

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.

11 To unravel nature's secrets we must simplify its abundant complexities and idiosyncrasies. The layers of natural history giving rise to an ecological community can be distilled – among many forms – into a network, where nodes represent species and links represent interactions between them. Networks are generally constructed for one type of interaction, such as food webs capturing predation^{1–3} or pollination networks capturing a specific mutualistic interaction⁴, and continues to lead to significant breakthroughs in our understanding of the dynamical consequences of community structure^{5–7}. This perspective has also been used to shed light on the generative processes driving the assembly of complex ecological communities^{8,9}.

25 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}, and differences in species' trophic niche^{15,16}, coupled with early establishment of fast/slow energy channels¹⁷, significantly impacts the long-term dynamics of the community. 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} drive colonization and extinction dynamics.

38 Recent interest in ‘multilayer networks’ comprising multiple interaction types (multiplex interactions) may provide additional insight into these processes^{26,27}. However, interactions where species affect others by altering

42 the environment in a lasting way have not yet been incorporated into models of ecological networks. These interactions, known as ecosystem engineering^{28,29} or more generally niche construction^{12,30}, are quite common in nature and exist in almost every ecosystem.

47 Diverse interactions occur not only between species but indirectly through the effects that species have on their environment^{29,31,32}. Elephants root out large saplings and small trees, enabling the formation and maintenance of grasslands³³ and creating habitat for smaller vertebrates³⁴. Burrowing rodents create shelter and promote primary production by aerating the soil³⁵, salmon and aquatic invertebrates create freshwater habitats by changing stream morphology³⁶, and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth³⁷. These examples illustrate ecosystem engineering, where the engineering organism alters the environment on timescales longer than its own³⁸. Engineers are widely acknowledged to have impacts on both small and large spatial scales³⁹, and may serve as important keystone species in many habitats⁴⁰.

63 Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth⁴¹. For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the Proterozoic roughly 2.5 Byrs BP^{41,42}, paving the way for the biological invasion of terrestrial habitats. In the oceans it is thought that rRNA and protein biogenesis of aquatic photoautotrophs drove the nitrogen:phosphorous ratio (the Redfield Ratio) to ca. 16:1 matching that of

73 plankton⁴³, illustrating that engineering clades can have 131 much larger, sometimes global-scale effects. 132
 74 The effect of the environment on species is commonly 133 included in models of ecological dynamics^{44–46} due to its 134 acknowledged importance and because it can – to first 135 approximation – be easily systematized. By compari- 136 son the way in which species engineer the environment 137 defies easy systematization due to the multitude of mech- 138 anisms by which engineering occurs. While interactions 139 between species and the abiotic environment have been 140 conceptually described^{32,47}, the absence of engineered ef- 141 fects in network models was addressed by Odling-Smee et 142 al.²⁹, where they outlined a conceptual framework that 143 included both species and abiotic compartments as nodes 144 of a network, with links denoting both biotic and abiotic 145 interactions.

146 **How does the assembly dynamics of species constrained 147 by multitype interactions impact community structure 148 and stability? How are these processes altered when 149 the presence of engineers modifies interactions?** Here 150 we model the assembly of an ecological network where 151 nodes represent ecological entities, including engineering 152 species, non-engineering species, and the effects of the 153 former on the environment, which we call abiotic *modi- 154 fiers*. The links of the network that connect both species 155 and modifiers represent trophic (*eat* interactions), ser- 156 vice (*need* interactions), and engineering dependencies, 157 respectively (Fig. 1; see Methods for a full descrip- 158 tion). Trophic interactions represent both predation as 159 well as parasitism, whereas service interactions account 160 for non-trophic interactions associated with reproduc- 161 tive facilitation such as pollination or seed dispersal. In 162 our framework a traditional mutualism (such as a plant- 163 pollinator interaction) consists of a service (need) inter- 164 action in one direction and a trophic (eat) interaction in 165 the other. These multitype interactions between species 166 and modifiers thus embed multiple dependent ecological 167 sub-systems into a single network (Fig. 1). Modifiers 168 in our framework overlap conceptually with the ‘abiotic 169 compartments’ described in Odling-Smee et al.²⁹. Fol- 170 lowing Pillai et al.⁴⁸, we do not track the abundances of 171 biotic or abiotic entities but track only their presence or 172 absence. We use this framework to explore the dynamics 173 of ecosystem assembly, where the colonization and ex- 174 tinction of species within a community depends on the 175 constraints imposed by the trophic, service, and engineer- 176 ing dependencies. We then show how observed network 177 structures emerge from the process of assembly, compare 178 their attributes with those of empirical systems, and ex- 179 amine the effects of ecosystem engineers.

180 Our results offer four key insights into the roles of 181 multitype interactions and ecosystem engineering in 182 driving community assembly. First, we show that the 183 assembly of communities in the absence of engineering 184 reproduces many features observed in empirical systems. 185 These include changes in the proportion of generalists 186 over the course of assembly that accord with measured 187 data and trophic diversity similar to empirical observa- 188

tions. Second, we show that increasing the frequency 131 of mutualistic interactions leads to the assembly of 132 ecological networks that are more nested, a common 133 feature of diverse mutualistic systems⁴⁹, but are also 134 prone to extinction cascades. Our third key result shows 135 that increasing the proportion of ecosystem engineers 136 within a community has nonlinear effects on observed 137 extinction rates. While we find that a low amount of 138 engineering increases extinction rates, a high amount of 139 engineering has the opposite effect. Finally we show that 140 redundancies in engineered effects promote community 141 diversity by lowering the barriers to colonization.

143 **Assembly without ecosystem engineering.** Com- 144 munities assemble by random colonization from a source 145 pool. A species from the source pool can colonize if it 146 finds at least one resource that it can consume (one *eat* 147 interaction is satisfied; cf. Ref. 50) and all of its non- 148 trophic needs are met (all *need* interactions are satisfied; 149 see Fig. 1). As such, the service interactions are as- 150 sumed to be obligate, whereas trophic interactions are 151 flexible. While a basal resource is always assumed to be 152 present (white node in Fig. 1b), following the establish- 153 ment of an autotrophic base, the arrival of mixotrophs 154 (i.e. mixing auto- and heterotrophy) and lower trophic 155 heterotrophs create opportunities for organisms occupy- 156 ing higher trophic levels to invade. This expanding niche 157 space initially serves as an accelerator for community 158 growth.

159 Following the initial colonization phase, extinctions be- 160 gin to slow the rate of community growth. Primary ex- 161 tinctions occur if a given species is not the strongest 162 competitor for at least one of its resources. A species’ 163 competition strength is determined by its interactions: 164 competition strength is enhanced by the number of need 165 interactions and penalized by the number of its resources 166 (favoring trophic specialists) and consumers (favoring 167 species with fewer predators). This encodes three key as- 168 sumptions: that mutualisms provide a fitness benefit⁵¹, 169 specialists are stronger competitors than generalists^{52–55}, 170 and many predators entail an energetic cost⁵⁶. Secondary 171 extinctions occur when species lose its last trophic or any 172 of its service requirements. See Fig. 1d,e for an illustra- 173 tion of the assembly process. As the colonization and ex- 174 tinction rates converge, the community reaches a steady 175 state around which it oscillates (Fig. 2a). See Methods 176 and Supplementary Appendix 1 for a complete descrip- 177 tion of the assembly process. Specific model parameteri- 178 zations are described in Supplementary Appendix 2.

179 Assembly of ecological communities in the absence of 180 engineering results in interaction networks with struc- 181 tures consistent with empirical observations. As the com- 182 munity reaches steady state, we find that the connectance 183 of trophic interactions ($C(t) = L(t)/S(t)^2$, where $S(t)$ 184 is species richness and $L(t)$ is the number of links at 185 time t) decays to a constant value (Fig. S1). Decaying 186 connectance followed by stabilization around a constant 187 value has been documented in the assembly of mangrove 188

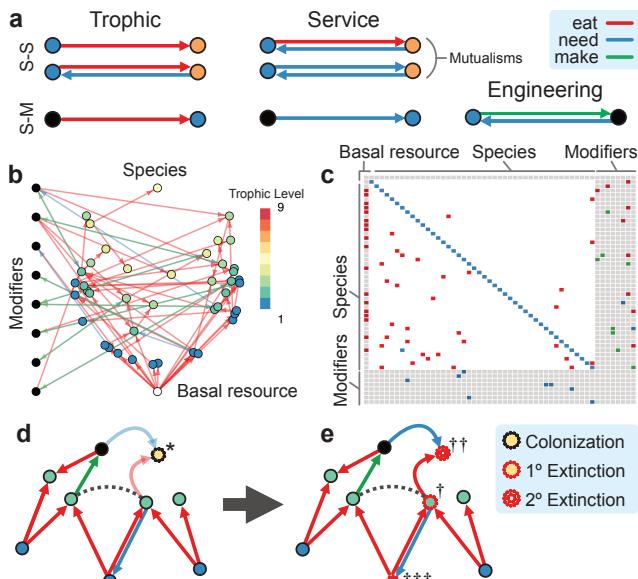


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mutualistic relationships define both species-species (S-S) and species-modifier (S-M) interactions; an engineering interaction is denoted by an engineer that makes a modifier, such 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.

communities¹⁶ and experimental aquatic mesocosms¹⁷. The initial decay is likely inevitable 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 model⁵⁷ 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^{16,50}. Here the trophic generality of species i is defined $G_i = k_i^{\text{in}}/(L/S)$ where k_i^{in} is the in-degree, or number of resources consumed, by species i ⁵⁷. A species is classified as a generalist if $G_i > 1$ and a specialist if $G_i < 1$. In empirical investigations, generality is often scaled to the steady state link density L^*/S^* . 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 func-

tioning 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 biogeography⁵⁰, 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 $\text{TL} = 1.6$. 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 $\text{TL}_{\max} (\pm \text{standard deviation}) = 11 \pm 2.8$ (Fig. 2c). While the maximum trophic level is higher than that measured in most predator-prey systems⁵⁸, it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers) are included⁵⁹. Overall, the most common trophic level among species at steady state is ca. $\text{TL} = 4.75$.

The distribution of trophic levels changes shape over the course of assembly. Early in assembly, we observe 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 models⁶⁰.

Structure and dynamics of mutualisms. Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks^{49,61–63}. Nestedness has been shown to maximize the structural stability of mutualistic networks⁶⁴, emerge naturally via adaptive foraging behaviors^{24,65} and neutral processes⁶⁶, and promote the influence of indirect effects in driving coevolutionary dynamics⁶⁷. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties^{68,69}, interaction asymmetry among species may promote nestedness in both trophic⁶³ and mutualistic systems⁷⁰. Processes that operate on different temporal and spatial scales may have a significant influence on these observations⁷¹. 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

268 that geographic insularity may reinforce this process⁷².

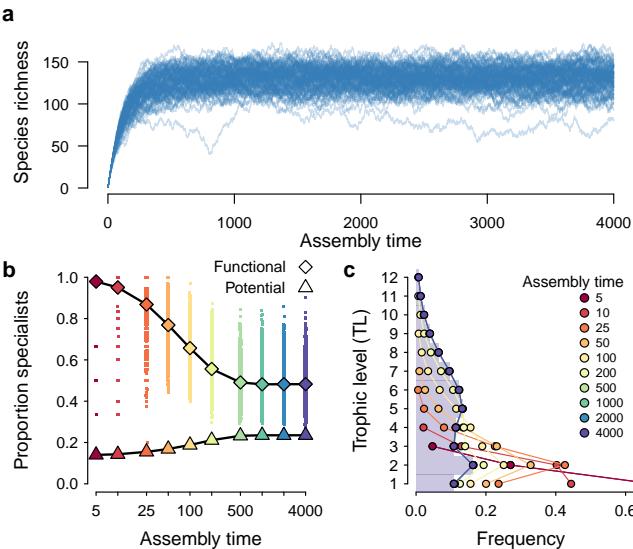


Figure 2. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index $G_i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

269 Does the assembly of ecological networks favor nested-
270 ness when mutualistic interactions are frequent? In the
271 absence of mutualisms, the trade-offs in our model pre-
272 clude high levels of nestedness because we assume that
273 generalists are at a competitive disadvantage when they
274 share the same resources with a specialist consumer. Yet
275 we find that as we increase the frequency of service inter-
276 actions (holding constant trophic interaction frequency;
277 see Supplementary Appendix 2), the assembled commu-
278 nity at steady state becomes more nested (Fig. 3a).
279 More service interactions increase a species' competition
280 strength, lowering its primary extinction risk. Participa-
281 tion in a mutualism thus delivers a fitness advantage to
282 the species receiving the service, compensating for the
283 lower competitive strength of generalists and allowing
284 generalists to share subsets of resources with specialists,
285 which promotes nestedness. However increases in mu-
286 tualisms also increase inter-species dependencies, which
287 raises the potential risk associated with losing mutual-

288 istic partners^{73,74}. While this shifting landscape of ex-
289 tinction risks lowers the steady state species richness of
290 highly mutualistic communities, we do not observe a di-
291 rect relationship between nestedness and richness (Fig.
292 S4).

293 When we examine the dynamics of the community as a
294 function of service interaction frequency, we observe that
295 mutualistic interactions have different effects on primary
296 versus secondary extinction rates. Because service de-
297 pendencies bolster the competitive strength of otherwise
298 susceptible species such as trophic generalists and species
299 with multiple predators, the rate of primary extinctions
300 is lowered, though this effect is weak (Fig. 3b). How-
301 ever, because mutualisms build rigid dependencies be-
302 tween species, more service interactions result in higher
303 frequencies of secondary extinctions (Fig. 3c). In com-
304 munities with many mutualistic interactions, this com-
305 bined influence yields extinctions that are less likely to
306 occur, but lead to larger cascades when they do.

307 An increased rate of secondary extinctions means that
308 the network is less robust to perturbation, which may im-
309 pact community turnover, or persistence. If we measure
310 persistence in terms of the proportion of time species
311 are established in the community, we find that higher
312 frequencies of service interactions lower average persis-
313 tence (increased species turnover; Fig. 3d). Analysis of
314 species-specific interactions reveals that it is the species
315 that require more services that have lower persistence
316 (Fig. S5). Observations of empirical systems appear
317 to support model predictions. For example, assem-
318 bling plant-pollinator systems have demonstrated high rates of
319 species and interaction turnover, both during the assem-
320 bly process and at the steady state⁷⁶.

321 We emphasize that we have restricted ourselves to
322 examining the effects of obligate mutualisms, although
323 the importance of non-obligate mutualisms has long
324 been recognized^{24,65,76,78,79}. We expect that the in-
325 creased rate of secondary extinctions attributable to
326 the loss of obligate mutualistic partners to have greater
327 impact on system stability than the potential loss of
328 non-obligate mutualistic partners. As such, we do not
329 expect inclusion of non-obligate mutualisms to alter the
330 qualitative nature of our findings.

331 **332 Assembly with ecosystem engineering.** The con-
333 cept of ecosystem engineering, or more generally niche
334 construction, has both encouraged an extended evo-
335 lutionary synthesis⁸⁰ while also garnering considerable
336 controversy^{81,82}. Models that explore the effects of
337 ecosystem engineering are relatively few, but have cov-
338 ered important ground^{29,38}. For example, engineering
339 has been shown to promote invasion⁸³, alter primary
340 productivity⁸⁴, and change the selective environment
341 over eco-evolutionary timescales^{85,86} which can lead to
342 unexpected outcomes such as the fixation of deleteri-
343 ous alleles⁸⁷. On smaller scales, microbiota construct
344 shared metabolic resources that have a significant influ-
345 ence on microbial communities⁸⁸, the dynamics of which

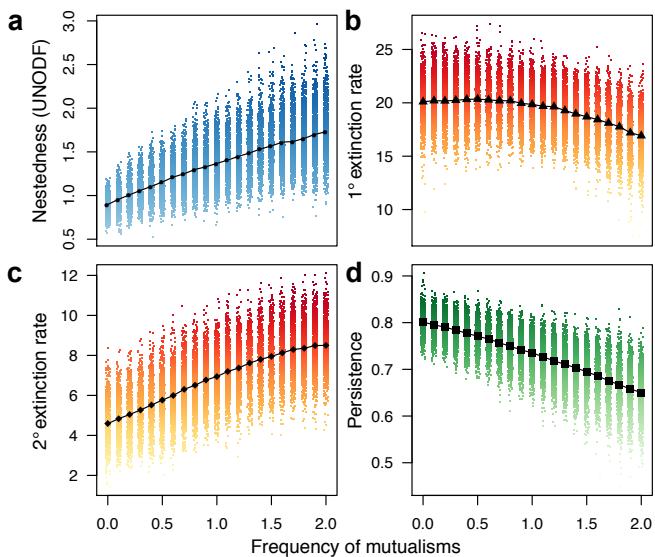


Figure 3. **a**, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)⁷⁷. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. **b**, Primary 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.

may even serve as the missing ingredient stabilizing some complex ecological systems⁸⁹.

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*)⁹⁰. Here, freshwater invertebrates are serviced by the habitat modifications engineered by the shipworm, linking species indirectly via an abiotic effect (in our framework via a modifier node). As the frequency of service interactions increases, the negative effects associated with rare engineers is diminished (Fig. 4a). Increasing service interactions both elevates the competitive strength of species receiving services (from species and/or modifiers), while creating more interdependences between and among species. As trophic interactions are replaced by service interactions, previously vulnerable species gain a competitive foothold and persist, lowering rates of primary extinctions (Fig. 4a). The costs of these added services to the community are an increased rate of secondary extinctions (Fig. 4b) and higher species turnover (Fig. 4c), such that extinctions are less common but lead to larger cascades.

While the importance of engineering timescales has been emphasized previously³⁸, redundant engineering has been assumed to be unimportant²⁸. We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when the effects of engineers increase their own fitness⁸³ as is generally assumed to be the case with niche construction⁸⁶.

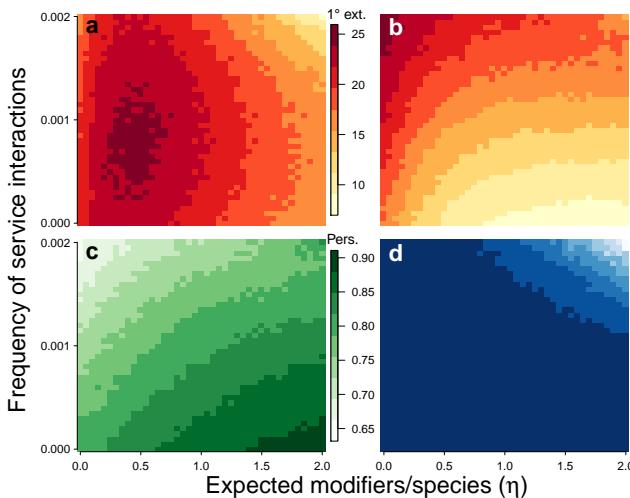


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade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

The vast majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant engineers appear rare²⁸. However if we consider longer timescales, increasing diversity of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification³⁰. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic^{41,42} among other large-scale engineering events in the history of life⁴¹. 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 descendants⁹¹. In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production⁹². In these systems, redundancy in the production of shared metabolic resources may play a key role in community structure and dynamics^{88,93}.

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 redundancy have lower species richness because species' trophic and service dependencies are unlikely to be fulfilled, precluding colonization (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, redundancy increases the temporal stability of species' niches while minimizing priority effects by allowing multiple engineers to fulfill dependencies. Our results thus suggest that redundant engineers may play important roles in assembling ecosystems by lowering the barriers to colonization thereby promoting community diversity.

We have shown that the dynamics of assembly driven by competitive forces influenced by 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 environments⁹⁴, 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.⁴⁸, we do not track the abundances of entities but track only their presence or absence (see also Refs. 19,20). The links of the

518 network represent interactions between pairs of entities (x,y). We 562 compute the competitive strength of species i as
 519 distinguish three types of such interactions: x eats y, x needs y to
 520 be present, x makes modifier y.

521 The assembly process entails two steps: first a source pool of
 522 species is created, followed by colonization/extinction into/from a
 523 local community. The model is initialized by creating S species
 524 and $M = \eta S$ modifiers, such that $N = S + M$ is the expected total
 525 number of entities (before considering engineering redundancies)
 526 and η is the expected number of modifiers made per species in the
 527 community, where the expectation is taken across replicates. For
 528 each pair of species (x,y) there is a probability p_e that x eats y
 529 and probability p_n that x needs y. For each pair of species x and
 530 modifier m, there is a probability q_e that species x eats modifier m
 531 and a probability q_n that species x needs modifier m. Throughout
 532 we assume that $p_e = q_e$ and $p_n = q_n$ for simplicity. Each species
 533 i makes a number of modifiers $M_i \sim \text{Poiss}(\eta)$ where η is the mean
 534 number of modifiers made per species. If engineering redundancies
 535 are allowed, once the number of modifiers per species is determined
 536 each modifier is assigned to a species independently to match its
 537 assigned number of modifiers. This means that multiple species
 538 may make the same modifier, and that there may be some modifiers
 539 that are not assigned to any species, which are eliminated from
 540 the pool. Accounting for engineering redundancies, the number of
 541 modifiers in the pool becomes $M' = \eta S(e - 1)/e$ where e is Euler's
 542 number. If engineering redundancies are not allowed, each modifier
 543 is made by a single engineer and $M' = M$.

544 In addition to interactions with ecosystem entities, there can be
 545 interactions with a basal resource, which is always present. The
 546 first species always eats this resource, such that there is always a
 547 primary producer in the pool. Other species eat the basal resource
 548 with probability p_e . Species with zero assigned trophic interac-
 549 tions are assumed to be primary producers. See Supplementary
 550 Appendix 1 for additional details on defining the source pool.

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

560 An established species is at risk of extinction if it is not the
 561 strongest competitor at least one of its resources that it eats. We

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

563 where n_i is the number of entities that species i needs, e_i is the
 564 number of entities from the pool that species i can eat, and v_i is
 565 the number of species in the community that eat species i . This
 566 captures the ecological intuition that mutualisms provide a fitness
 567 benefit⁵¹, specialists are stronger competitors than generalists⁵⁴,
 568 and many predators entail an energetic cost⁵⁶. The coefficients
 569 c_n , c_e , c_v describe the relative effects of these contributions to
 570 competition strength. In the following, we use the relationship
 571 $c_n > c_e > c_v$, such that the competitive benefit of adding an addi-
 572 tional mutualism is greater than the detriment incurred by adding
 573 another prey or predator. A species at risk of extinction leaves the
 574 community stochastically in time at rate r_e .

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

581 The model described here can be simulated efficiently with an
 582 event-driven simulation utilizing a Gillespie algorithm. In these
 583 types of simulations, one computes the rates r_j of all possible events
 584 j in a given step. One then selects the time at which the next
 585 event happens by drawing a random number from an exponential
 586 distribution with mean $1/\sum_j r_j$. At this time, an event occurs
 587 that is randomly selected from the set of possible events such that
 588 the probability of event a is $r_a / \sum_j r_j$. The effect of the event
 589 is then realized and the list of possible events is updated for the
 590 next step. This algorithm is known to offer a much better ap-
 591 proximation to the true stochastic continuous time process than
 592 a simulation in discrete time steps, while providing a much higher
 593 numerical efficiency⁹⁵. Simulations described in the main text have
 594 default parameterizations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$,
 595 $c_v = 1$, and 4000 iterations. Replicates are defined as the indepen-
 596 dent assembly of independently drawn source pools with a given
 597 parameterization.

598 Data availability

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

600

601 Code availability

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

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- 605 [1] Paine, R. T. Food web complexity and species diversity. *622 Am. Nat.* **100**, 65–75 (1966).
- 606 [2] Dunne, J. A., Williams, R. J. & Martinez, N. D. Food- 623 web structure and network theory: the role of con-
 608 nectance and size. *Proc Natl Acad Sci USA* **99**, 12917– 624 12922 (2002).
- 611 [3] Pascual, M. & Dunne, J. *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Ox- 625 ford University Press, Oxford, UK, 2006). URL 626 <http://www.google.com/search?client=safari&rls=en-us&q=Ecological+Networks&ie=UTF-8&oe=UTF-8>.
- 616 [4] Bascompte, J. & Jordano, P. *Mutualistic Networks*. 627 Monographs in Population Biology (Princeton Univer- 628 sity Press, Princeton, NJ, 2013). URL 629 <https://books.google.com/books?id=xVWzAAAAQBAJ>.
- 620 [5] May, R. M. Will a large complex system be stable? *Nature* 630 **238**, 413–414 (1972).
- 622 [6] Gross, T., Levin, S. A. & Dieckmann, U. Generalized models reveal stabilizing factors in food webs. *Science* 623 **325**, 747–750 (2009).
- 625 [7] Allesina, S. & Tang, S. Stability criteria for complex 626 ecosystems. *Nature* **483**, 205–208 (2012).
- 627 [8] Montoya, J. M. & Solé, R. V. Topological properties of 628 food webs: from real data to community assembly mod- 629 els. *Oikos* **102**, 614–622 (2003).
- 631 [9] Bascompte, J. & Stouffer, D. The assembly and disas- 632 sembly of ecological networks. *Philos. T. Roy. Soc. B* 633 **364**, 1781 (2009).
- 635 [10] Hubbell, S. *The unified neutral theory of biodi- 636 versity and biogeography* (Princeton Univ Press, 637 2001). URL <http://www.google.com/search?client=safari&rls=en-us&q=The+unified+neutral+theory+of+biodiversity&ie=UTF-8&oe=UTF-8>.
- 638 [11] Tilman, D. Niche tradeoffs, neutrality, and community

- 639 structure: a stochastic theory of resource competition, 703
 640 invasion, and community assembly. *Proceedings of the 704 National Academy of Sciences* **101**, 10854–10861 (2004). 705
- 642 [12] Fukami, T. Historical Contingency in Community As- 706
 643 sembly: Integrating Niches, Species Pools, and Priority 707
 644 Effects. *Annu Rev Ecol Evol Syst* **46**, 1–23 (2015). 708
- 645 [13] Kraft, N. J. B., Valencia, R. & Ackerly, D. D. Functional 709 Traits and Niche-Based Tree Community Assembly in an 710
 646 Amazonian Forest. *Science* **322**, 580–582 (2008). 711
- 648 [14] O'Dwyer, J. P., Lake, J., Ostling, A., Savage, V. M. & 712
 649 Green, J. An integrative framework for stochastic, size- 713
 650 structured community assembly. *Proc. Natl. Acad. Sci. 714 USA* **106**, 6170 (2009). 715
- 652 [15] Brown, J. H., Kelt, D. A. & Fox, B. J. As- 716
 653 sembly Rules and Competition in Desert Rodents. 717
<http://dx.doi.org.proxy.lib.sfu.ca/10.1086/679735> 718
 654 815–818 (2002).
- 656 [16] Piechnik, D. A., Lawler, S. P. & Martinez, N. D. 720
 657 Food-web assembly during a classic biogeographic study: 721
 658 species“trophic breadth” corresponds to colonization or- 722
 659 der. *Oikos* **117** (2008).
- 660 [17] Fahimipour, A. K. & Hein, A. M. The dynamics of as- 724
 661 sembling food webs. *Ecol. Lett.* **17**, n/a–n/a (2014). 725
- 662 [18] Barbier, M., Arnoldi, J.-F., Bunin, G. & Loreau, M. 726
 663 Generic assembly patterns in complex ecological com- 727
 664 munities. *Proc. Natl. Acad. Sci. USA* **115**, 2156–2161 728
 665 (2018).
- 666 [19] Campbell, C., Yang, S., Albert, R. & Shea, K. A network 730
 667 model for plant-pollinator community assembly. *Proc. 731
Natl. Acad. Sci. USA **108**, 197–202 (2011).*
- 669 [20] Hang-Kwang, L. & Pimm, S. L. The assembly of eco- 733
 670 logical communities: A minimalist approach. *Journal of 734
Animal Ecology **62**, 749–765 (1993).*
- 672 [21] Law, R. & Morton, R. D. Permanence and the Assembly 736
 673 of Ecological Communities. *Ecology* **77**, 762–775 (1996).
- 674 [22] Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, 738
 675 L., Urbani, P. & Dunne, J. A. Consequences of adaptive 739
 676 behaviour for the structure and dynamics of food webs. 740
Ecol. Lett. **13**, 1546–1559 (2010).
- 678 [23] Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de 742
 679 EspanÁls, P. & Flores, J. D. Topological plas- 743
 680 ticity increases robustness of mutualistic networks. 744
Journal of Animal Ecology **81**, 896–904 (2012).
- 682 arXiv:<https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/j.2745.2006.01132.x>. 747
- 684 [24] Valdovinos, F. S. et al. Niche partitioning due to adaptive 748
 685 foraging reverses effects of nestedness and connectance on 749
 686 pollination network stability. *Ecol Lett* **19**, 1277–1286 750
 687 (2016).
- 688 [25] Ponisio, L. C. et al. A network perspective for community 752
 689 assembly. *Front Ecol Evol* **7**, 103 (2019).
- 690 [26] Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A. & 754
 691 Berlow, E. L. How structured is the entangled bank? 755
 692 the surprisingly simple organization of multiplex ecologi- 756
 693 cal networks leads to increased persistence and resilience. 757
PLoS Biol **14**, e1002527 (2016).
- 695 [27] Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The 759
 696 multilayer nature of ecological networks. *Nature Ecol 760
Evol **1**, 0101 (2017).*
- 698 [28] Lawton, J. H. What do species do in ecosystems? *Oikos* 762
 699 **71**, 367–374 (1994).
- 700 [29] Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feld- 764
 701 man, M. W. & Laland, K. N. Niche construction theory: 765
 702 a practical guide for ecologists. *Q Rev Biol* **88**, 4–28 766
 (2013).
- [30] Odling-Smee, F., Laland, K. & Feldman, M. *Niche Con- 704
 struction: The Neglected Process in Evolution (MPB-37)*. 705
 Monographs in Population Biology (Princeton University Press, Princeton, NJ, 2013). URL <https://books.google.com/books?id=0k-NujtWMZOC>.
- [31] Jones, C. G., Lawton, J. H. & Shachak, M. Organisms 709 as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
- [32] Olff, H. et al. Parallel ecological networks in ecosystems. *Philos T Roy Soc B* **364**, 1755 (2009).
- [33] Haynes, G. Elephants (and extinct relatives) as earth- 713
 movers and ecosystem engineers. *Geomorphology* **157–158**, 99 – 107 (2012).
- [34] Pringle, R. M. Elephants as agents of habitat creation for 716
 small vertebrates at the patch scale. *Ecology* **89**, 26–33 718
 (2008).
- [35] Reichman, O. & Seabloom, E. W. The role of pocket go- 719
 phers as subterranean ecosystem engineers. *Trends Ecol 720
Evol **17**, 44 – 49 (2002).*
- [36] Moore, J. W. Animal Ecosystem Engineers in Streams. *BioScience* **56**, 237–246 (2006). 723
 arXiv:<http://oup.prod.sis.lan/bioscience/article-pdf/56/3/237/26897844/56-3-237.pdf>.
- [37] Meyer, S. T., Leal, I. R., Tabarelli, M. & Wirth, R. 726
 Ecosystem engineering by leaf-cutting ants: nests of atta 727
 cephalotes drastically alter forest structure and microcli- 728
 mate. *Ecol Entomol* **36**, 14–24 (2011).
- [38] Hastings, A. et al. Ecosystem engineering in space and 730
 time. *Ecol Lett* **10**, 153–164 (2007).
- [39] Wright, J. P., Jones, C. G., Boeken, B. & Shachak, 731
 M. Predictability of ecosystem engineering effects on 732
 species richness across environmental variability and 733
 spatial scales. *Journal of Ecology* **94**, 815–824 (2006). 734
 arXiv:<https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/j.2745.2006.01132.x>.
- [40] Jones, C. & Lawton, J. *Linking Species & Ecosystems* 736
 (Springer US, 2012). URL https://books.google.com/books?id=Dm__dBwAAQBAJ.
- [41] Erwin, D. H. Macroevolution of ecosystem engineering, 738
 niche construction and diversity. *Trends Ecol Evol* **23**, 739
 304 – 310 (2008).
- [42] Schirrmeyer, B. E., de Vos, J. M., Antonelli, 740
 A. & Bagheri, H. C. Evolution of multicel- 741
 lular organisms coincided with increased diversification 742
 of cyanobacteria and the great oxidation event. 743
Proc Natl Acad Sci USA **110**, 1791–1796 (2013). 744
 arXiv:<https://www.pnas.org/content/110/5/1791.full.pdf>.
- [43] Loladze, I. & Elser, J. J. The origins of the Red- 745
 field nitrogen-to-phosphorus ratio are in a homoeostatic 746
 protein-to-rRNA ratio. *Ecol Lett* **14**, 244–250 (2011).
- [44] Woodward, G., Perkins, D. M. & Brown, L. E. Climate 747
 change and freshwater ecosystems: impacts across mul- 748
 tiple levels of organization. *Philos T Roy Soc B* **365**, 749
 2093–2106 (2010).
- [45] Brose, U. et al. Climate change in size-structured ecosys- 750
 tems. *Philos T Roy Soc B* **367**, 2903–2912 (2012).
- [46] Gibert, J. P. Temperature directly and indirectly influ- 751
 ences food web structure. *Sci Rep-UK* **9**, 5312 (2019).
- [47] Getz, W. M. Biomass transformation webs provide a 752
 unified approach to consumer-resource modelling. *Ecol 753
Lett **14**, 113–124 (2011).*
- [48] Pillai, P., Gonzalez, A. & Loreau, M. Metacommunity 754
 theory explains the emergence of food web complexity. 755
Proc Natl Acad Sci USA **108**, 19293–19298 (2011).

- [49] Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. The nested assembly of plant-animal mutualistic networks. *Proc Natl Acad Sci USA* **100**, 9383–9387 (2003).
- [50] Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. Trophic theory of island biogeography. *Ecol Lett* **14**, 1010–1016 (2011).
- [51] Bronstein, J. L. Conditional outcomes in mutualistic interactions. *Trends in ecology & evolution* **9**, 214–217 (1994).
- [52] MacArthur, R. & Levins, R. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the United States of America* **51**, 1207 (1964).
- [53] Dykhuizen, D. & Davies, M. An experimental model: bacterial specialists and generalists competing in chemostats. *Ecology* **61**, 1213–1227 (1980).
- [54] Futuyma, D. J. & Moreno, G. The evolution of ecological specialization. *Annual review of Ecology and Systematics* **19**, 207–233 (1988).
- [55] Costa, A. *et al.* Generalisation within specialization: inter-individual diet variation in the only specialized salamander in the world. *Scientific reports* **5**, 1–10 (2015).
- [56] Brown, J. S., Kotler, B. P. & Valone, T. J. Foraging under predation - a comparison of energetic and predation costs in rodent communities of the negev and sonoran deserts. *Australian Journal of Zoology* **42**, 435–448 (1994).
- [57] Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* **404**, 180–183 (2000).
- [58] Williams, R. & Martinez, N. Limits to trophic levels and omnivory in complex food webs: Theory and data. *Am Nat* **163**, 458–468 (2004). arXiv:<https://doi.org/10.1086/381964>.
- [59] Lafferty, K. D., Dobson, A. P. & Kuris, A. M. Parasites dominate food web links. *Proc Natl Acad Sci USA* **103**, 11211–11216 (2006).
- [60] Turney, S. & Buddle, C. M. Pyramids of species richness: the determinants and distribution of species diversity across trophic levels. *Oikos* **125**, 1224–1232 (2016).
- [61] Bascompte, J., Jordano, P. & Olesen, J. M. Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science* **312**, 431–433 (2006).
- [62] Guimarães Jr, P. R., Rico-Gray, V., Furtado dos Reis, S. & Thompson, J. N. Asymmetries in specialization in ant-plant mutualistic networks. *Proc. Roy. Soc. B* **273**, 2041 (2006).
- [63] Araújo, M. S. *et al.* Nested diets: a novel pattern of individual-level resource use. *Oikos* **119**, 81–88 (2010).
- [64] Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497–1253497 (2014).
- [65] Valdovinos, F. S. Mutualistic networks: moving closer to a predictive theory. *Ecol Lett* **0** (2019).
- [66] Krishna, A., Guimarães Jr, P. R., Jordano, P. & Bascompte, J. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* **117**, 1609–1618 (2008).
- [67] Guimarães Jr, P. R., Pires, M. M., Jordano, P., Bascompte, J. & Thompson, J. N. Indirect effects drive co-evolution in mutualistic networks. *Nature* **18**, 586 (2017).
- [68] Stouffer, D. B. Compartmentalization increases food-web persistence. *Proc Natl Acad Sci USA* **108**, 3648–3652 (2011).
- [69] Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J. & Gonzalez, A. Effects of network modular-
ity on the spread of perturbation impact in experimental metapopulations. *Science* **357**, 199–201 (2017).
- [70] Pires, M. M., Prado, P. I. & Guimarães Jr, P. R. Do food web models reproduce the structure of mutualistic networks? *PLoS ONE* **6**, e27280 (2011).
- [71] Massol, F. *et al.* Linking community and ecosystem dynamics through spatial ecology. *Ecol Lett* **14**, 313–323 (2011).
- [72] Yeakel, J. D., Guimarães Jr, P. R., Bocherens, H. & Koch, P. L. The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. *Proc Roy Soc B* **280**, 20130239–20130239 (2013).
- [73] Bond, W. J., Lawton, J. H. & May, R. M. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Phil Trans Roy Soc B* **344**, 83–90 (1994).
- [74] Colwell, R. K., Dunn, R. R. & Harris, N. C. Coextinction and persistence of dependent species in a changing world. *Ann Rev Ecol Evol Sys* **43**, 183–203 (2012).
- [75] Dátilo, W., Guimaraes Jr, P. R. & Izzo, T. J. Spatial structure of ant-plant mutualistic networks. *Oikos* **122**, 1643–1648 (2013).
- [76] Ponisio, L. C., Gaiarsa, M. P. & Kremen, C. Opportunistic attachment assembles plant–pollinator networks. *Ecol Lett* **20**, 1261–1272 (2017).
- [77] Cantor, M. *et al.* Nestedness across biological scales. *PloS one* **12** (2017).
- [78] Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de Españo, P. & Flores, J. D. Topological plasticity increases robustness of mutualistic networks. *J Anim Ecol* **81**, 896–904 (2012).
- [79] Vieira, M. C. & Almeida Neto, M. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecol Lett* **18**, 144–152 (2015).
- [80] Laland, K. N. *et al.* The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc Roy Soc B* **282**, 20151019 (2015).
- [81] Gupta, M., Prasad, N., Dey, S., Joshi, A. & Vidya, T. Niche construction in evolutionary theory: the construction of an academic niche? *J Gen* **96**, 491–504 (2017).
- [82] Feldman, M. W., Odling-Smee, J. & Laland, K. N. Why Gupta et al.'s critique of niche construction theory is off target. *J Gen* **96**, 505–508 (2017).
- [83] Cuddington, K. Invasive engineers. *Ecol Model* **178**, 335–347 (2004).
- [84] Wright, J. P. & Jones, C. G. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**, 2071–2081 (2004).
- [85] Kylafis, G. & Loreau, M. Ecological and evolutionary consequences of niche construction for its agent. *Ecol Lett* **11**, 1072–1081 (2008).
- [86] Krakauer, D. C., Page, K. M. & Erwin, D. H. Diversity, dilemmas, and monopolies of niche construction. *Am Nat* **173**, 26–40 (2009).
- [87] Laland, K. N., Odling-Smee, F. J. & Feldman, M. W. Evolutionary consequences of niche construction and their implications for ecology. *Proc Natl Acad Sci USA* **96**, 10242–10247 (1999).
- [88] Kallus, Y., Miller, J. H. & Libby, E. Paradoxes in leaky microbial trade. *Nat Commun* **8**, 1361 (2017).
- [89] Butler, S. & O'Dwyer, J. P. Stability criteria for complex microbial communities. *Nature Communications* **9**, 2970 (2018).

- 895 [90] Shipway, J. R. *et al.* A rock-boring and rock-ingesting
 896 freshwater bivalve (shipworm) from the philippines. *Proc
 897 Roy Soc B* **286**, 20190434 (2019).
- 898 [91] Kidwell, S. M. Taphonomic feedback in Miocene assem-
 899 blages: testing the role of dead hardparts in benthic com-
 900 munities. *Palaios* **1**, 239–255 (1986).
- 901 [92] Polz, M. F., Alm, E. J. & Hanage, W. P. Horizontal
 902 gene transfer and the evolution of bacterial and archaeal
 903 population structure. *Trends Genet* **29**, 170 – 175 (2013).
- 904 [93] Muscarella, M. E. & O'Dwyer, J. P. Ecological insights
 905 from the evolutionary history of microbial innovations.
 906 *bioRxiv* 220939 (2017).
- 907 [94] Corlett, R. T. The anthropocene concept in ecology and
 908 conservation. *Trends in Ecology & Evolution* **30**, 36 – 41
 909 (2015).
- 910 [95] Gillespie, D. T. Exact stochastic simulation of coupled
 911 chemical reactions. *J Phys Chem* **81**, 2340–2361 (1977).
- 912 [96] Williams, R. J. & Purves, D. W. The probabilistic niche
 913 model reveals substantial variation in the niche structure
 914 of empirical food webs. *Ecology* **92**, 1849–1857 (2011).
- 915 [97] Warren, C. P., Pascual, M., Lafferty, K. D. & Kuris,
 916 A. M. The inverse niche model for food webs with para-
 917 sites. *Theor Ecol* **3**, 285–294 (2010).

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940

941

942 Author contributions

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

947

948 Competing interests

949 The authors declare no competing interests.

950

SUPPLEMENTARY METHODS

951

Appendix 1: Building the source pool

952 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 a pair of species (x, y) there is the same.

953 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

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

$$M' = \eta S \left(1 - \frac{1}{e}\right). \quad (\text{S1})$$

955 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

$$p_m = \frac{\eta}{S (1 + \eta - \frac{\eta}{e})^2}. \quad (\text{S2})$$

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

957 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.

958 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

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

959 such that the proportion of redundant modifiers ϕ is

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

960 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.

961 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 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 modifier $M' < M$. To determine the number of modifiers in the pool, for each species a set number of modifiers is drawn, where step, equal to the number of entities that meet the criteria for each species $M_i \sim \text{Poiss}(\eta)$. 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

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Appendix 2: Model parameterizations

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).

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 $p_n = 0.002$.

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

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

We compared certain structural features of ENIgMa at steady state to those of the Niche Model⁵⁷. Comparisons were restricted 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

(S3) $\eta = 0$ We compared certain structural features of ENIgMa at steady state to those of the Niche Model⁵⁷. Comparisons were restricted 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

1070 there are many similarities, there are also some important differ- 1116 nity. Because trophic links can now exist between species-modifiers
 1071 ences, some of which are highlighted in the main text. While we 1117 as well as species-species, there are different ways of accounting
 1072 consider a comparison of our framework with other food web mod- 1118 for structure, making direct comparisons with non-engineered food
 1073 els such as the Niche Model relevant, we emphasize that the mo- 1119 webs somewhat difficult. We note that we exclude service interac-
 1074 tions underlying both are distinct. Our approach is intended 1120 tions in this case to best match the structural analysis described in
 1075 to provide a deeper understanding into how multitype dependen- 1121 the main text and shown in Fig. 2. While the inclusion of engineers
 1076 cies between species and the environment impact the dynamics of 1122 ($\eta = 2$) does have an impact on stability in terms of primary versus
 1077 community assembly. While capturing general qualitative features 1123 secondary extinction rates, there is not a strong effect of engineer-
 1078 of empirical systems demonstrates that the dynamics we consider 1124 ing on steady state species richness (Fig. S6a; species richness is
 1079 are ecologically relevant, the goal of our approach is distinct from 1125 shown in blue, modifier richness is shown in red).
 1080 that of static food web models, which aim to maximize structural
 1081 similarities between model and empirical systems^{57,96}.

1082 We compared steady state ecological networks that emerge from 1127 duction of engineering, depending on how specialization is defined.
 1083 ENIGMa (described in Methods, main text) with food webs con- 1128 As in the main text, a specialist is defined when its generality
 1084 structed from the Niche Model⁵⁷ with similar species richness and 1129 index $G_i < 1$ relative to the steady state link density. When engi-
 1085 neering. Because species richness and connectance of the 1130 neered modifiers are included, we account for a trophic interaction
 1086 Niche Model are often altered by eliminating disconnected species, 1131 between a species and another's modifier as an interaction that
 1087 we compared *i*) species richness, *ii*) connectance, *iii*) mean species 1132 occurs between those two species indirectly through the modifier
 1088 degree, *iv*) standard deviation of out-degree distributions, and *v*) 1133 intermediary. So if a species *B* makes a modifier *M*, and *A* eats
 1089 standard deviation of in-degree distributions averaged across 1000 1134 *M*, then we set *A* to (indirectly) eat *B*. This accounting of both
 1090 replicates for each model.

1091 We found that all measures resulted in fairly similar values be- 1136 compared to *i*) the direct trophic link density of the community,
 1092 tween ENIGMa and the Niche Model food webs with a some im- 1137 or *ii*) the direct + indirect trophic link density of the community,
 1093 portant differences (Figs. S2,S3). While similar, ENIGMa pro- 1138 and some insights can be gained from both approaches.

1094 duces consistently lower values of connectance, mean species de-
 1095 gree, as well as standard deviations of the in- and out-degree dis- 1139 In the first case, where G_i is determined relative to L_{direct}^*/S^* ,
 1096 tributions. This means that the food webs produced by ENIGMa 1140 we find that there are no potential specialists that colonize the
 1097 are more sparsely connected with less variance between species. 1141 community, and (as in the main text) functional specialists colonize
 1098 These results were expected, as the Niche Model assumes system- 1142 first, but (not as in the main text) become functional generalists
 1099 atically increasing dietary ranges with higher niche values, whereas 1143 at steady state (mean proportion specialists at steady state is 0.04;
 1100 the trophic interactions assigned to species in the source pool of 1144 Fig. S6b). This means that the indirect links that define trophic in-
 1101 ENIGMa are drawn independently. An important difference be- 1145 teractions between species and modifiers increase the link-density of
 1102 tween the Niche Model and ENIGMa is that we do not distinguish 1146 the network relative to that defined only by direct trophic interac-
 1103 between predators and parasites. A different framework known 1147 tions. In words, modifiers serve to connect otherwise disconnected
 1104 as the Inverse Niche Model⁹⁷ has been proposed to address par- 1148 species, formalizing the otherwise indirect relationships that struc-
 1105 asitic interactions. The Inverse Niche Model assumes increasing 1149 ture the role of engineers in the community. In the second case,
 1106 specialization with feeding hierarchies, which would serve to lower 1150 where G_i is determined relative to $L_{\text{indirect}}^*/S^*$, we find that the
 1107 the average generality of species (lower degree). In addition, the 1151 changes in both functional and potential specialists over the course
 1108 Inverse Niche model outputs lower standard deviations of in- and 1152 of assembly (Fig. S6c) follow those observed for non-engineered
 1109 out-degree distributions. Together these trends suggest that the 1153 food webs (Fig. 2b).

1110 qualitative structural differences that we observe for the assembly
 1111 and Niche model may reflect an important structural distinction 1154 Finally, we observe that while the number of trophic levels in-
 1112 between food webs that do and do not include parasitic species. 1155 crease in the presence of species-modifier interactions, the overall
 1113 Appendix 4: The structure of engineered food webs 1156 trophic structure of the community advances over the course of as-
 1114 We examined whether and to what extent the structure of food 1161 species, the mean trophic level of the community is systematically
 1115 webs was altered when engineers are introduced into the commu- 1162 elevated.

1126 The role of specialists *does* and *does not* change with the intro-
 1127 duction of engineering, depending on how specialization is defined.
 1128 As in the main text, a specialist is defined when its generality
 1129 index $G_i < 1$ relative to the steady state link density. When engi-
 1130 neered modifiers are included, we account for a trophic interaction
 1131 between a species and another's modifier as an interaction that
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 1134 *M*, then we set *A* to (indirectly) eat *B*. This accounting of both
 1135 direct and indirect trophic interactions between species can then be

1136 In the first case, where G_i is determined relative to L_{direct}^*/S^* ,
 1137 we find that there are no potential specialists that colonize the
 1138 community, and (as in the main text) functional specialists colonize
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 1141 the trophic interactions assigned to species in the source pool of 1142 Fig. S6b). This means that the indirect links that define trophic in-
 1142 teractions between species and modifiers increase the link-density of
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 1153 out-degree distributions. Together these trends suggest that the 1154 food webs (Fig. 2b).

1155 Finally, we observe that while the number of trophic levels in-
 1156 crease in the presence of species-modifier interactions, the overall
 1157 trophic structure of the community advances over the course of as-
 1158 sembly in much the same way as it does without engineers (Fig.
 1159 S6d). Trophic levels are calculated with respect to indirect species
 1160 interactions through modifier intermediaries. Because species at
 1161 any trophic level can engineer modifiers used as resources by other

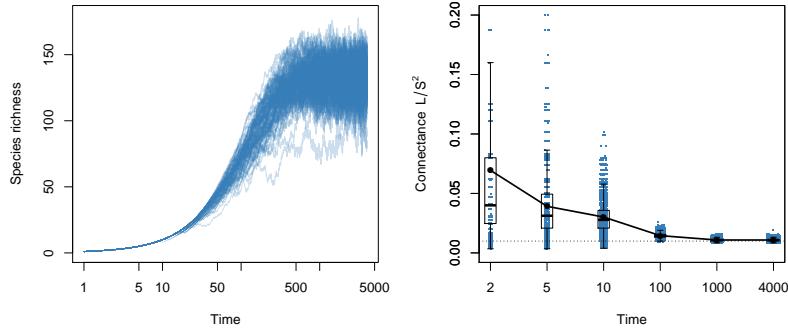


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because a small number of species interact with each other such that the proportion of realized interactions (out of all possible interactions)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

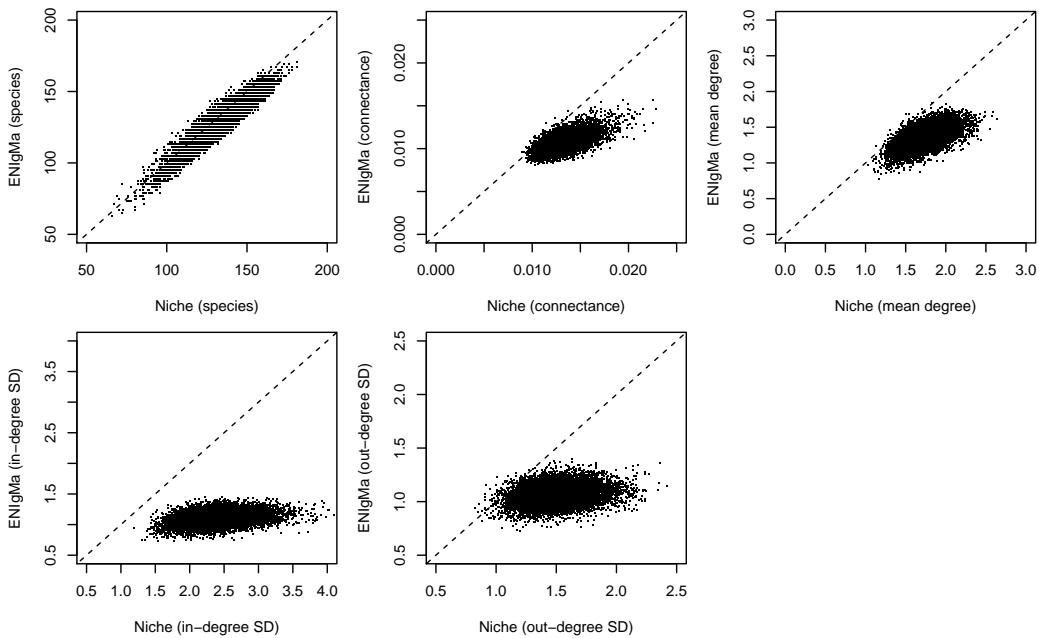


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in-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

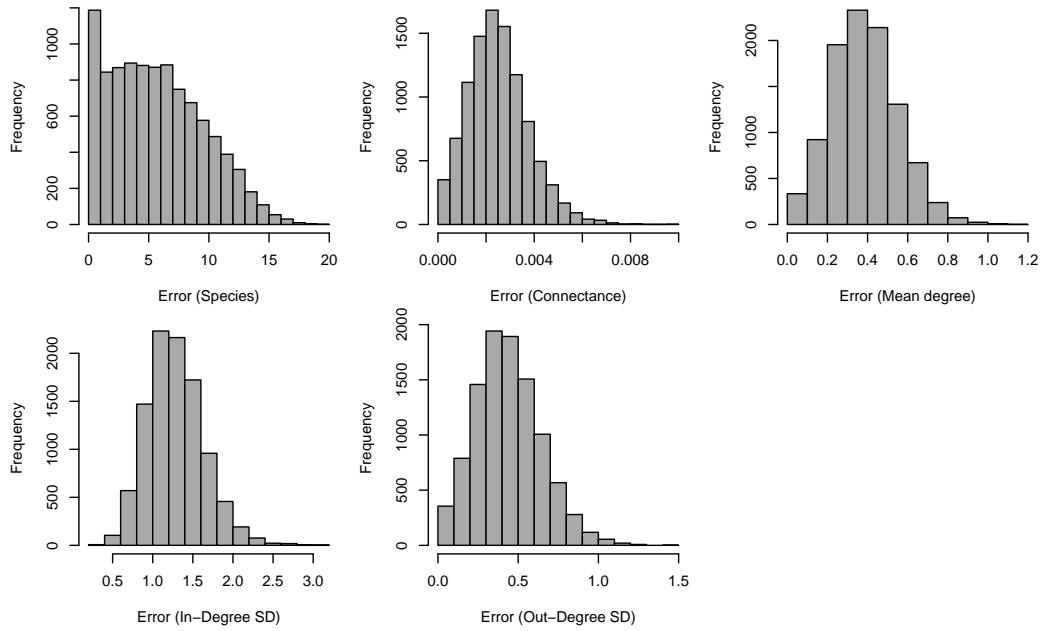


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as $\sqrt{(m_i - m_j)^2}$, where m_i and m_j are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model was used to assess metrics.

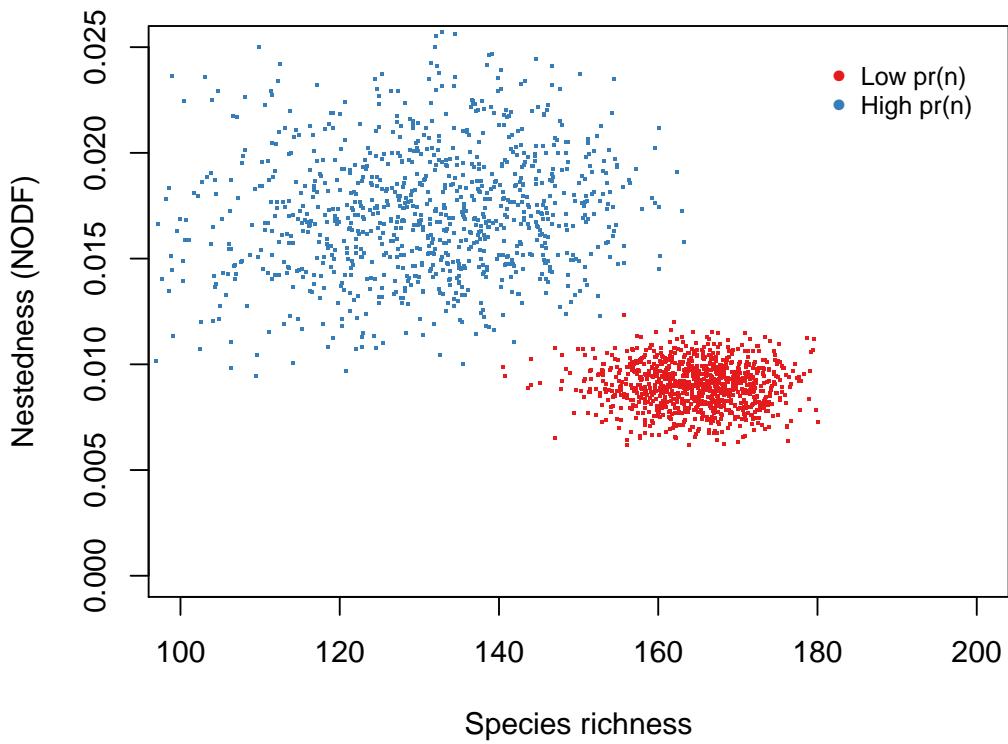


Figure S4. Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities with low (red) and high (blue) frequency of service interactions. While higher frequencies of service interactions does lower steady state species richness (due to increasing secondary extinction rates), there is not a relationship between nestedness and species richness across replicates for a given service interaction frequency.

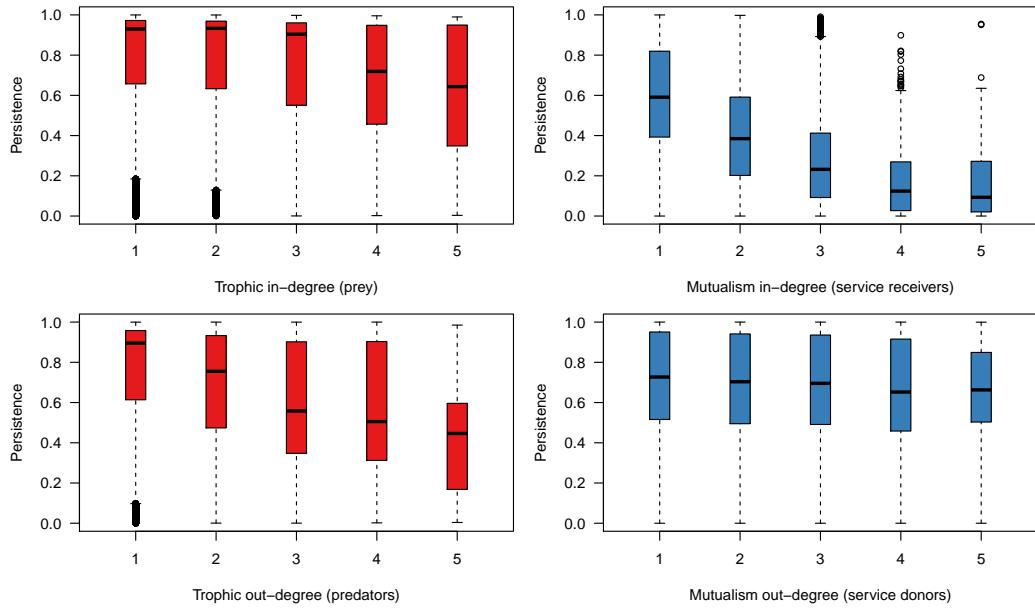


Figure S5. Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top) and out-degree (the number of predators a species has; bottom). Right column: species-specific persistence as a function of the mutualism in-degree (the number of service receivers 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.

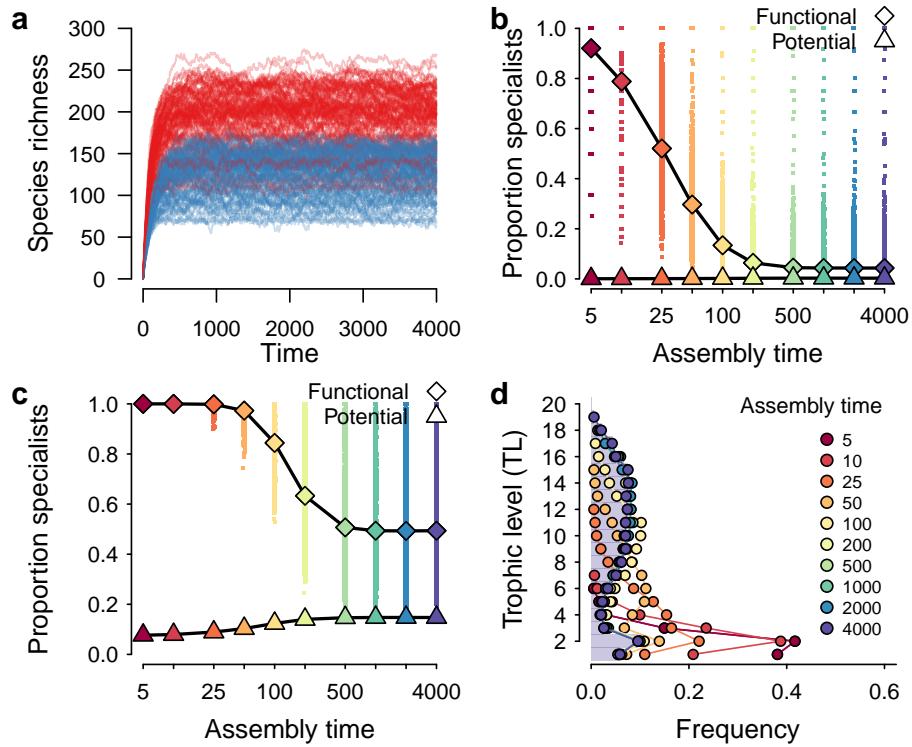


Figure S6. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$ relative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

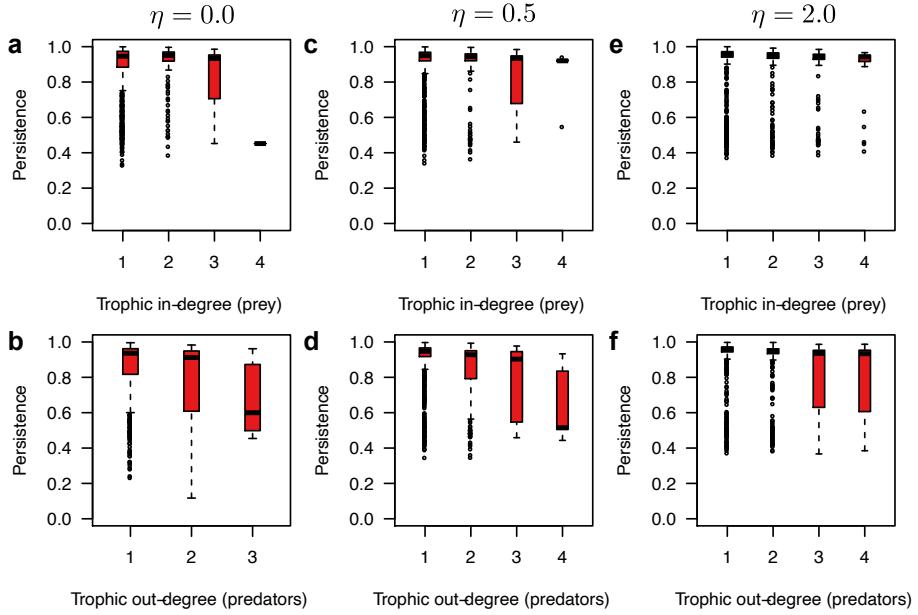


Figure S7. Species-specific persistence as a function of **a** trophic in-degree (number of resources a species has; top) and **b** out-degree (number of consumers that eat the species; bottom) when there are no engineers in the community. Species-specific persistence as a function of **c** trophic in-degree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

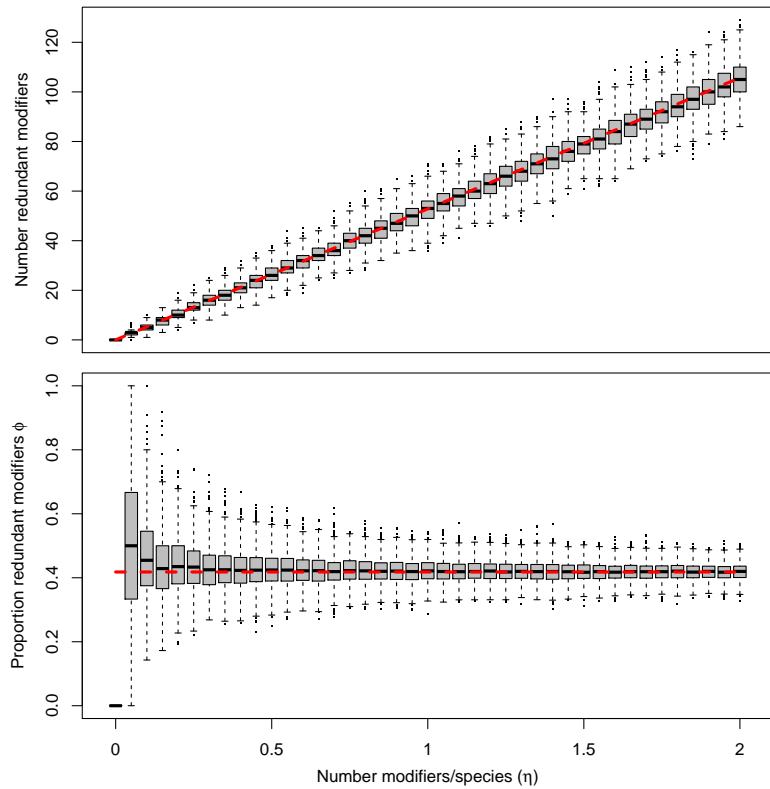


Figure S8. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the source pool as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

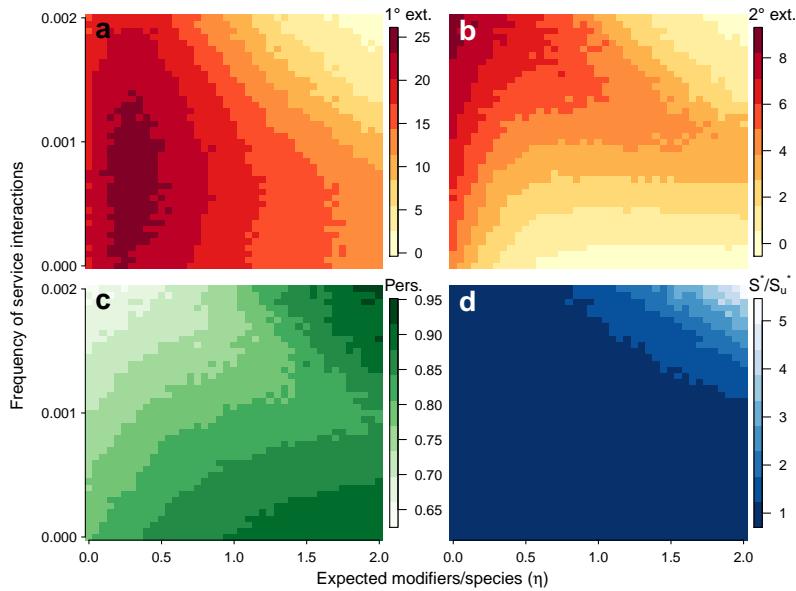


Figure S9. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers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

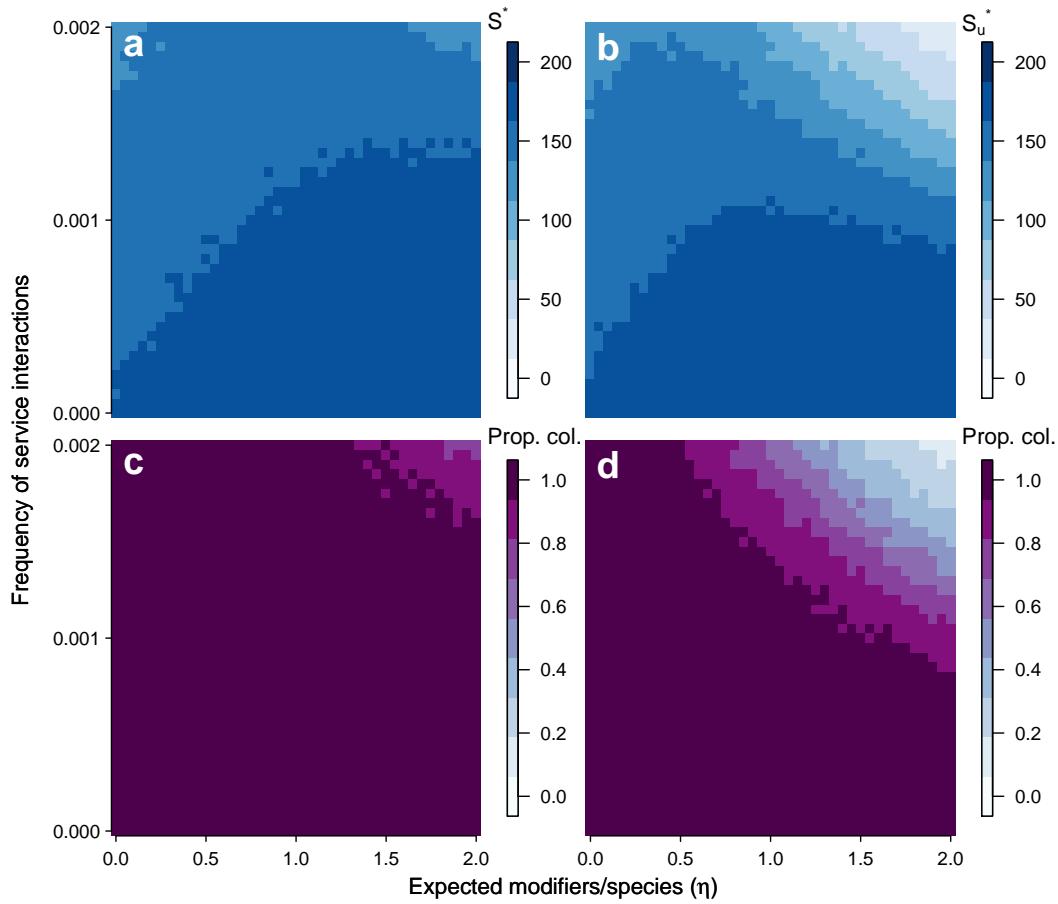


Figure S10. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**,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