaction networks with struc-

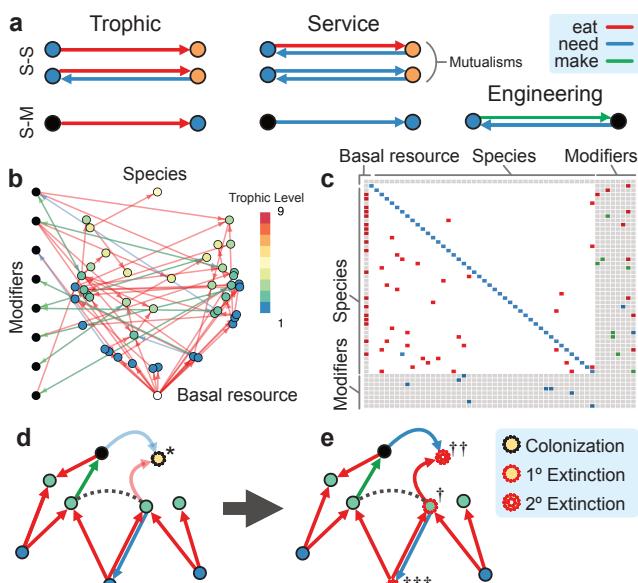


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mutualistic relationships define both species-species (S-S) and species-modifier (S-M) interactions; an engineering interaction is denoted by an engineer that makes a modifier, such that the modifier needs the engineer to persist. **b**, An assembling 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 exclusion (competition denoted by dashed line) to species (†). The extinction of species (†) will cascade to affect those connected by trophic (††) and service (†††) dependencies.

tures consistent with empirical observations. As the community reaches steady state, we find that the connectance of trophic interactions ($C(t) = L(t)/S(t)^2$, where $S(t)$ is species richness and $L(t)$ is the number of links at time t) decays to a constant value (Fig. S1). Decaying connectance followed by stabilization around a constant value has been documented in the assembly of mangrove communities¹⁶ and experimental aquatic mesocosms¹⁷. The initial decay is likely inevitable in sparse webs as early in the assembly process the small set of tightly interacting species will have a high link density from which

it will decline as the number of species increases. Compared to trophic networks constructed using the Niche model⁶⁰ given similar species richness and connectance, our framework results in networks with degree distributions of similar means but with reduced variance (Supplementary Appendix 3).

Recent empirical work has suggested that generalist species may dominate early in assembly, whereas specialists colonize after a diverse resource base has accumulated^{16,53}. Here the trophic generality of species

i is defined as $G_i(t) = k_i^{in}(t)/(L^*/S^*)^{60}$, where $k_i^{in}(t)$ is the number of species consumed by species i at time t , which is scaled by the steady state link density L^*/S^* , as is typically done in empirical investigations¹⁶. A species is classified as a generalist if $G_i > 1$ and a specialist if $G_i < 1$. If generality is evaluated with respect to the steady state link density, we find that species with many potential trophic interactions realize only a subset of them, thereby functioning as specialists early in the assembly process (Fig. 2b). As the community grows, more potential interactions become realized, and functional specialists become functional generalists. Moreover, as species assemble the available niche space expands, and the proportion of potential trophic specialists grows (Fig. 2b). This confirms expectations from the trophic theory of island biogeography⁵³, where communities with lower richness (i.e. early assembly) are less likely to support specialist consumers than species-rich communities (i.e. late assembly). At steady state the proportion of functional specialists is ca. 56%, which is similar to empirical observations of assembling food webs¹⁶.

The dominance of functional specialists early in assembly 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 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 $TL_{max} (\pm \text{standard deviation}) = 11 \pm 2.8$ (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 con-

fers 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.

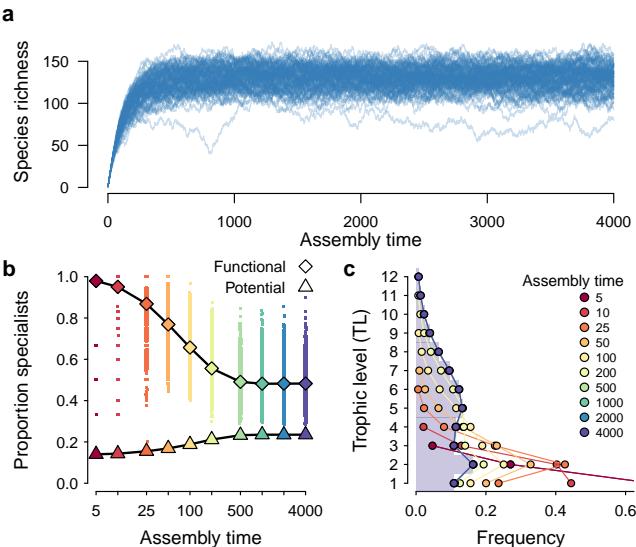


Figure 2. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index $G_i < 1$. 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 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.

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 cov-

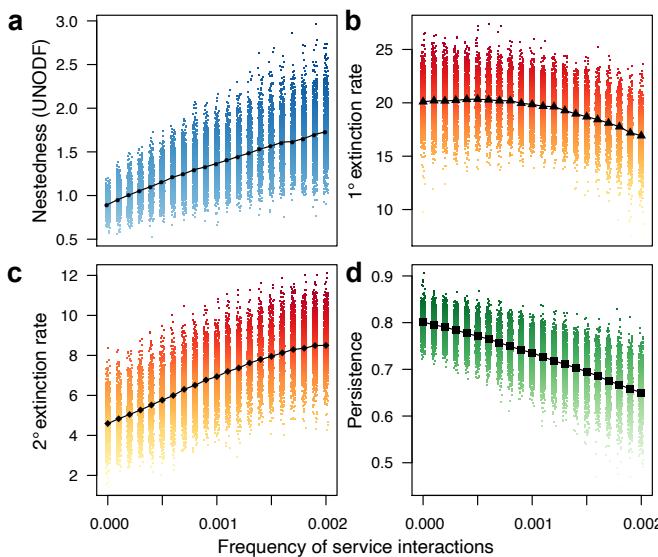


Figure 3. **a**, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)⁷⁹. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. **b**, Primary 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.

ered 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 (modifiers without a maker) 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 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). 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 interdependences between and among species. As trophic interactions are replaced by service interactions, previously vulnera-

434 ble species gain a competitive foothold and persist, low-
 435 ering rates of primary extinctions (Fig. 4a). The costs of
 436 these added services to the community are an increased
 437 rate of secondary extinctions (Fig. 4b) and higher species
 438 turnover (Fig. 4c), such that extinctions are less common
 439 but lead to larger cascades.

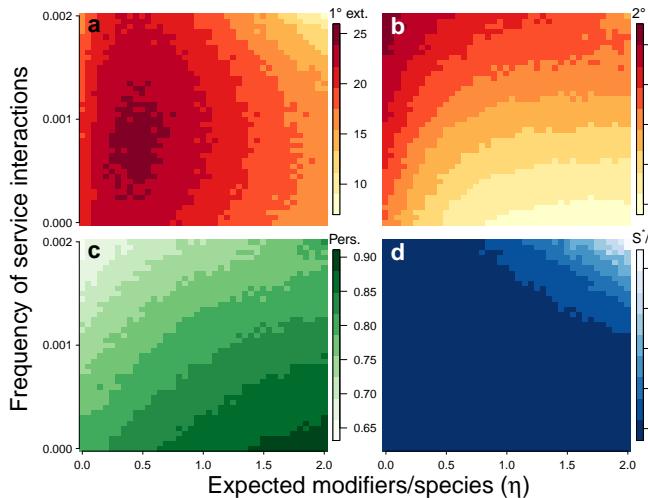


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade 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.

440 While the importance of engineering timescales has
 441 been emphasized previously⁴¹, redundant engineering
 442 has been assumed to be unimportant²⁹. We argue that
 443 redundancy may be an important component of highly
 444 engineered systems, and particularly relevant when the
 445 effects of engineers increase their own fitness⁸⁵ as is gen-
 446 erally assumed to be the case with niche construction⁸⁸.

447 The vast majority of contemporary ecosystem engineer-
 448 ing case studies focus on single taxa, such that redundant
 449 engineers appear rare²⁹. However if we consider longer
 450 timescales, increasing diversity of engineering clades may
 451 promote redundancy, and in some cases this may feed
 452 back to accelerate diversification³¹. Such positive feed-
 453 back mechanisms likely facilitated the global changes in-
 454 duced by cyanobacteria in the Proterozoic^{44,45} among
 455 other large-scale engineering events in the history of
 456 life⁴⁴. Engineering redundancies are likely important on
 457 shorter timescales as well. For example, diverse sessile

458 epifauna on shelled gravels in shallow marine environ-
 459 ments are facilitated by the engineering of their ances-
 460 tors, such that the engineered effects of the clade de-
 461 termine the future fitness of descendants⁹⁶. In the mi-
 462 crobiome, redundant engineering may be very common
 463 due to the influence of horizontal gene transfer in struc-
 464 turing metabolite production⁹⁷. In these systems, re-
 465 dundancy in the production of shared metabolic re-
 466 sources may play a key role in community structure and
 467 dynamics^{90,91}.

468 When there are few engineers, each modifier in the
 469 community tends to be unique to a particular engineer-
 470 ing species. Engineering redundancies increase linearly
 471 with η (Supplementary Appendix 1; Fig. S8), such that
 472 the loss of an engineer will not necessarily lead to the
 473 loss of engineered modifiers. We examine the effects of
 474 this redundancy by comparing our results to those pro-
 475 duced by the same model, but where each modifier is
 476 uniquely produced by a single species. Surprisingly, the
 477 lack of engineering redundancies does not alter the gen-
 478 eral relationship between engineering and measures of
 479 community stability (Fig. S9). However we find that
 480 redundancies play a central role in maintaining species
 481 diversity. When engineering redundancies are allowed,
 482 steady state community richness S^* does not vary con-
 483 siderably with increasing service interactions and engi-
 484 neering (Fig. S10a). In contrast, when redundant engi-
 485 neering is not allowed, steady state community richness
 486 S_u^* declines sharply (Figs. 4d, S10b).

487 Communities lacking redundant engineering have lower
 488 species richness because species' trophic and service de-
 489 pendencies are unlikely to be fulfilled given a particu-
 490 lar assemblage (Fig. S10c,d). Colonization occurs only
 491 when trophic and service dependencies are fulfilled. As
 492 such, a species requiring multiple engineered modifiers,
 493 each uniquely produced, means that each required entity
 494 must precede colonization. This magnifies the role of pri-
 495 ority effects in constraining assembly order¹², precluding
 496 many species from colonizing. In contrast, redundant
 497 engineering increases the temporal stability of species'
 498 niches while minimizing priority effects by allowing mul-
 499 tiple engineers to fulfill the dependencies of a particular
 500 species. Our results thus suggest that redundant engi-
 501 neers may play important roles in assembling ecosystems
 502 by lowering the barriers to colonization, promoting com-
 503 munity diversity.

504 We have shown that the dynamics of assembly driven
 505 by competitive forces influenced by multitype interac-
 506 tions can produce communities with realistic structures
 507 and dynamics. Moreover, the inclusion of ecosystem
 508 engineering by way of modifier nodes reveals that low
 509 levels of engineering may be expected to produce higher
 510 rates of extinction while limiting the size of extinction
 511 cascades, and that engineering redundancy – whether
 512 it is common or rare – serves to promote colonization
 513 and by extension diversity. We suggest that including
 514 the effects of engineers, either explicitly as we have
 515 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 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 $M_i \sim \text{Poiss}(\eta)$ where η is the mean number of modifiers made per species. 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

$$\sigma_i = c_{nn} n_i - c_{ee} e_i - c_{vv} v_i, \quad (1)$$

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>.

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929

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931 Author contributions

932 JDY and TG conceived of the model framework. JDY, MMP,
 933 MAMA, and TG designed the analyses. JDY, MMP, MAMA,
 934 JLOD, PRG, DG, and TG analyzed the results and contributed
 935 to multiple versions of the manuscript.

936

937 Competing interests

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SUPPLEMENTARY METHODS

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Appendix 1: Building the source pool

964 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,y) 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 m is highest for at least one of their resources: these species are ing trophic and service interactions for both species-species and species-modifier interactions is the same.

965 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

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

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

(S1)

967 To set interactions between species and modifiers in the pool, we must know the frequency of each directed interaction type. 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

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

(S2)

968 The frequency of the null interaction is then calculated by $p_\emptyset = 1 - (p_e + p_n)$ for species-species interactions and $p_\emptyset = 1 - (p_e + p_n + p_m)$

969 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 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.

970 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 $M'_{\text{unique}} = \eta S e^{-1}$. The number of modifiers made by multiple engineers is calculated as $M' - M'_{\text{unique}}$, such that

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

971 such that the proportion of redundant modifiers ϕ is

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

972 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.

973 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 in the community that do not have a competition strength that 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 event. The rates at which each event occurs change at each step, equal to the number of entities that meet the criteria for each event at that point in time. The species/modifier that colonizes a species (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

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

975 $M' = \eta S \left(1 - \frac{1}{e}\right)$. For example, if the community is empty, and 50 species are

976 able to colonize, the probability of drawing ‘colonization’ is 1, and the colonizer would be randomly drawn from the 50 capable of colonizing. Another example: if 20 species are able to

977 colonize, 10 species are not superior competitors for any one of their resources, and 30 species do not meet their dependencies,

978 $\sum_j r_j = 60$, and $r_{\text{colonize}} = 1/3$, $r_{\text{primary extinction}} = 1/6$, and $r_{\text{secondary extinction}} = 1/2$. In this case, the most probable event is a secondary extinction. After this single event takes place, the

979 community is updated depending on which event occurred, and the simulation proceeds to 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

980 providing a much higher numerical efficiency⁹⁹.

Appendix 2: Model parameterizations

981 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 (time-steps).

982 **Assembly without ecosystem engineering** Here we set the average number of modifiers made per species $\eta = 0$ and the probability of need interactions in the species pool $p_n = 0.002$.

983 **Structure and dynamics of mutualisms** Again we used the default parameterizations but set $\eta = 0$, while varying $p_n \in [0, 0.002]$.

984 **Assembly with ecosystem engineering** Here we used the default parameterizations but varied $\eta \in [0, 2]$ and $p_n \in [0, 0.002]$.

Appendix 3: Comparison to Niche Model

985 We compared certain structural features of ENIGMa at steady state to those of the Niche Model⁶⁰. Comparisons were restricted

986 to networks constructed in the absence of engineering because engineers introduce indirect effects that are not considered in static food web models, and may make such comparisons irrelevant. While

987 (S3) 1077 We compared certain structural features of ENIGMa at steady state to those of the Niche Model⁶⁰. Comparisons were restricted

988 (S4) 1078 to networks constructed in the absence of engineering because engineers introduce indirect effects that are not considered in static food web models, and may make such comparisons irrelevant. While

1082 there are many similarities, there are also some important differ- 1126 **Appendix 4: The structure of engineered food webs**
 1083 ences, some of which are highlighted in the main text. While we
 1084 consider a comparison of our framework with other food web mod-
 1085 els such as the Niche Model relevant, we emphasize that the mo-
 1086 tivations underlying both are distinct. Our approach is intended
 1087 to provide a deeper understanding into how multitype dependen-
 1088 cies between species and the environment impact the dynamics of
 1089 community assembly. While capturing general qualitative features
 1090 of empirical systems demonstrates that the dynamics we consider
 1091 are ecologically relevant, the goal of our approach is distinct from
 1092 that of static food web models, which aim to maximize structural
 1093 similarities between model and empirical systems^{60,100}.

1127 We examined whether and to what extent the structure of food
 1128 webs was altered when engineers are introduced into the commu-
 1129 nity. Because trophic links can now exist between species-modifiers
 1130 as well as species-species, there are different ways of accounting
 1131 for structure, making direct comparisons with non-engineered food
 1132 webs somewhat difficult. We note that we exclude service interac-
 1133 tions in this case to best match the structural analysis described in
 1134 the main text and shown in Fig. 2. While the inclusion of engineers
 1135 ($\eta = 2$) does have an impact on stability in terms of primary versus
 1136 secondary extinction rates, there is not a strong effect of engineer-
 1137 ing on steady state species richness (Fig. S6a; species richness is
 1138 shown in blue, modifier richness is shown in red).

1139 The role of specialists *does* and *does not* change with the intro-
 1140 duction of engineering, depending on how specialization is defined.
 1141 As in the main text, a specialist is defined when its generality
 1142 index $G_i < 1$ relative to the steady state link density. When engi-
 1143 neered modifiers are included, we account for a trophic interaction
 1144 between a species and another's modifier as an interaction that
 1145 occurs between those two species indirectly through the modifier
 1146 intermediary. So if a species B makes a modifier M , and A eats
 1147 M , then we set A to (indirectly) eat B . This accounting of both
 1148 direct and indirect trophic interactions between species can then be
 1149 compared to *i*) the direct trophic link density of the community,
 1150 or *ii*) the direct + indirect trophic link density of the community,
 1151 and some insights can be gained from both approaches.

1094 We compared steady state ecological networks that emerge from
 1095 ENIgMa (described in Methods, main text) with food webs con-
 1096 structed from the Niche Model⁶⁰ with similar species richness and
 1097 connectance. Because species richness and connectance of the
 1098 Niche Model are often altered by eliminating disconnected species,
 1099 we compared *i*) species richness, *ii*) connectance, *iii*) mean species
 1100 degree, *iv*) standard deviation of out-degree distributions, and *v*)
 1101 standard deviation of in-degree distributions averaged across 1000
 1102 replicates for each model.

1103 We found that all measures resulted in fairly similar values be-
 1104 tween ENIgMa and the Niche Model food webs with a some im-
 1105 portant differences (Figs. S2,S3). While similar, ENIgMa pro-
 1106 duces consistently lower values of connectance, mean species de-
 1107 gree, as well as standard deviations of the in- and out-degree dis-
 1108 tributions. This means that the food webs produced by ENIgMa
 1109 are more sparsely connected with less variance between species.
 1110 These results were expected, as the Niche Model assumes system-
 1111 atically increasing dietary ranges with higher niche values, whereas
 1112 the trophic interactions assigned to species in the source pool of
 1113 ENIgMa are drawn independently. An important difference be-
 1114 tween the Niche Model and ENIgMa is that we do not distinguish
 1115 between traditional consumers and parasites. A different frame-
 1116 work known as the Inverse Niche Model¹⁰¹ has been proposed to
 1117 address parasitic interactions. The Inverse Niche Model assumes in-
 1118 creasing specialization with feeding hierarchies, which would serve
 1119 to lower the average generality of species (lower degree). In ad-
 1120 dition, the Inverse Niche model outputs lower standard deviations
 1121 of in- and out-degree distributions. Together these trends suggest
 1122 that the qualitative structural differences that we observe for the
 1123 assembly and Niche model may reflect an important structural dis-
 1124 tinction between food webs that do and do not include parasitic
 1125 species.

1167 Finally, we observe that while the number of trophic levels in-
 1168 crease in the presence of species-modifier interactions, the overall
 1169 trophic structure of the community advances over the course of as-
 1170 sembly in much the same way as it does without engineers (Fig.
 1171 S6d). Trophic levels are calculated with respect to indirect species
 1172 interactions through modifier intermediaries. Because species at
 1173 any trophic level can engineer modifiers used as resources by other
 1174 species, the mean trophic level of the community is systematically
 1175 elevated.

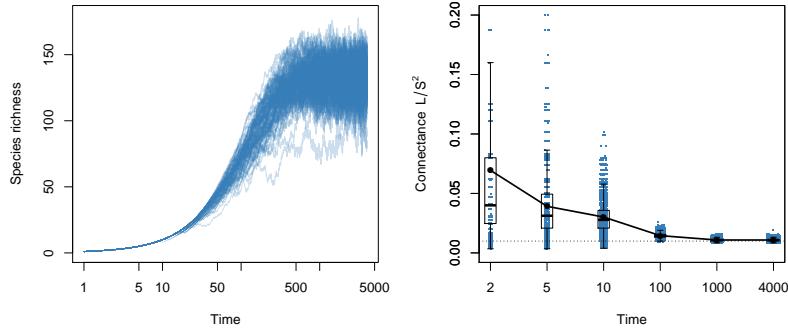


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because a small number of species interact with each other such that the proportion of realized interactions (out of all possible interactions)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

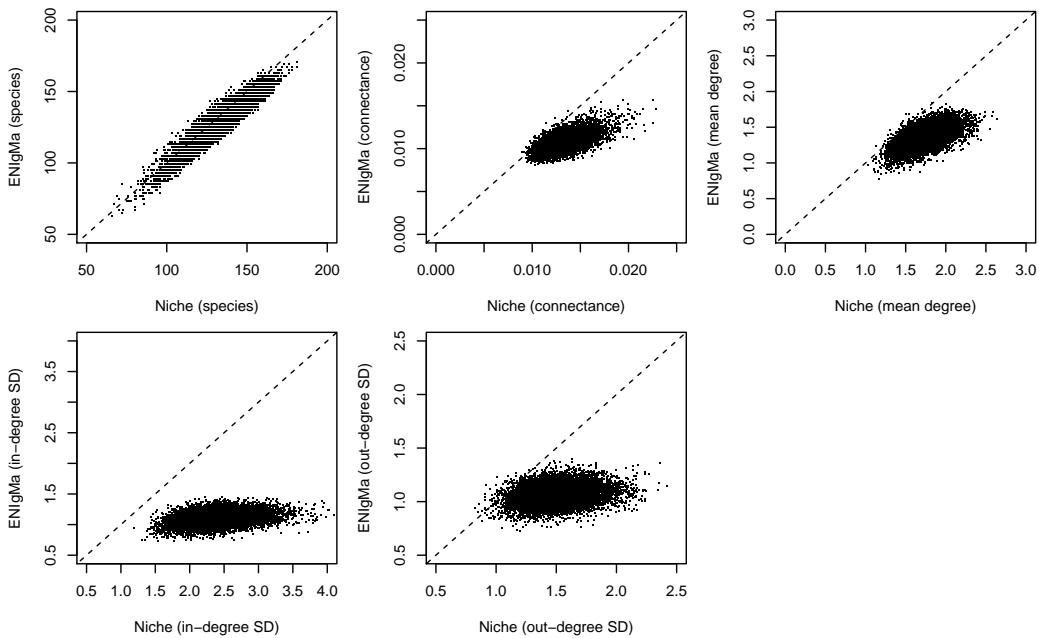


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in-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

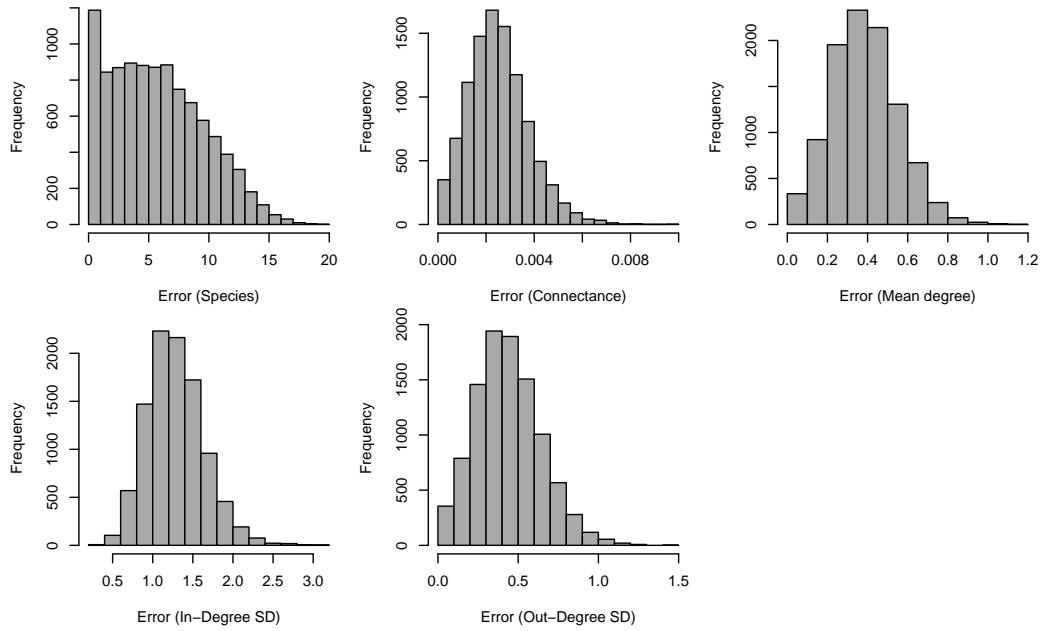


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as $\sqrt{(m_i - m_j)^2}$, where m_i and m_j are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model was used to assess metrics.

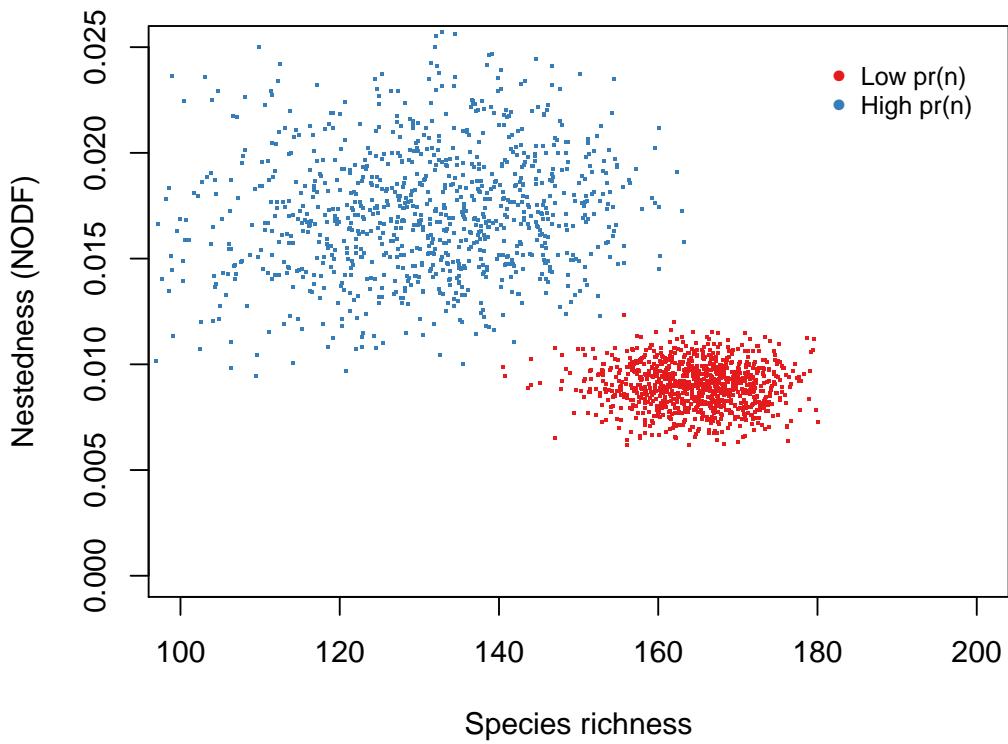


Figure S4. Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities without service interactions ($p_n = 0$) compared to those with a high frequency of service interactions ($p_n = 0.002$). While higher frequencies of service interactions do lower steady state species 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.

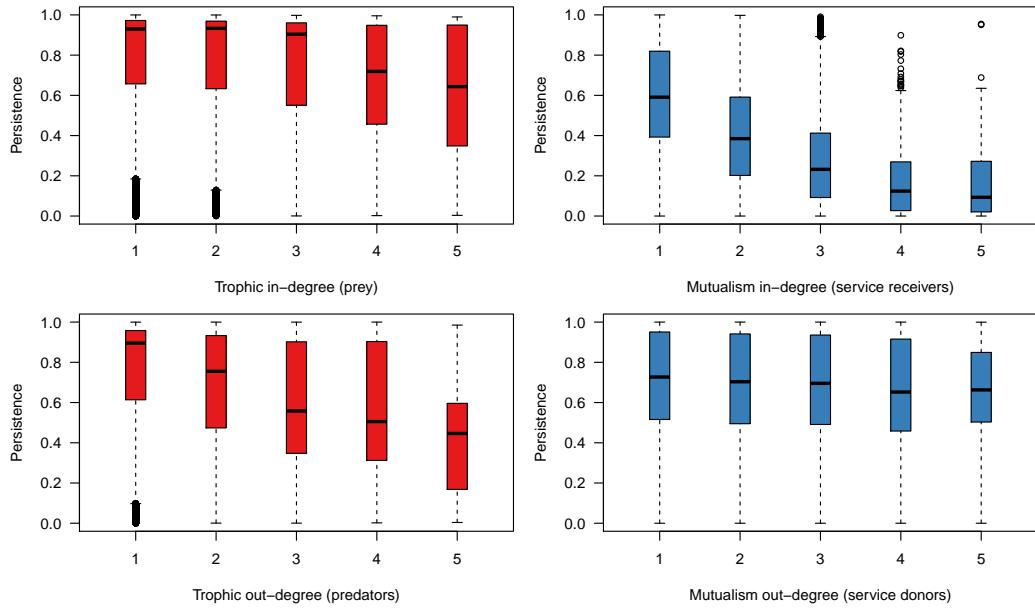


Figure S5. Persistence as a function of trophic and service in/out-degree for communities with higher densities of service interactions ($p_e = 0.01$; $p_n = 0.002$). Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top) and out-degree (the 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.

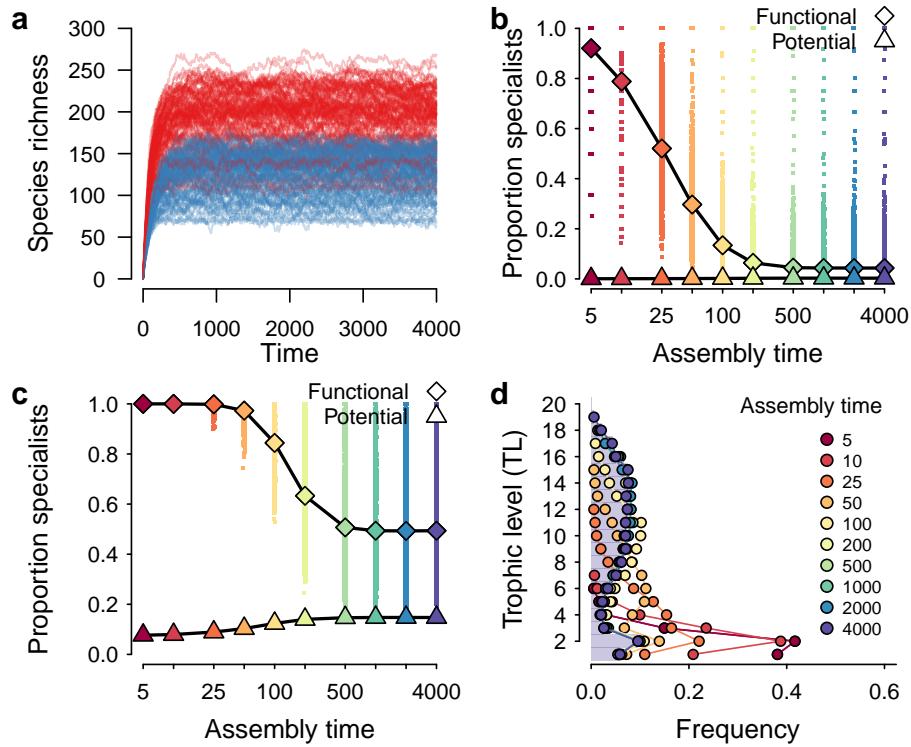


Figure S6. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$ relative 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.

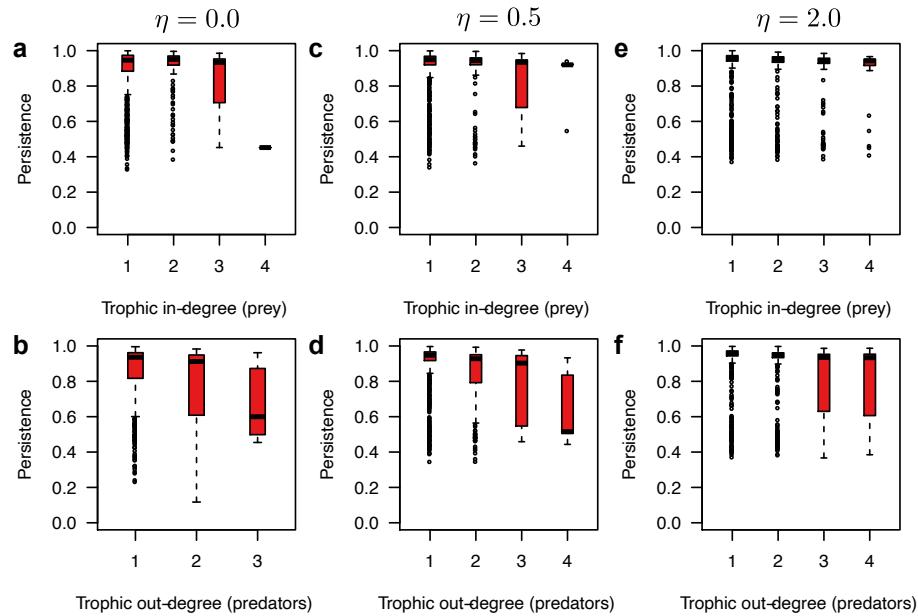


Figure S7. Species-specific persistence as a function of **a** trophic in-degree (number of resources a species has; top) and **b** out-degree (number of consumers that eat the species; bottom) when there are no engineers in the community. Species-specific persistence as a function of **c** trophic in-degree (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.

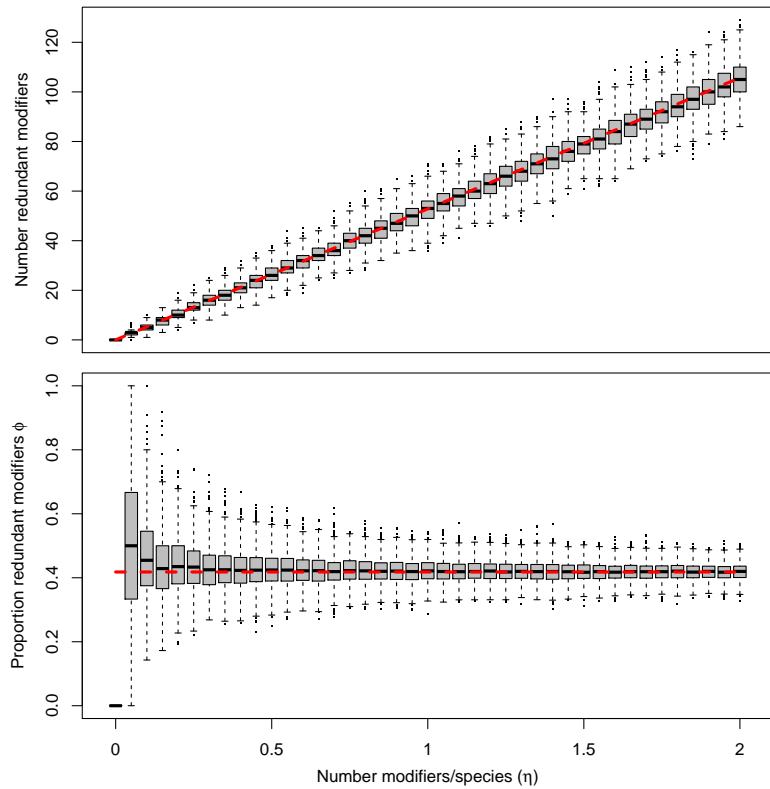


Figure S8. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the source pool as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

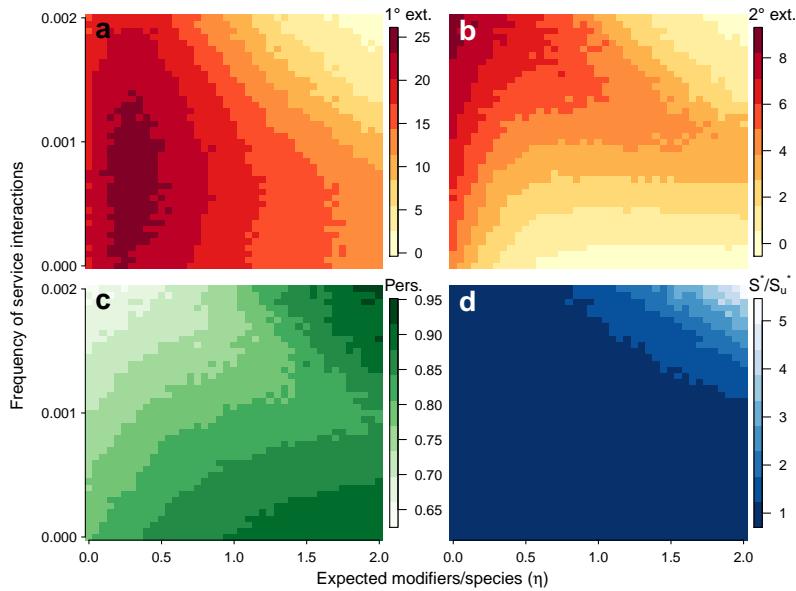


Figure S9. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers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

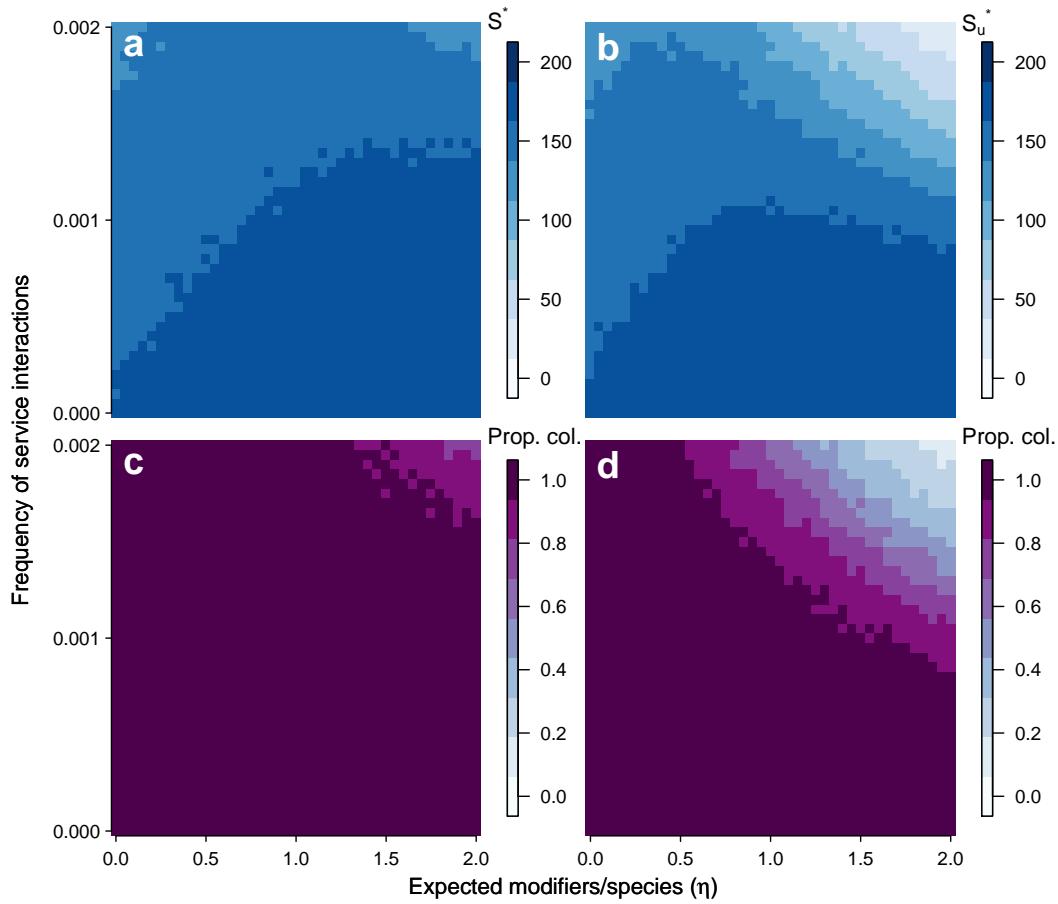


Figure S10. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**,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