

1 Diverse interactions and ecosystem engineering stabilize community assembly

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

11 To unravel nature's secrets we must simplify its abundant complexities and idiosyncrasies. The layers of natural history giving rise to an ecological community can be distilled – among many forms – into a network, where nodes represent species and links represent interactions between them. Networks are generally constructed for one type of interaction, such as food webs capturing predation^{1–3} or pollination networks capturing a specific mutualistic interaction⁴, and continues to lead to significant breakthroughs in our understanding of the dynamical consequences of community structure^{5–7}, assembly⁸, and coevolution⁹.

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

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

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

43 mote primary production by aerating the soil²⁰, salmon
44 and aquatic invertebrates create freshwater habitats by
45 changing stream morphology²¹, and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth²². These examples illustrate ecosystem engineering, where the engineering organism alters the environment on timescales longer than its own²³. Engineers are widely acknowledged to have impacts on both small and large spatial scales²⁴, and may serve as important keystone species in many habitats²⁵.

53 Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth²⁶. For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the Proterozoic roughly 2.5 Byrs BP^{26,27}, 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 plankton²⁸, illustrating that engineering clades can have much larger, sometimes global-scale effects.

65 The effect of the environment on species is commonly included in models of ecological dynamics^{29–31} due to its acknowledged importance and because it can – to first approximation – be easily systematized. By comparison the way in which species engineer the environment defies easy systematization due to the multitude of mechanisms by which engineering occurs. While interactions between species and the abiotic environment have been conceptually described^{17,32}, the absence of engineered effects in network models was addressed by Odling-Smee et

75 al.¹³, where they outlined a conceptual framework that 133 pool. A species from the source pool can colonize if it
 76 included both species and abiotic compartments as nodes 134 finds at least one resource that it can consume (one *eat*
 77 of a network, with links denoting both biotic and abiotic 135 interaction is satisfied; cf. Ref. 35) and all of its non-
 78 interactions. 136 trophic needs are met (all *need* interactions are satisfied;
 137 see Fig. 1). As such, the service interactions are as-
 138 sumed to be obligate, whereas trophic interactions are
 139 flexible. While a basal resource is always assumed to be
 140 present, (white node in Fig. 1b) following the establish-
 141 ment of an autotrophic base, the arrival of mixotrophs
 142 (i.e. mixing auto- and heterotrophy) and lower trophic
 143 heterotrophs create opportunities for organisms occupy-
 144 ing higher trophic levels to invade. This expanding niche
 145 space initially serves as an accelerator for community
 146 growth.

79 Here we model the assembly of an ecological network 147 Following the initial colonization phase, extinctions be-
 80 where nodes represent ecological entities, including en- 148 gin to slow the rate of community growth. Primary ex-
 81 gineering species, non-engineering species, and the ef- 149 tions occur if a given species is not the strongest
 82 fects of the former on the environment, which we call 150 competitor for at least one of its resources (see Meth-
 83 abiotic *modifiers*. The links of the network that con- 151 ods). A species' competition strength is determined by
 84 nect both species and modifiers represent trophic (eat 152 its interactions: competition strength is enhanced by
 85 interactions), service (*need* interactions), and engineer- 153 the number of need interactions and penalized by the
 86 ing dependencies, respectively (Fig. 1; see Materials and 154 number of its resources(favoring trophic specialists) and
 87 Methods for a full description). Trophic interactions rep- 155 consumers(favoring species with fewer predators). Sec-
 88 resent both predation as well as parasitism, whereas ser- 156 ondary extinctions occur when species lose its last trophic
 89 vice interactions account for non-trophic interactions as- 157 or any of its service requirements. See Fig. 1d, e for an
 90 sociated with reproductive facilitation such as pollination 158 illustration of the assembly process. As the colonization
 91 or seed dispersal. In our framework a traditional mutual- 159 and extinction rates converge, the community reaches a
 92 ism (such as a plant-pollinator interaction) consists of a 160 steady state around which it oscillates (Fig. 2a). See
 93 service (need) interaction in one direction and a trophic 161 Methods and Supplementary Appendix 1 for a complete
 94 (eat) interaction in the other. These multitype interac- 162 description of the assembly process. Specific model pa-
 95 tions between species and modifiers thus embed multiple 163 rameterizations for each section are described in Supple-
 96 dependent ecological sub-systems into a single network 164 mentary Appendix 2.
 97 (Fig. 1). Modifiers in our framework overlap conceptu-
 98 ally with the 'abiotic compartments' described in Odling-
 99 Smee et al.¹³. Following Pillai et al.³³, we do not track
 100 the abundances of biotic or abiotic entities but only track
 101 their presence or absence. We use this framework to ex-
 102 plore the dynamics of ecosystem assembly, where the col-
 103 onization and extinction of species within a community
 104 depends on the constraints imposed by the trophic, ser-
 105 vice, and engineering dependencies. We then show how
 106 observed network structures emerge from the process of
 107 assembly, compare their attributes with those from em-
 108 pirical systems, and examine the effects of ecosystem en-
 109 gineers.

110 Our results offer four key insights into the roles of 165 Assembly of ecological communities in the absence of
 111 multitype interactions and ecosystem engineering in 166 engineering results in interaction networks with struc-
 112 driving community assembly. First, we show that the 167 tures consistent with empirical observations. As the com-
 113 assembly of communities in the absence of engineering 168 munity reaches steady state, we find that the connectance
 114 reproduces many features observed in empirical systems. 169 of trophic interactions ($C(t) = L(t)/S(t)^2$, where $S(t)$ is
 115 These include changes in the proportion of generalists 170 species richness and $L(t)$ is the number of links at time t)
 116 over the course of assembly that accord with measured 171 decays to a value similar to that of the source pool over
 117 data and trophic diversity similar to empirical observa- 172 time (Fig. S1). Decaying connectance has been docu-
 118 tions. Second, we show that increasing the frequency 173 mented in the assembly of mangrove communities³⁶, how-
 119 of mutualistic interactions leads to the assembly of 174 ever this decay is likely inevitable as early in the assem-
 120 ecological networks that are more nested, a common 175 bly process the small set of tightly interacting species will
 121 feature of diverse mutualistic systems³⁴, but are also less 176 have a high link density from which it will decline as the
 122 stable. Our third key result shows that increasing the 177 number of species increases. Compared to trophic net-
 123 proportion of ecosystem engineers within a community 178 works constructed using the Niche model³⁷ given similar
 124 has nonlinear effects on observed extinction rates. While 179 species richness and connectance, our framework results
 125 we find that a low amount of engineering increases 180 in networks with degree distributions of similar means
 126 extinction rates, a high amount of engineering has the 181 but with reduced variance (Supplementary Appendix 3).
 127 opposite effect. Finally we show that redundancies 182 Recent empirical work has suggested that general-
 128 in engineered effects promote community diversity by 183 ist species may dominate early in assembly, whereas
 129 lowering the barriers to colonization. 184 specialists colonize after a diverse resource base has
 130

131 **Assembly without ecosystem engineering.** Com- 185 accumulated^{35,36}. Here the trophic generality of species
 132 munities assemble by random colonization from a source 186 i is defined $G_i = k_i^{\text{in}}/(L/S)$ where k_i^{in} is the in-degree, or
 187 number of resources consumed, by species i ³⁷. A species
 188 is classified as a generalist if $G_i > 1$ and a specialist if
 189 $G_i < 1$. In empirical investigations, generality is often
 190 scaled to the steady state link density L^*/S^* . If gener-

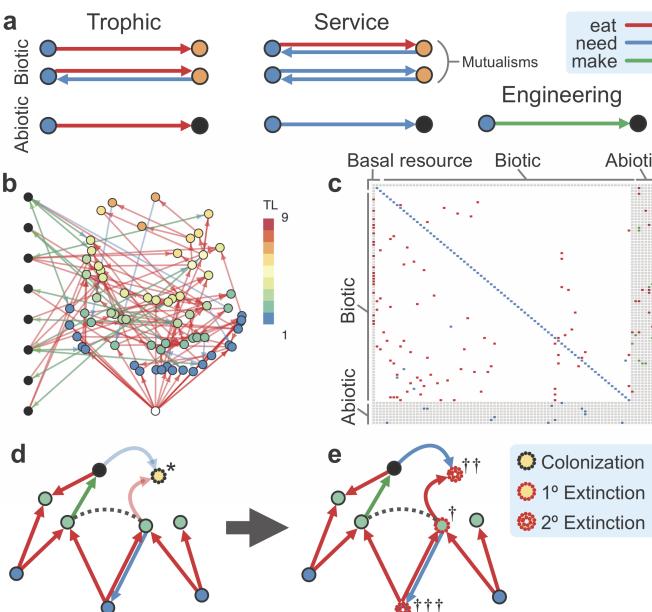


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). **b**, An assembling food web with species (colored nodes; color denotes trophic level, TL) and modifiers (black nodes). The basal resource is the white node rooted at the bottom of the network.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

ability 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 biogeography³⁵, 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 webs³⁶.

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 predator-prey systems³⁸, it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers) are included³⁹. 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 models⁴⁰.

Structure and dynamics of mutualisms. Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks³⁴ and are defined by asymmetric interactions between species^{34,41–43}. A nested structure has been shown to maximize the structural stability of mutualistic networks⁴⁴, emerge naturally via adaptive foraging behaviors^{45,46} and neutral processes⁴⁷, and promote the influence of indirect effects in driving coevolutionary dynamics⁹. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties^{48,49}, interaction asymmetry among species may promote nestedness in both trophic⁴³ and mutualistic systems⁵⁰. Processes that operate on different temporal and spatial scales may have a significant influence on these observations⁵¹. For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity⁵², and there is some evidence from Pleistocene food webs that geographic insularity may reinforce this process⁵³.

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 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

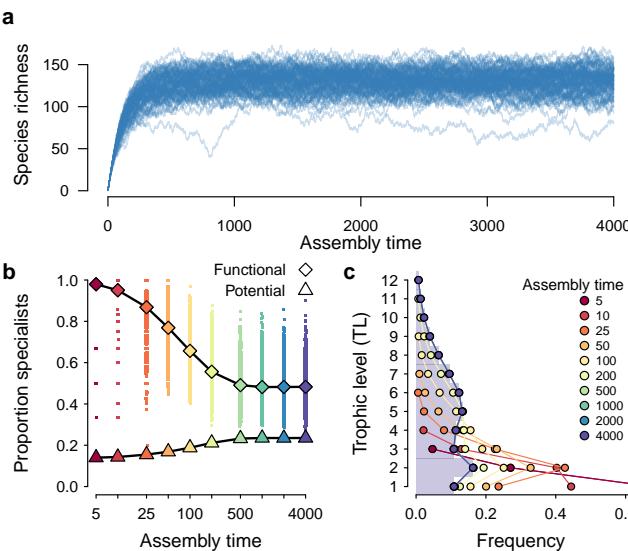


Figure 2. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index $G_i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

272 raises the potential risk associated with losing mutualistic
 273 partners^{54,55}. While this shifting landscape of extinction
 274 risks lowers the steady state species richness of communi-
 275 ties with high frequencies of service interactions, there is
 276 not a direct relationship between nestedness and richness
 277 (Fig. S5).

278 Increasing the frequency of mutualisms affects extinc-
 279 tion dynamics within the community in conflicting ways.
 280 Consider two motifs composed of trophic and mutualis-
 281 tic interactions, respectively (Fig. 3, inset). In a trophic
 282 motif with no mutualisms, species with high vulnerabil-
 283 ity (multiple predators) are at greater risk of primary
 284 extinction via competitive exclusion. This will result in
 285 the secondary extinction of the specialist consumer. If
 286 the interactions are instead mutualisms the costs of vul-
 287 nerability are compensated by services, and it is now the
 288 low vulnerability species with fewer trophic partners that
 289 is at greater risk of exclusion, preserving the core of the
 290 motif at the expense of the periphery. Preservation of
 291 the core species also emerges in larger nested motifs (Fig.
 292 S4), and has been observed in ant-plant mutualistic sys-
 293 tems where nested structures are thought to arise from
 294 shifting competitive exclusion to the periphery⁵⁶. The
 295 effects of mutualisms will differ across motifs, but they
 296 will generally serve to increase competitive advantages of
 297 species receiving services, while creating additional struc-

298 tural dependencies within the community.

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

313 An increased rate of secondary extinctions means that
 314 the network is less robust to perturbation, which may im-
 315 pact community turnover, or persistence. If we measure
 316 persistence in terms of the proportion of time species
 317 are established in the community, we find that higher
 318 frequencies of service interactions lower average persis-
 319 tence (increased species turnover; Fig. 3d). Analysis of
 320 species-specific interactions reveals that it is the species
 321 that require more services that have lower persistence
 322 (Fig. S6). Observations of empirical systems appear
 323 to support model predictions. For example, assembling
 324 plant-pollinator systems have demonstrated high rates of
 325 species and interaction turnover, both during the assem-
 326 bly process and at the steady state⁸.

327 We emphasize that we have restricted ourselves to
 328 examining the effects of obligate mutualisms, although
 329 the importance of non-obligate mutualisms has long
 330 been recognized^{8,45,46,58,59}. We expect that the increased
 331 rate of secondary extinctions attributable to the loss of
 332 obligate mutualistic partners to have greater impact on
 333 system stability than the potential loss of non-obligate
 334 mutualistic partners. As such, we do not expect inclu-
 335 sion of non-obligate mutualisms to alter the qualitative
 336 nature of our findings.

337 **338 Assembly with ecosystem engineering.** The con-
 339 cept of ecosystem engineering, or more generally niche
 340 construction, has both encouraged an extended evo-
 341 lutionary synthesis⁶⁰ while also garnering considerable
 342 controversy^{61,62}. Models that explore the effects of
 343 ecosystem engineering are relatively few, but have cov-
 344 ered important ground^{13,23}. For example, engineering
 345 has been shown to promote invasion⁶³, alter primary
 346 productivity⁶⁴, and change the selective environment
 347 over eco-evolutionary timescales^{65,66} which can lead to
 348 unexpected outcomes such as the fixation of deleteri-
 349 ous alleles⁶⁷. On smaller scales, microbiota construct
 350 shared metabolic resources that have a significant influ-
 351 ence on microbial communities⁶⁸, the dynamics of which
 352 may even serve as the missing ingredient stabilizing some
 353 complex ecological systems⁶⁹.

354 We next explore the effects of ecosystem engineering
 355 by allowing species to produce abiotic modifiers as addi-

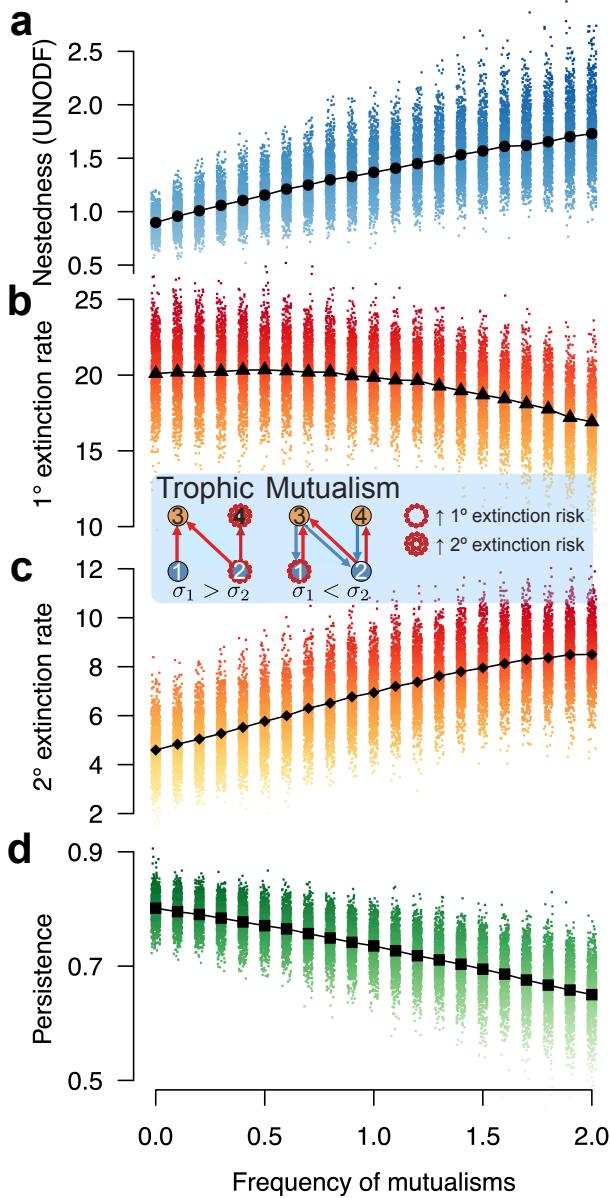


Figure 3. **a**, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)⁵⁷. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. Inset: A trophic and mutualistic nested motif for resource species 1, 2 and consumer species 3, 4. Whether the interactions are trophic or mutualistic impacts the susceptibility of each species to primary extinctions (based on differences in competitive strength σ_i) and secondary extinctions (which result from lost dependencies associated with primary extinctions). **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.

tional 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. S7), 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 for food webs without engineering, we measure community stability by assessing *i*) rates of primary versus secondary extinctions, *ii*) species persistence, and *iii*) steady state community diversity.

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. S8).

415 Increasing the frequency of service interactions pro-
 416 motes service interactions between species and engi-
 417 neered modifiers (Fig. 1). A topical example of the latter
 418 is the habitat provided to invertebrates by the recently
 419 discovered rock-boring teredinid shipworm (*Lithoredo*
 420 *abatanica*)⁷⁰. Here, freshwater invertebrates are serviced
 421 by the habitat modifications engineered by the shipworm,
 422 linking species indirectly via an abiotic effect (in our
 423 framework via a modifier node). As the frequency of
 424 service interactions increases, the negative effects asso-
 425 ciated with rare engineers is diminished (Fig. 4a). In-
 426 creasing service interactions both elevates the competi-
 427 tive strength of species receiving services (from species
 428 and/or modifiers), while creating more interdependen-
 429 cies between and among species. As trophic interactions
 430 are replaced by service interactions, previously vulnera-
 431 ble species gain a competitive foothold and persist (Fig.
 432 3, inset), lowering rates of primary extinctions (Fig. 4a).
 433 The costs of these added services to the community are
 434 an increased rate of secondary extinctions (Fig. 4b) and
 435 higher species turnover (Fig. 4c). Low rates of primary
 436 extinction coupled with high rates of secondary extinc-
 437 tion mean that extinctions are less common but lead to
 438 larger cascades.

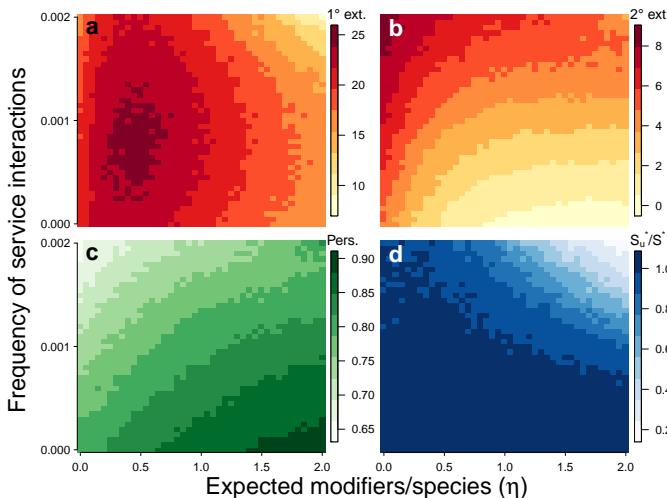


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade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

439 While the importance of engineering timescales has
 440 been emphasized previously²³, redundant engineering
 441 has been assumed to be unimportant¹². We argue that

442 redundancy may be an important component of highly
 443 engineered systems, and particularly relevant when the
 444 effects of engineers increase their own fitness⁶³ as is gen-
 445 erally assumed to be the case with niche construction⁶⁶.
 446 The vast majority of contemporary ecosystem engineer-
 447 ing case studies focus on single taxa, such that redundant
 448 engineers appear rare¹². However if we consider longer
 449 timescales, increasing diversity of engineering clades may
 450 promote redundancy, and in some cases this may feed
 451 back to accelerate diversification¹⁴. Such positive feed-
 452 back mechanisms likely facilitated the global changes in-
 453 duced by cyanobacteria in the Proterozoic^{26,27} among
 454 other large-scale engineering events in the history of
 455 life²⁶. Engineering redundancies are likely important on
 456 shorter timescales as well. For example, diverse sessile
 457 epifauna on shelled gravels in shallow marine environ-
 458 ments are facilitated by the engineering of their ances-
 459 tors, such that the engineered effects of the clade de-
 460 termine the future fitness of descendants⁷¹. In the mi-
 461 crobiome, redundant engineering may be very common
 462 due to the influence of horizontal gene transfer in struc-
 463 turing metabolite production⁷². In these systems, re-
 464 dundancy in the production of shared metabolic re-
 465 sources may play a key role in community structure and
 466 dynamics^{68,73}.

467 When there are few engineers, each modifier in the
 468 community tends to be unique to a particular engineer-
 469 ing species. Engineering redundancies increase linearly
 470 with η (Supplementary Appendix 1; Fig. S9), such that
 471 the loss of an engineer will not necessarily lead to the
 472 loss of engineered modifiers. We examine the effects of
 473 this redundancy by comparing our results to those pro-
 474 duced by the same model, but where each modifier is
 475 uniquely produced by a single species. Surprisingly, the
 476 lack of engineering redundancies does not alter the gen-
 477 eral relationship between engineering and measures of
 478 community stability (Fig. S10). However we find that
 479 redundancies play a central role in maintaining species
 480 diversity. When engineering redundancies are allowed,
 481 steady state community richness S^* does not vary con-
 482 siderably with increasing service interactions and engi-
 483 neering (Fig. S11A). In contrast, when redundant engi-
 484 neering is not allowed, steady state community richness
 485 S_u^* declines sharply (Figs. 4D, S11B).

486 Communities lacking redundancy have lower species
 487 richness because species' trophic and service dependen-
 488 cies are unlikely to be fulfilled, precluding colonization
 489 (Fig. S11C,D). Colonization occurs only when trophic
 490 and service dependencies are fulfilled. A species requiring
 491 multiple engineered modifiers, each uniquely produced,
 492 means that each required entity must precede coloniza-
 493 tion. This magnifies the role of priority effects in con-
 494 straining assembly order¹⁵, precluding many species from
 495 colonizing. In contrast, redundancy increases the tempo-
 496 ral stability of species' niches while minimizing priority
 497 effects by allowing multiple engineers to fulfill depen-
 498 dencies. Our results thus suggest that redundant engineers
 499 may play important roles in assembling ecosystems by

lowering the barriers to colonization thereby promoting community diversity.

We have shown that the dynamics of assembly driven by multitype interactions can produce model communities with realistic structures and dynamics. Moreover, the inclusion of ecosystem engineering by way of modifier nodes reveals that low levels of engineering may be expected to produce higher rates of extinction while limiting the size of extinction cascades, and that engineering redundancy – whether it is common or rare – may have considerable dynamical implications.

We suggest that including the effects of engineers, either explicitly as we have done here, or otherwise, is vital for understanding the inter-dependencies that define ecological systems. As past ecosystems have fundamentally altered the landscape on which contemporary communities interact, future ecosystems will be defined by the influence of engineering today. Given the rate and magnitude that humans are currently engineering environments⁷⁴, understanding the role of ecosystem engineers is tantamount to understanding our own.

Methods

We model an ecological system with a network where nodes represent ecological entities such as populations of species and/or the presence of abiotic modifiers affecting species. Following Pilai et al.³³, we do not track the abundances of entities but only track their presence or absence. The links of the network represent interactions between pairs of entities (x,y). We distinguish three types of such interactions: x eats y, x needs y to be present, x makes modifier y.

The assembly process entails two steps: first a source pool of species is created, followed by colonization/extinction into/from a local community. The model is initialized by creating S species and $M = \eta S$ modifiers, such that $N = S + M$ is the average total number of entities and η is the average number of modifiers per species in the system. For each pair of species (x,y) there is a probability p_e that x eats y and probability p_n that x needs y. For each pair of species x and modifier m, there is a probability q_e that x eats m and a probability q_n that species x needs modifier m. Additionally, each species makes a number of modifiers that is drawn from a Poisson distribution with mean $\mu = \eta e / (e - 1)$ where e is Euler's number. Once the number of modifiers per species is determined, each modifier is assigned to a species independently. This means that multiple species may make the same modifier, and that there may be some modifiers that are not made by any species, which are eliminated from the pool.

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

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

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

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

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

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 created immediately, 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 efficiency⁷⁵. 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.

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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- 873 JDY and TG conceived of the model framework. JDY, MMP,
874 MAMA, and TG designed the analyses. JDY, MMP, MAMA,
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879

880 Competing interests

881 The authors declare no competing interests.

882

SUPPLEMENTARY METHODS

936

Appendix 2: Model parameterizations

883

Appendix 1: Building the source pool

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

895 In these two quadrants, the expected frequency of eat interactions
 896 $E\{p_e\}$ and the expected frequency of need interactions $E\{p_n\}$ are
 897 free parameters, as is the expected number of modifiers made per
 898 species $E\{M_i\} = \eta$. Here and throughout, we simplify this pa-
 899 rameter space by assuming that the frequency of eat and need in-
 900 teractions for species-species (SS) interactions and species-modifier
 901 (SM) interactions are equivalent, such that $E_{SS}\{p_e\} = E_{SM}\{p_e\}$
 902 and $E_{SS}\{p_n\} = E_{SM}\{p_n\}$. For each species, a set number of modi-
 903 fiers is drawn from $Pois(\eta)$, such that the expected proportion of
 904 species that are engineers (species that make modifiers) is $1 - e^{-\eta}$.
 905 If a particular modifier is randomly and independently drawn for
 906 a given engineer from a complete list of all possible modifiers, such
 907 that multiple species – with some probability – can make the same
 908 modifier, the expected number of modifiers is

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

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

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

911 Finally the frequency of the non-interaction is calculated as
 912 $E_{SS}\{p_\emptyset\} = 1 - E_{SS}\{p_e\} + E_{SS}\{p_n\}$ and $E_{SM}\{p_\emptyset\} = 1 - E_{SM}\{p_e\} +$
 913 $E_{SM}\{p_n\} + E_{SM}\{p_m\}$ for species-species and species-modifier in-
 914 teractions, respectively. Pairwise interactions are assigned ran-
 915 domly from these probabilities between species-species and species-
 916 modifiers independently in both quadrants, such that the source
 917 pool matrix has no imbued structure apart from the number of
 918 species, the number of modifiers, and the frequency of each direc-
 919 tional interaction type. Each source pool is provided a *basal re-*
 920 *source* (the first row/column). A species with a trophic interaction
 921 to this resource is identified as an autotroph (or mixotroph depend-
 922 ing on its other trophic interactions). If they do not have service
 923 dependencies with other species/modifiers, it is these species that
 924 are uniquely able to initiate assembly.

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

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

930 such that the proportion of redundant modifiers ϕ is

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

931 Accordingly, we find that the number of redundant modifiers in-
 932 creases linearly with η , while the proportion of modifiers that are
 933 redundant is fixed. Figure S9A,B shows both analytical expecta-
 934 tions and numerically-derived measures for $E\{M_P\}_{\text{redundant}}$ and
 935 ϕ , respectively.

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

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

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

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

947 Appendix 3: Comparison to Niche Model

948 We compared certain structural features of ENIgMa at steady
 949 state to those of the Niche Model³⁷. Comparisons were restricted
 950 to networks constructed in the absence of engineering because engi-
 951 neers introduce indirect effects that are not considered in static food
 952 web models, and may make such comparisons irrelevant. While
 953 there are many similarities, there are also some important differ-
 954 ences, some of which are highlighted in the main text. While we
 955 consider a comparison of our framework with other food web mod-
 956 els such as the Niche Model relevant, we emphasize that the mo-
 957 tivations underlying both are distinct. Our approach is intended
 958 to provide a deeper understanding into how multitype depen-
 959 dencies between species and the environment impact the dynamics of
 960 community assembly. While capturing general qualitative features
 961 of empirical systems demonstrates that the dynamics we consider
 962 are ecologically relevant, the goal of our approach is distinct from
 963 that of static food web models, which aim to maximize structural
 964 similarities between model and empirical systems^{37,76}.

965 We compared steady state ecological networks that emerge
 966 from ENIgMa (described in Materials and Methods, main text)
 967 with food webs constructed from the Niche Model³⁷ with simi-
 968 lar species richness and connectance. Because species richness and
 969 connectance of the Niche Model are often altered by eliminating dis-
 970 connected species, we compared *i*) species richness, *ii*) connectance,
 971 *iii*) mean species degree, *iv*) standard deviation of out-degree dis-
 972 tributions, and *v*) standard deviation of in-degree distributions av-
 973 eraged across 1000 replicates for each model.

974 We found that all measures resulted in fairly similar values be-
 975 tween ENIgMa and the Niche Model food webs with a some im-
 976 portant differences (Figs. S2,S3). While similar, ENIgMa pro-
 977 duces consistently lower values of connectance, mean species de-
 978 gree, as well as standard deviations of the in- and out-degree dis-
 979 tributions. This means that the food webs produced by ENIgMa
 980 are more sparsely connected with less variance between species.
 981 These results were expected, as the Niche Model assumes system-
 982 atically increasing dietary ranges with higher niche values, whereas
 983 the trophic interactions assigned to species in the source pool of
 984 ENIgMa are drawn independently. An important difference be-
 985 tween the Niche Model and ENIgMa is that we do not distinguish
 986 between predators and parasites. A different framework known
 987 as the Inverse Niche Model⁷⁷ has been proposed to address par-
 988 asitic interactions. The Inverse Niche Model assumes increasing
 989 specialization with feeding hierarchies, which would serve to lower
 990 the average generality of species (lower degree). In addition, the
 991 Inverse Niche model outputs lower standard deviations of in- and
 992 out-degree distributions. Together these trends suggest that the
 993 qualitative structural differences that we observe for the assembly
 994 and Niche model may reflect an important structural distinction
 995 between food webs that do and do not include parasitic species.

996 Appendix 4: The structure of engineered food webs 1015 two species. So if a species B makes a modifier M , and A eats M ,
 1016 then we set A to (indirectly) eat B . This accounting of both di-
 1017 rect and indirect trophic interactions between species can then be
 1018 compared to *i*) the direct trophic link density of the community,
 1019 or *ii*) the direct + indirect trophic link density of the community,
 1020 and some insights can be gained from both approaches.

997 We examined whether and to what extent the structure of food 1021 webs was altered when engineers are introduced into the commu-
998 nity. Because trophic links can now exist between species-modifiers 1022 as well as species-species, there are different ways of accounting
999 for structure, making direct comparisons with non-engineered food 1023 webs somewhat difficult. We note that we exclude service interac-
1000 tions in this case to best match the structural analysis described in 1024 the main text and shown in Fig. 2. While the inclusion of engineers
1001 ($\eta = 2$) does have an impact on stability in terms of primary versus 1025 secondary extinction rates, there is not a strong effect of engineer-
1002 ing on steady state species richness (Fig. S7a; species richness is 1026 shown in blue, modifier richness is shown in red).

1003 The role of specialists *does* and *does not* change with the intro- 1027 duction of engineering, depending on how specialization is defined. 1028 formalizing the otherwise indirect relationships that structure the
1004 role of engineers in the community.

1005 As in the main text, a specialist is defined when its generality index 1029 $G_i < 1$ relative to the steady state link density. When engineered 1030 modifiers are included, we account for a trophic interaction between 1031 those observed for non-engineered food webs (Fig. 2b).

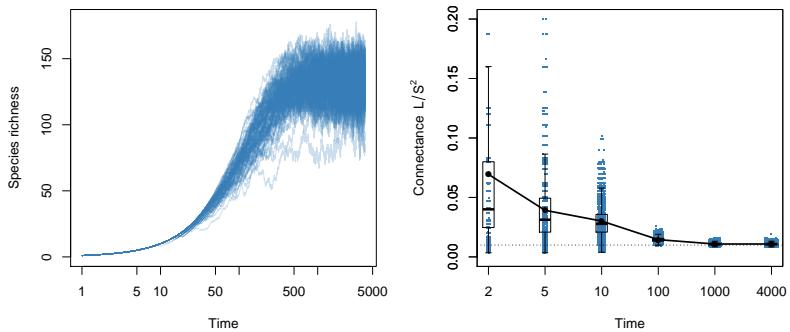


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because few species are tightly connected. Over time, connectance decays as species richness increases, and the density of trophic interactions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

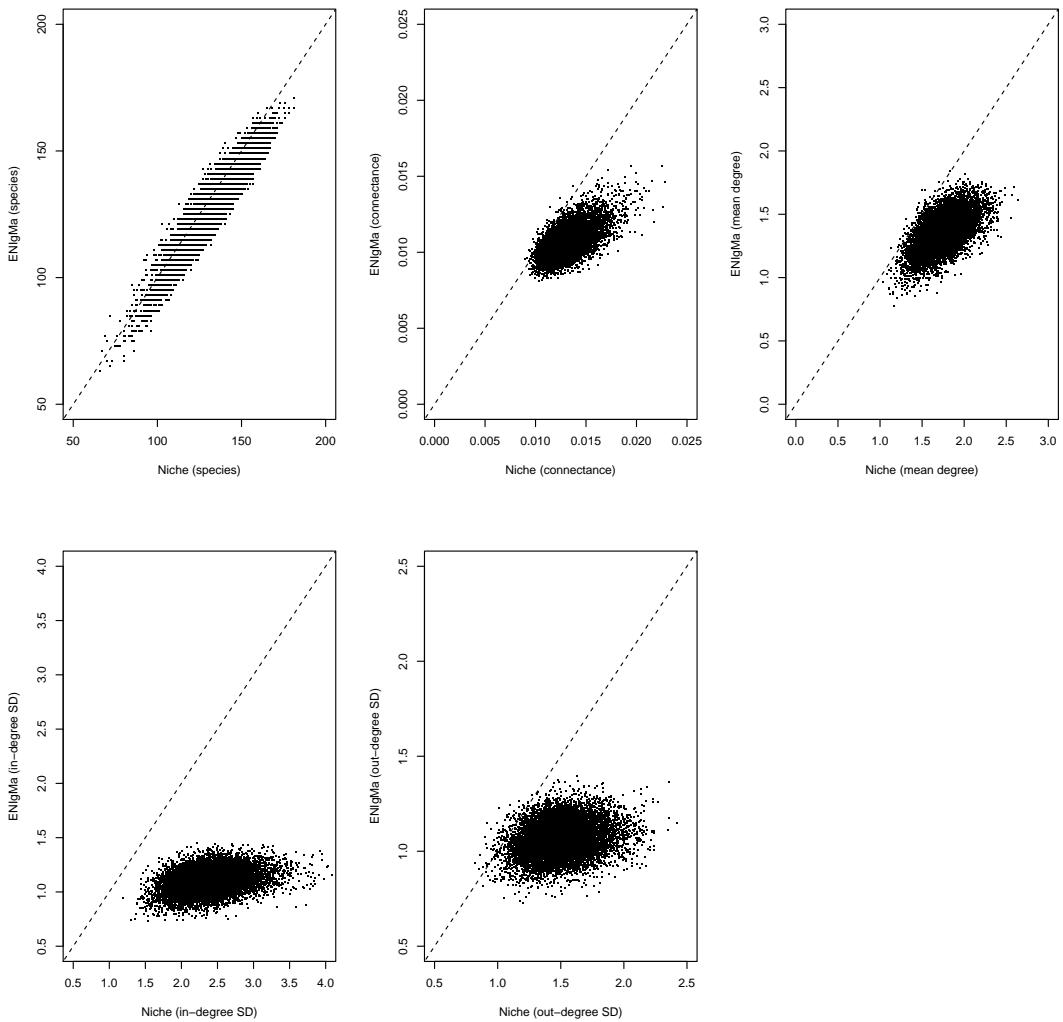


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in-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

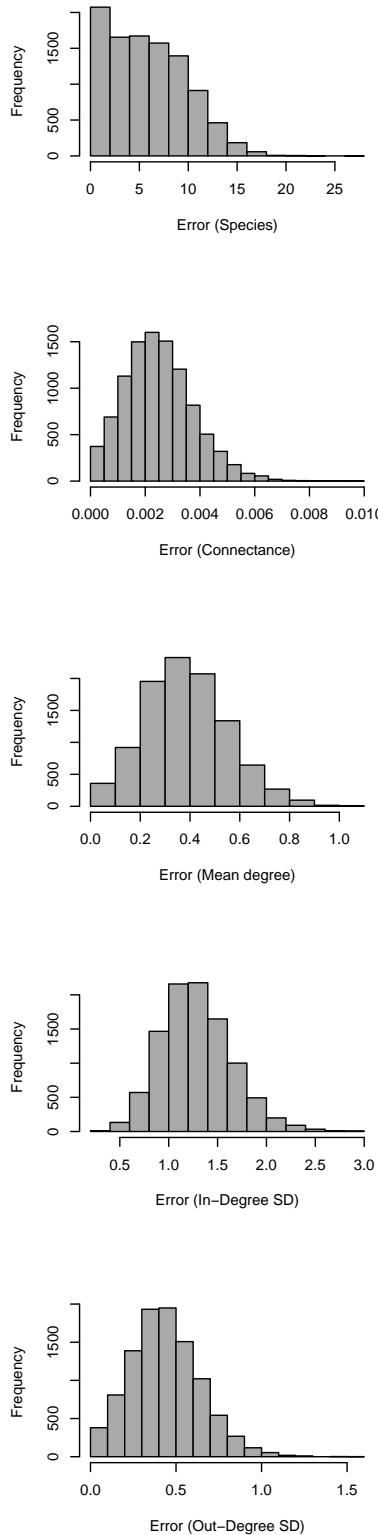


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as $\sqrt{(m_i - m_j)^2}$, where m_i and m_j are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model used to assess metrics.

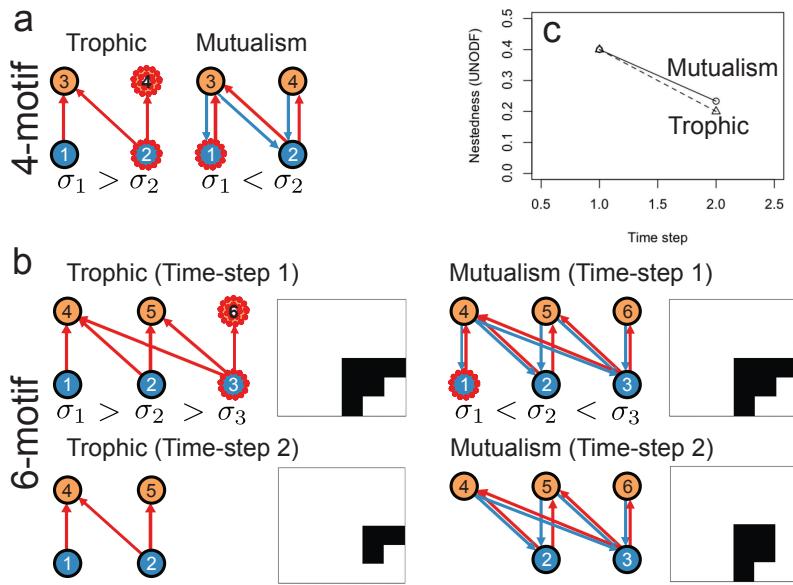


Figure S4. **a**, The 4-species nested trophic and mutualistic motif described in the main text. **b**, A 6-species nested trophic and mutualistic motif. For the trophic motif at time-step 1, it is the core species of the motif that are at greatest risk of extinction. For the mutualistic motif at time-step 1 it is the peripheral species at greatest risk. **c**, Nestedness (UNODF) of the 6-species trophic and mutualistic motif over the course of the two time-steps illustrated in **b**. While nestedness decays in both following the primary and secondary extinctions, it decays more slowly for the mutualistic motif. While suggesting that the dynamics of a single (among many possible) motif cannot simply be extended to the entire network, we suggest that the maintenance of asymmetric interactions among species engaged in mutualistic interactions may be important for the observed increase in nestedness when service interactions are frequent.

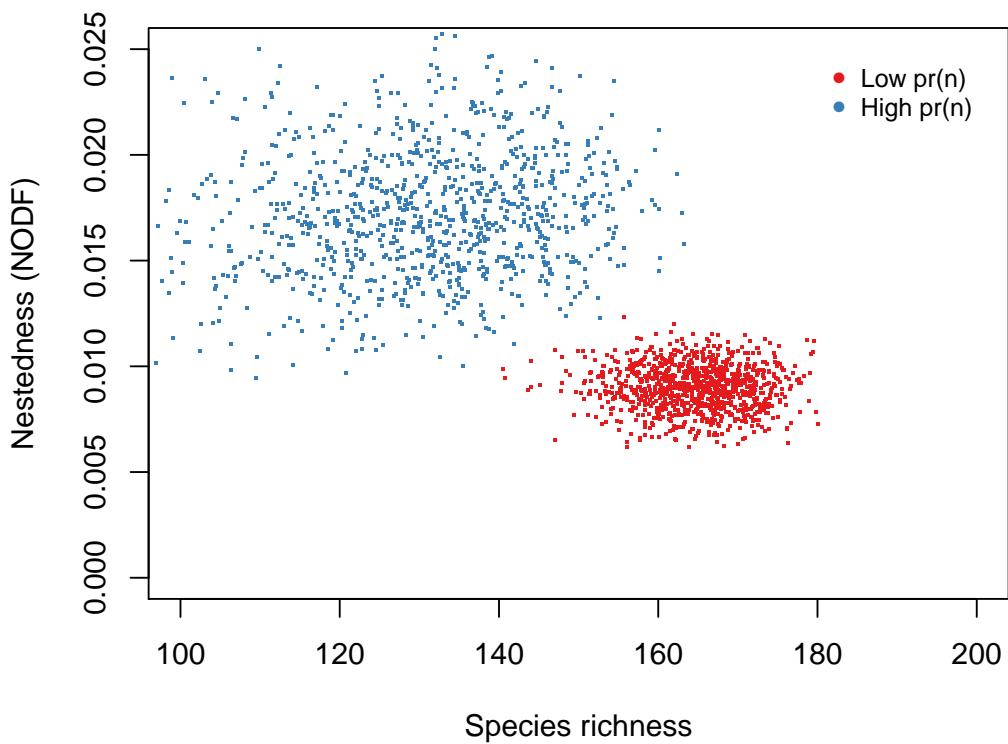


Figure S5. Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities with low (red) and high (blue) frequency of service interactions. While higher frequencies of service interactions does lower steady state species richness (due to increasing secondary extinction rates), there is not a relationship between nestedness and species richness across replicates for a given service interaction frequency.

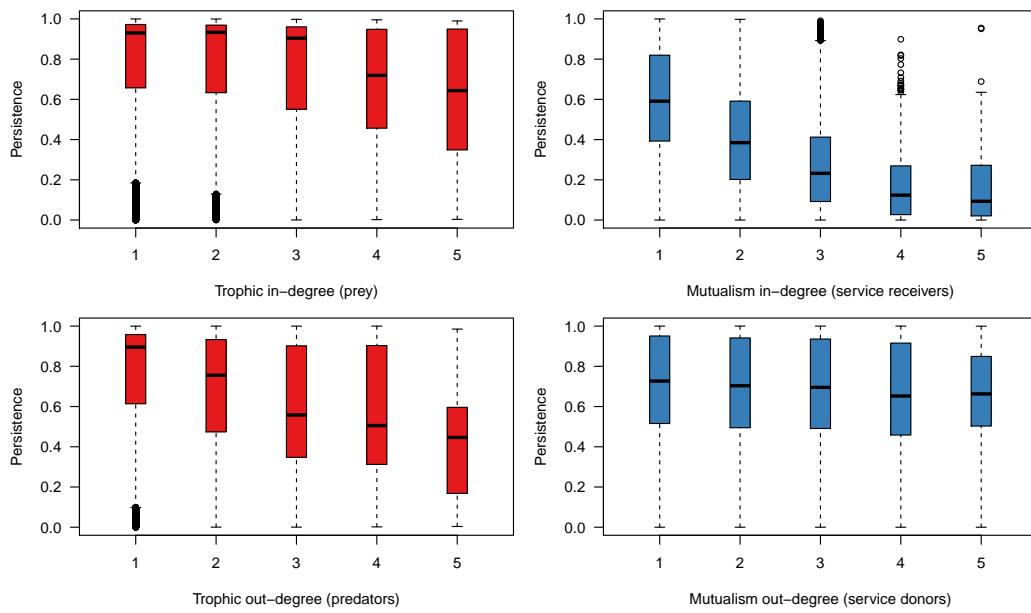


Figure S6. Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top) and out-degree (the number of predators a species has; bottom). Right column: species-specific persistence as a function of the mutualism in-degree (the number of service receivers 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.

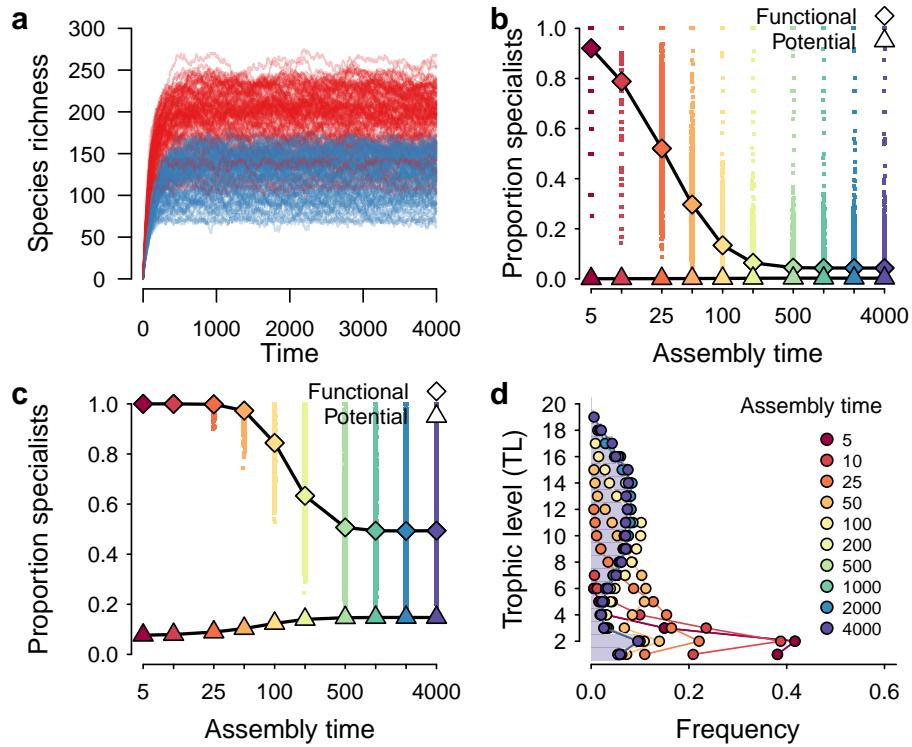


Figure S7. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$ relative 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 Materials and Methods for parameter values.

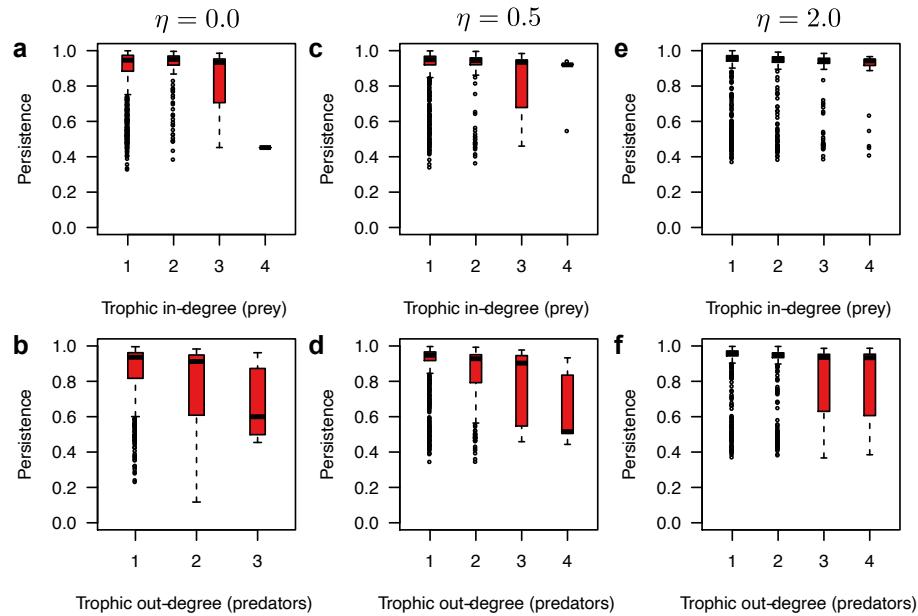


Figure S8. **a,b**, Species-specific persistence as a function of trophic in-degree (number of resources a species has; top) and out-degree (number of consumers that eat the species; bottom) when there are no engineers in the community. **c,d**, Species-specific persistence as a function of trophic in-degree (number of resources a species has; top) and 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 increase in species with higher numbers of consumers. **e,f**, Species-specific persistence as a function of trophic in-degree (number of resources a species has; top) and 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.

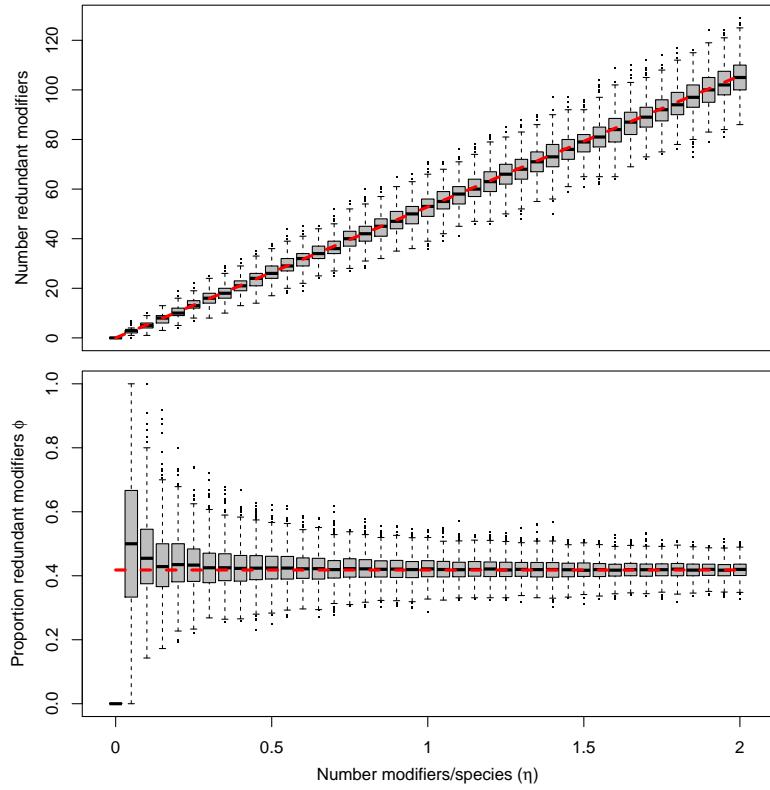


Figure S9. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the source pool as 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).

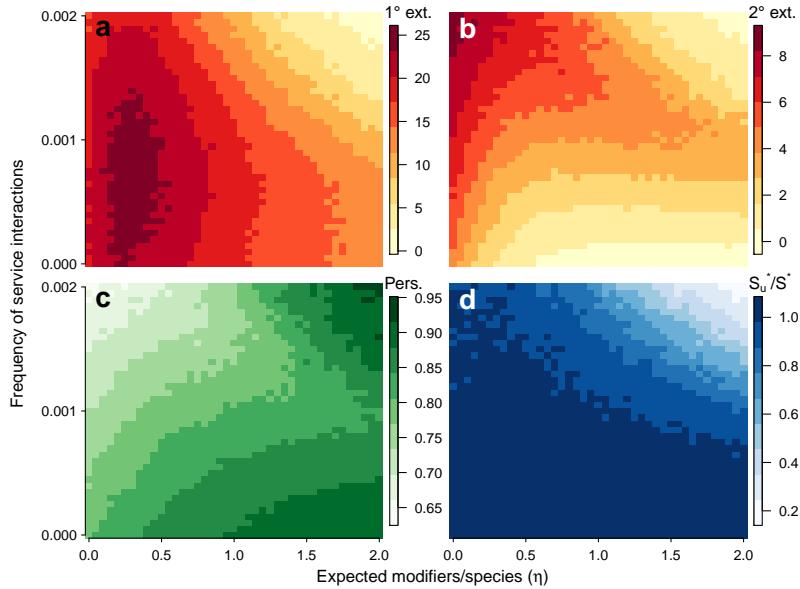


Figure S10. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence, defined as the percent simulation time the community is occupied by a given species, averaged across all species that successfully colonize. **d**, The ratio S_u^*/S^* , where S_u^* denotes steady states for systems where all engineered modifiers are unique to each engineer, and S^* denote steady states for systems with redundant engineering. Lower values of S_u^*/S^* mean that systems with redundant engineers have higher steady states than those without redundancies. Values are averaged over 50 replicates for each parameterization. See Materials and Methods for default parameter values.

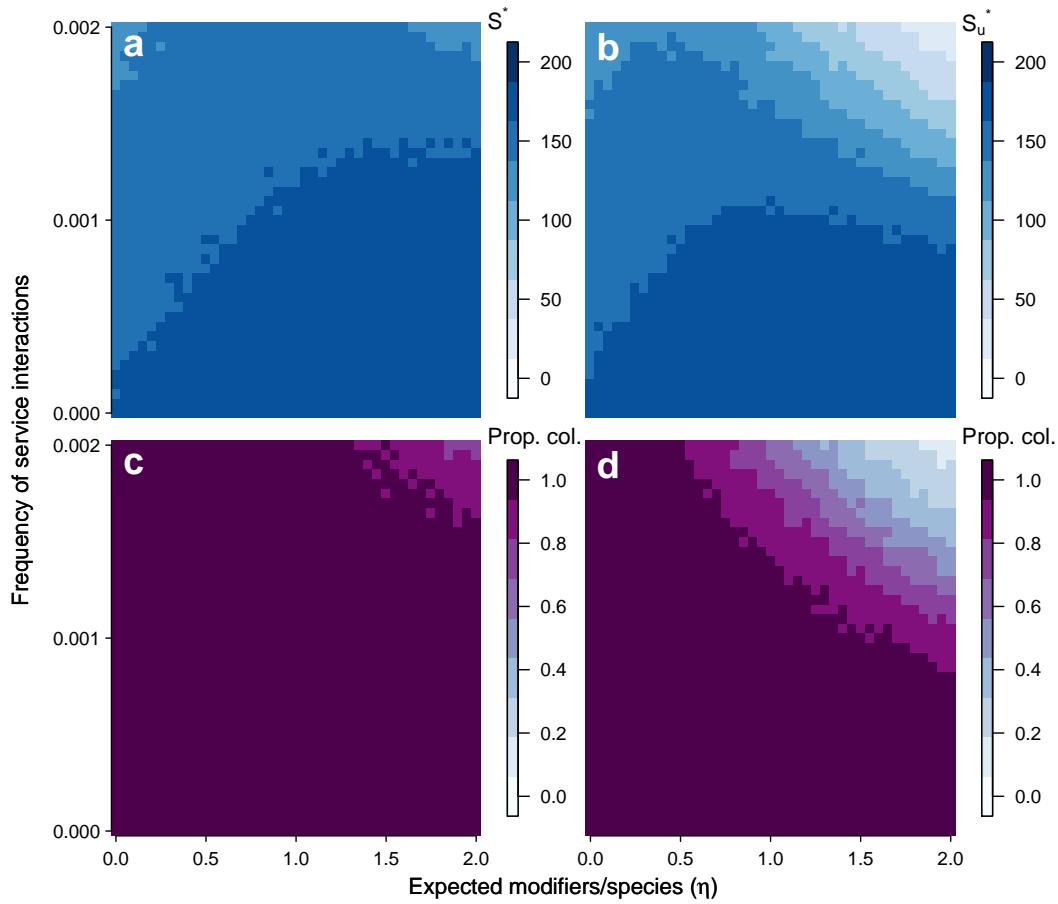


Figure S11. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (without redundant engineering).