

1 Diverse interactions and ecosystem engineering can stabilize community assembly

2 Justin D. Yeakel,^{1,2} Mathias M. Pires,³ Marcus A. M. de Aguiar,³ James L.
3 O'Donnell,⁴ Paulo R. Guimarães Jr.,⁵ Dominique Gravel,⁶ and Thilo Gross^{7,8,9,10}

4 ¹University of California Merced, 5200 Lake Rd, Merced, CA 95340, USA

5 ²Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

6 ³Universidade Estadual de Campinas, Cidade Universitária Zeferino Vaz - Barão Geraldo, Campinas - SP, 13083-970, Brazil

7 ⁴University of Washington, Seattle, WA 98195, USA

8 ⁵Universidade de São Paulo, Butanta, São Paulo - State of São Paulo, Brazil

9 ⁶Université de Sherbrooke, 2500 Boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada

10 ⁷University of California, Davis, Davis, CA 95616, USA

11 ⁸Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung

12 ⁹Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB),

13 Ammerländer Heerstrasse 231, 26129 Oldenburg, Germany

14 ¹⁰University of Oldenburg, ICBM, 26129 Oldenburg, Germany

15 Correspondence and requests for materials should be addressed to J.D.Y. (email: jdyeakel@gmail.com)

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 directly with each other but and indirectly through environmental effects, however the role of these ecosystem engineers has not yet been considered in models of ecological networksecological network models. Here we explore the dynamics of ecosystem assembly, where the species 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 mutualismsmutualistic interactions. 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 frequencyprimary extinctions, 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 reducing primary extinctions and extinction cascade magnitude. Our results suggest that ecological engineers may enhance community diversity while increasing persistence by facilitating colonization and limiting competitive exclusion.

16 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
17 be distilled – among many forms – into a network, where nodes represent species and links represent interactions
18 between them. Networks are generally constructed for one type of interaction, such as food webs capturing
19 predation^{1–3} or pollination networks capturing a specific
20 mutualistic interaction⁴, and continuescontinue to lead
21 to significant breakthroughs in our understanding of the
22 dynamical consequences of community structure^{5–7}. This
23 perspective has also been used to shed light on the generative processes driving the assembly of complex ecological
24 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}, while differences in species' trophic niche^{15,16}, coupled with early establishment of fast/slow energy channels¹⁷, appear to significantly impact long-term community dynamics. There has been growing interest in understanding the combined role of trophic and mutualistic interactions in driving assembly^{18,19}, where the establishment of species from a source pool^{19–21} and the plasticity of

41 species interactions^{22–25} constrain colonization and extinction dynamics. Despite these advances While recent
42 interest in 'multilayer networks' comprising multiple
43 interaction types (multitype interactions) may provide
44 additional insight into these processes^{26,27}, there is not
45 yet a well-defined theory for the assembly of communities
46 that incorporates multiple interaction types and both
47 biotic/multitype interactions as well as both biotic and
48 abiotic components from which functioning ecosystems
49 are composed (cf. Ref.²⁸).

50 Recent interest in 'multilayer networks' comprising multiple interaction types (multitype interactions) may provide additional insight into these processes^{26,27}. However, interactions where species affect others by altering the abiotic environment in a lasting way have not yet been incorporated into models of ecological networks. These interactions, known as ecosystem engineering^{31,94} or more generally niche construction^{12,95}, are quite common in nature and exist in almost every ecosystem.

51 Diverse interactions occur not only between species but indirectly through the effects that species have on their the abiotic environment^{29–31}. Elephants root out large saplings and small trees, enabling the formation and maintenance of grasslands^{32,33} and creating habitat for smaller vertebrates³⁴. Burrowing rodents such as go-

66 phers and African mole rats create shelter and promote 124 primary production by aerating the soil^{35,36}, salmon 125 bed multiple dependent ecological sub-systems into a sin-
 67 and aquatic invertebrates create freshwater habitats by 126 gle network ([Fig.-Figure 1](#)). Modifiers in our framework
 68 changing stream morphology³⁷, and leaf-cutter ants al- 127 overlap conceptually with the ‘abiotic compartments’ de-
 69 ter microclimates, influencing seedling survival and plant 128 scribed in Odling-Smee et al.³¹. Following Pillai et al.⁴⁹,
 70 growth³⁸. These examples illustrate ecosystem engineer- 129 we do not track the abundances of biotic or abiotic en-
 71 ing, where the engineering organism alters the environ- 130 tities but track only their presence or absence. We use
 72 ment on timescales longer than its own³⁹. Engineers are 131 this framework to explore the dynamics of ecosystem as-
 73 widely acknowledged to have impacts on both small and 132 sembly, where the colonization and extinction of species
 74 large spatial scales⁴⁰, and likely serve as important key- 133 within a community depends on the constraints imposed
 75 stone species in many habitats⁴¹. 134 by the trophic, service, and engineering dependencies.
 76

77 Ecosystem engineering not only impacts communities 135 We then show how observed network structures emerge
 78 on ecological timescales, but has profoundly shaped the 136 from the process of assembly, compare their attributes
 79 evolution of life on Earth⁴². For example, the emergence 137 with those of empirical systems, and examine the effects
 80 of multicellular cyanobacteria fundamentally altered the 138 of ecosystem engineers.
 81 atmosphere during the Great Oxidation Event of the 139 Our results offer four key insights into the roles of
 82 Proterozoic roughly 2.5 Byrs BP^{42,43}, paving the way 140 multitype interactions and ecosystem engineering in
 83 for the biological invasion of terrestrial habitats. In the 141 driving community assembly. First, we show that the
 84 oceans it is thought that rRNA and protein biogenesis of 142 assembly of communities in the absence of engineer-
 85 aquatic photoautotrophs drove the nitrogen:phosphorous 143 ing reproduces many features observed in empirical
 86 ratio (the Redfield Ratio) to ca. 16:1 matching that of 144 systems. These include changes in the proportion of
 87 plankton⁴⁴, illustrating that engineering clades can have 145 generalists over the course of assembly that accord
 88 much larger, sometimes global-scale effects. 146 with measured data and trophic diversity similar to
 89 The effect of abiotic environmental conditions on 147 empirical observations. Second, we show that increasing
 90 species is commonly included in models of ecological 148 the frequency of mutualistic interactions leads to the
 91 dynamics^{45–47} due to its acknowledged importance and 149 assembly of ecological networks that are more nested,
 92 because it can – to first approximation – be easily sys- 150 a common feature of diverse mutualistic systems⁵⁰,
 93 tematized. By comparison the way in which species engineer 151 but [that](#) are also prone to extinction cascades. Our
 94 the environment defies easy systemization due to the mul- 152 third key result shows that increasing the proportion of
 95 titude of mechanisms by which engineering occurs. While 153 ecosystem engineers within a community has nonlinear
 96 interactions between species and the abiotic environ- 154 effects on observed extinction rates. While we find that
 97 ment have been conceptually described^{30,48}, the absence 155 a low amount of engineering increases extinction rates,
 98 of engineered effects in network models was [addressed](#) 156 a high amount of engineering has the opposite effect.
 99 [described](#) by Odling-Smee et al.³¹, where they outlined 157 Finally we show that redundancies in engineered effects
 100 a conceptual framework that included both species and 158 promote community diversity by lowering the barriers
 101 abiotic compartments as nodes of a network, with links 159 to colonization.

102 denoting both biotic and abiotic interactions.

103 How does the assembly of species constrained by multi- 160 **Results**
 104 type interactions impact community structure and stabil-
 105 ity? How are these processes altered when the presence 161 **Assembly without ecosystem engineering.** Our
 106 of engineers modifies species’ dependencies within the 162 framework assumes that communities assemble by ran-
 107 community? Here we model the assembly of an ecologi- 163 dom colonization from a source pool. A species from
 108 cal network where nodes represent ecological entities, in- 164 the source pool can colonize if it finds at least one re-
 109 cluding engineering species, non-engineering species, and 165 source that it can consume (one [eat eat](#) interaction is
 110 the effects of the former on the environment, which we 166 satisfied; cf. Ref.⁵¹) and all of its non-trophic needs
 111 call abiotic [modifiers](#)⁵². The links of the network 167 are met (all [need need](#) interactions are satisfied; see [Fig.-Figure 1](#)). As such, service interactions are assumed to
 112 that connect both species and modifiers represent trophic 168 be obligate, whereas trophic interactions are flexible –
 113 ([eat eat](#) interactions), service ([need ‘need’](#) interactions), 169 except in the case of a consumer with [only just](#) a sin-
 114 and engineering dependencies, respectively ([Fig.-Figure 1](#); 170 gle resource. While [a-an abiotic](#) basal resource is always
 115 see Methods for a full description). Trophic inter- 171 assumed to be present (white node in [Fig.-Figure 1b](#)),
 116 actions represent both predation as well as parasitism, 172 following the establishment of an autotrophic base, the
 117 whereas service interactions account for non-trophic in- 173 arrival of mixotrophs (i.e. mixing auto- and heterotro-
 118 teractions associated with reproductive facilitation such 174 phy) and lower trophic heterotrophs create opportunities
 119 as pollination or seed dispersal. In our framework a tradi- 175 for organisms occupying higher trophic levels to invade.
 120 tional mutualism (such as a plant-pollinator interaction) 176 This expanding niche space initially serves as an acceler-
 121 consists of a service (need) interaction in one direction 177 ator for community growth.
 122 and a trophic (eat) interaction in the other. These multi- 178

123 type interactions between species and modifiers thus em- 179 Following the initial colonization phase, extinctions be-
 180 gin to slow the rate of community growth. Primary ex-
 181 tinctions occur if a given species is not the strongest

162 framework assumes that communities assemble by ran-
 163 dom colonization from a source pool. A species from
 164 the source pool can colonize if it finds at least one re-
 165 source that it can consume (one [eat eat](#) interaction is
 166 satisfied; cf. Ref.⁵¹) and all of its non-trophic needs
 167 are met (all [need need](#) interactions are satisfied; see [Fig.-Figure 1](#)). As such, service interactions are assumed to
 168 be obligate, whereas trophic interactions are flexible –
 169 except in the case of a consumer with [only just](#) a sin-
 170 gle resource. While [a-an abiotic](#) basal resource is always
 171 assumed to be present (white node in [Fig.-Figure 1b](#)),
 172 following the establishment of an autotrophic base, the
 173 arrival of mixotrophs (i.e. mixing auto- and heterotro-
 174 phy) and lower trophic heterotrophs create opportunities
 175 for organisms occupying higher trophic levels to invade.
 176 This expanding niche space initially serves as an acceler-
 177 ator for community growth.
 178

competitor for at least one of its resources. A species' competition strength is determined by its interactions: competition strength is enhanced by the number of need interactions (where the number of potential and realized interactions are equivalent) and penalized by the number of its resources (favoring realized resources (i.e. those resources present in the local community, favoring functional trophic specialists) and consumers (favoring species with fewer predators realized predators (i.e. those predators present in the local community)). This encodes three key assumptions: that mutualisms provide a fitness benefit⁵², specialists are stronger competitors than generalists^{53–56}, and many predators entail having many predators entails an energetic cost⁵⁷. Secondary extinctions occur when a species loses its last trophic or any of its service requirements. See Fig. 1d,e for an illustration of the assembly process. As the colonization and extinction rates converge, the community reaches a steady state around which it oscillates (Fig. Figure 2a). See Figure 1d,e for an illustration of the assembly process, and the Methods and Supplementary Appendix Note 1 for a complete description of the assembly process. Specific model parameterizations are described in Supplementary Appendix Note 2.

Assembly of ecological communities in the absence of engineering results in interaction networks with structures consistent with empirical observations. As the community reaches steady state (Fig. Figure 2a), we find that the connectance of trophic interactions ($C(t) = L(t)/S(t)^2$, where $S(t)$ is species richness and $L(t)$ is the number of links at time t) decays to a constant value (Fig. ??). Supplementary Figure 1. Decaying connectance followed by stabilization around a constant value has been documented in the assembly of mangrove communities¹⁶ and experimental aquatic mesocosms¹⁷. The initial decay is likely inevitable in sparse webs as early in the assembly process the small set of tightly interacting species will have a high link density from which it will decline as the number of species increases.

Compared to trophic networks constructed using In Supplementary Note 3 we include a brief comparison of assembly model food webs with those produced by the Niche model⁵⁸ given similar species richness and connectance, our framework results in networks with degree distributions of similar means but with reduced variance (Supplementary Appendix). While the aims of these approaches are quite distinct, we provide this comparison as a reference point to traditional food web models, and to emphasize that both approaches result in food webs with similar structures (Supplementary Figures 2,3).

Recent empirical work has suggested that generalist species may dominate early in assembly, whereas specialists colonize after a diverse resource base has accumulated^{16,51}. Here the trophic generality of species i is defined as $G_i(t) = k_i^{\text{in}}(t)/(L^*/S^*)$ ⁵⁸, where $k_i^{\text{in}}(t)$ is the number of species consumed by species i resource species linked

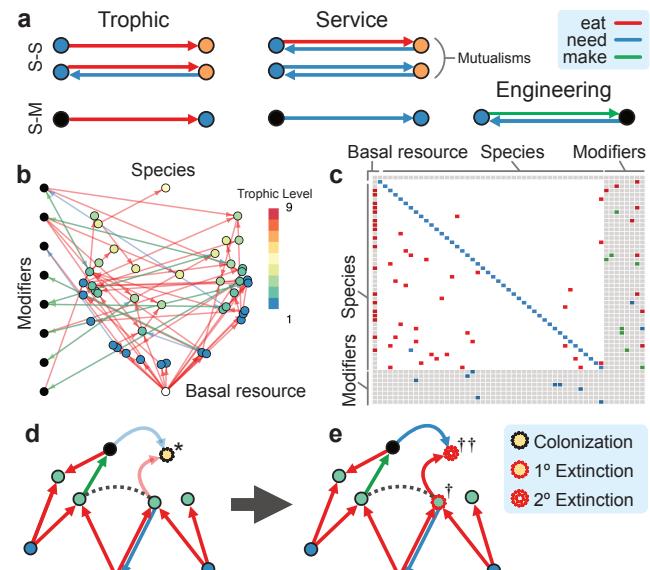


Figure 1. Model framework for ecological networks with multitype interactions and ecosystem engineering. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mutualistic relationships define both species-species (S-S) and species-modifier (S-M) 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.

to consumer i at time simulation time-step t , which is scaled by the steady state link density L^*/S^* , as is typically done performed in empirical investigations¹⁶. Only trophic links between species are considered here, such that we ignore links to the abiotic basal resource in our evaluation of trophic generality. A species is classified as a generalist if $G_i > 1$ and a specialist if $G_i < 1$. If generality is evaluated with respect to the steady state link density, we find that species with many potential trophic interactions realize only a subset of them, thereby functioning as specialists early in the assembly process (Fig. Figure 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. Figure 2b). This latter observation confirms expectations from the trophic theory of island biogeography⁵¹, where communities with lower richness (i.e. early assembly) are less

likely to support specialist consumers than species-rich communities (late assembly). At steady state the portion of functional specialists is ca. 5648%, which is similar to empirical observations of assembling mangrove island food webs¹⁶.

The dominance of functional specialists early in assembly is primarily following the initial assembly of autotrophs is due to the initial colonization by autotrophs. This is evident when we observe that the colonization of lower-trophic consumers with few resources, where the observed trophic level (TL) distribution early in assembly ($t = 5$) has an average TL = 1.6. Four trophic levels are typically established by $t = 50$, where colonization is still dominant, and by the time communities reach steady state the interaction networks are characterized by an average TL_{max} (\pm standard deviation) = 11 ± 2.8 (Fig. Figure 2c). While the maximum trophic level is higher than that measured in most consumer-resource systems⁵⁹, it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers) are included⁶⁰. 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. Figure 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 models⁶¹.

Structure and dynamics of mutualisms. Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks^{50,62–64}. Nestedness has been shown to maximize the structural stability of mutualistic networks⁶⁵, emerge naturally via adaptive foraging behaviors^{24,66} and neutral processes⁶⁷, and promote the influence of indirect effects in driving coevolutionary dynamics⁶⁸. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties^{69,70}, interaction asymmetry among species may promote nestedness in both trophic⁶⁴ and mutualistic systems⁷¹. Processes that operate on different temporal and spatial scales may have a significant influence on these observations⁷². For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity²⁵, and there is some evidence from Pleistocene food webs that geographic insularity may reinforce this process⁷³.

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

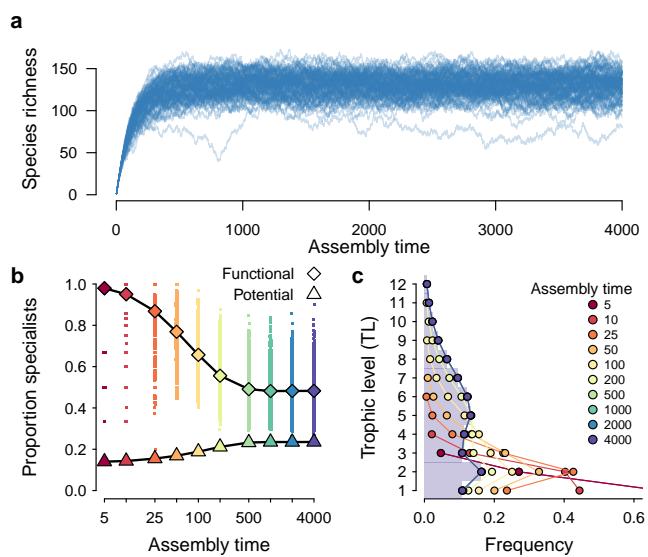


Figure 2. Food web structure over the course of assembly. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by $t = 250$. **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is 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.

that generalists are at a competitive disadvantage when they share the same resources with a specialist consumer. Yet we find that as we increase the frequency of service interactions (holding constant trophic interaction frequency; see Supplementary Appendix Note 2), the assembled community at steady state becomes more nested (Fig. Figure 3a). More service interactions increase a species' competition strength, lowering its primary extinction risk. Participation in a mutualism thus delivers a fitness advantage to the species receiving the service, compensating for the lower competitive strength of generalists and allowing generalists to share subsets of resources with specialists, which promotes nestedness. However increases in mutualisms also increase inter-species dependencies, which raises the potential risk associated with losing mutualistic partners^{74,75}. While this shifting landscape of extinction risks lowers the steady state species richness of highly mutualistic communities, we do not observe a direct relationship be-

336 tween nestedness and richness (Fig. ??).
 337 **Supplementary Figure 4.**

338 When we examine the dynamics of the community
 339 as a function of service interaction frequency, we ob-
 340 serve that mutualistic interactions have different effects
 341 on primary versus secondary extinction rates. Because
 342 service dependencies bolster the competitive strength of
 343 otherwise susceptible species such as trophic generalists
 344 and species with multiple predators, the rate of primary
 345 extinctions is lowered, though this effect is weak (Fig.
 346 Figure 3b). However, because mutualisms build rigid de-
 347 pendencies between species, more service interactions re-
 348 sult in higher frequencies of secondary extinctions (Fig.
 349 Figure 3c). In communities with many mutualistic inter-
 350 actions, this combined influence yields extinctions that
 351 are less likely to occur, but that lead to larger cascades
 352 when they do.

353 An increased rate of secondary extinctions means that
 354 the network is less robust to perturbation, which may im-
 355 pact community turnover, or persistence. If we measure
 356 persistence in terms of the proportion of time species
 357 are established in the community, we find that higher
 358 frequencies of service interactions lower average persis-
 359 tence (increased species turnover; Fig. Figure 3d). Anal-
 360 ysis of species-specific interactions reveals that it is the
 361 species that require more services that have lower persis-
 362 tence (Fig. ??). **Supplementary Figure 5.** Observations
363 of Some empirical systems appear to support model
364 predictions. For example, assembling plant-pollinator
365 long-term observations of ant-plant mutualistic systems
366 have demonstrated high rates of species and interaction
367 turnover, both during the assembly process and at the
368 steady state⁷⁶.

369 turnover among service-receivers (plants) relative to
370 service-donors (ants)⁷⁶.

371 We emphasize that we have restricted ourselves to
 372 examining the effects of obligate mutualisms, although
 373 the importance of non-obligate mutualisms has long
 374 been recognized^{23,24,66,78,79}. We expect that the in-
 375 creased rate of secondary extinctions attributable to
 376 the loss of obligate mutualistic partners to have greater
 377 impact on system stability than the potential loss of
 378 non-obligate mutualistic partners. As such, we do not
 379 expect inclusion of non-obligate mutualisms to alter the
 380 qualitative nature of our findings.

381 **Assembly with ecosystem engineering.** The con-
 382 cept of ecosystem engineering, or more generally niche
 383 construction, has both encouraged an extended evo-
 384 lutionary synthesis⁸⁰ while also garnering considerable
 385 controversy^{81,82}. Models that explore the effects of
 386 ecosystem engineering are relatively few, but have cov-
 387 ered important ground^{31,39}. For example, engineering
 388 has been shown to promote invasion⁸³, alter primary
 389 productivity⁸⁴, and change the selective environment
 390 over eco-evolutionary timescales^{85,86} which can lead to
 391 unexpected outcomes such as the fixation of deleterious
 392 alleles⁸⁷. On smaller scales, microbiota construct shared

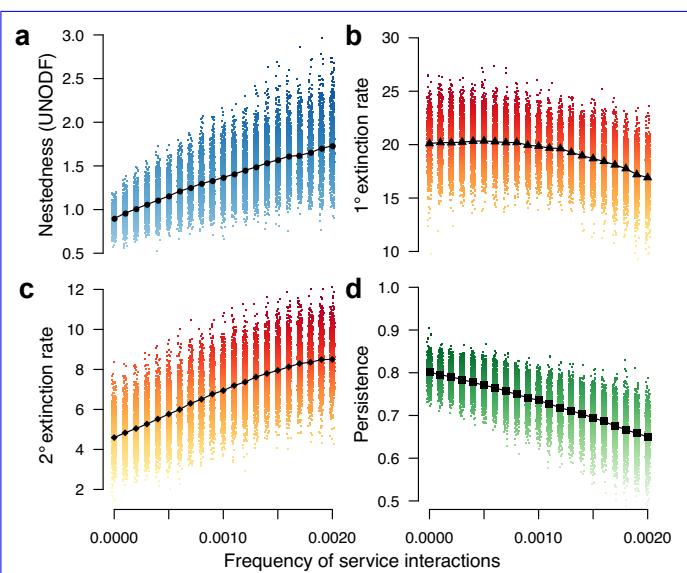


Figure 3. **Community structure and stability as a function of the frequency of service interactions.** a, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)⁷⁷. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. b, Primary extinction Mean rate of primary extinction (where primary extinctions occur from competitive exclusion of consumers over shared resources) and c, secondary extinction rate (which cascade from primary extinctions) as a function of service interaction frequency. d, Species persistence as a function of service interaction frequency. Primary and secondary extinction rates were evaluated at the community level, whereas persistence was determined for each species and averaged across the community. Measures were evaluated for 10^4 replicates; see Methods and Supplementary Appendix Note 2 for parameter values.

394 metabolic resources that have a significant influence
 395 on microbial communities⁸⁸, the dynamics of which may
 396 even serve as the missing ingredient stabilizing some com-
 397 plex ecological systems⁸⁹. **The soil** Soil is one place where
 398 these macro- and microbiotic systems intersect⁹⁰. Many
 399 microbes and detritivores transform and deliver organic
 400 matter into the macrobiotic food web, themselves hosting
 401 a complex network of trophic and service dependencies
 402 between species and abiotic entities^{91,92}.

403 We next explore the effects of ecosystem engineering
 404 by allowing species to produce abiotic modifiers as ad-
 405 ditional nodes in the ecological network (Fig. Figure 1).
 406 These modifier nodes produced by engineers can serve to
 407 fulfill resource or service requirements for other species.
 408 The parameter η defines the mean number of modifiers
 409 produced per species in the pool, drawn from a Poisson
 410 distribution (see Methods and Supplementary Appendix
 411 Note 1 for details). If a species makes ≥ 1 modifier, we
 412 label it an engineer. As the mean number of modifier-
 413 s/species η increases, both the number of engineers in the
 414 pool as well as the number of modifiers made per engi-
 415 neer increases. As detailed in Supplementary Appendix

⁴¹⁶ Note 1, multiple engineers can make the same modifier, such that engineering redundancies are introduced when η is large. When an engineer colonizes the community, so do its modifiers, which other species in the system may interact with. When engineers are lost, their modifiers will also be lost, though can linger in the community for a period of time inversely proportional to the density of disconnected modifiers in the community (see ⁴²⁴ Supplementary Note 1).

⁴²⁵ While the inclusion of engineering does not significantly impact the structure of species-species interactions within assembling food webs (see ⁴²⁷ Supplementary Appendix Note 4 and Fig. ??⁴²⁸Supplementary Figure 6), 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.

⁴³⁴ As the number of engineers increases, mean rates of primary extinction are first elevated and then decline (⁴³⁶Fig.–Figure 4a). At the same time, the mean rates of secondary extinction systematically decline and persistence systematically increases (⁴³⁸Fig.–Figure 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 (⁴⁵²Fig.–Figure 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 (⁴⁵⁸Figure 4b). 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. ??⁴⁵⁹–Supplementary Figure 7).

⁴⁶² Increasing the frequency of service interactions promotes service interactions between species and engineered modifiers (⁴⁶⁴Fig.–Figure 1). A topical example of the latter is the habitat provided to invertebrates by the recently discovered rock-boring teredinid shipworm (*Lithoredo abatanica*)⁹³. 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 (⁴⁷²Fig.⁴⁷³ Figure 4a). Increasing service interactions both elevates

⁴⁷⁴ the competitive strength of species receiving services (from species and/or modifiers), while creating more interdependencies between and among species. As trophic interactions are replaced by service interactions, previously vulnerable species gain a competitive foothold and persist, lowering rates of primary extinctions (Fig.–Figure 4a). The cost of these added services to the community is an increased rate of secondary extinctions (Fig.–Figure 4b) and higher species turnover (Fig.–Figure 4c), such that extinctions are less common but lead to larger cascades.

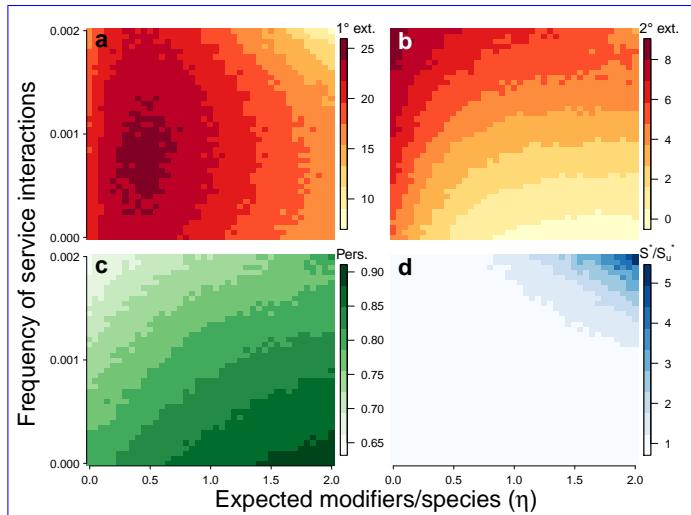


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence. **d**, The ratio S^*/S_u^* , where S_u^* denotes steady states for systems where all engineered modifiers are unique to each engineer, and S^* denote steady states for systems with redundant engineering. Higher values of S^*/S_u^* mean that systems with redundant engineers have higher richness at the steady state than those without redundancies. Primary and secondary extinction rates were evaluated at the community level, whereas persistence was determined for each species and averaged across the community. Each measure reports the expectation taken across 50 replicates. See Methods and ⁴⁸⁵Supplementary Appendix Note 2 for parameter values.

⁴⁸⁵ While the importance of engineering timescales has been emphasized previously³⁹, redundant engineering has been assumed to be unimportant⁹⁴. 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. If ecosystem engineering also includes, for example, biogeochemical processes such as nitrogen-fixing among plants and mycorrhizal fungi, redundancy may be perceived as the rule rather than the exception. Moreover, the vast majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant engi-

neers appear rare⁹⁴. If we consider longer timescales, diversification of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification⁹⁵. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic^{42,43} among other large-scale engineering events in the history of life⁴². Engineering redundancies are likely important on shorter timescales as well. For example, diverse sessile epifauna on shelled gravels in shallow marine environments are facilitated by the engineering of their ancestors, such that the engineered effects of the clade determine the future fitness of descendants⁹⁶. In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production⁹⁷. In these systems, redundancy in the production of shared metabolicic resources may play a key role in community structure and dynamics^{88,89}.

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 Note 1; Fig. ??Supplementary Figure 8), 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. ??). Supplementary Figure 9). 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. ??a) Supplementary Figure 10a). In contrast, when redundant engineering is not allowed (each modifier is unique to an engineer, denoted by the subscript 'u'), steady state community richness S_u^* declines sharply (Figs. Figure 4d, ??b) Supplementary Figure 10b).

Communities lacking redundant engineering have lower species richness because species' trophic and service dependencies are unlikely to be fulfilled within a given assemblage (Fig. ??c) Supplementary Figure 10c,d). Colonization occurs only when trophic and service dependencies are fulfilled. A species requiring multiple engineered modifiers, each uniquely produced, means that each required entity must precede colonization. This magnifies the role of priority effects in constraining assembly order¹², precluding many species from colonizing. In contrast, redundant engineering increases the temporal stability of species' niches while minimizing priority effects by allowing multiple engineers to fulfill the dependencies of a particular species. Our results thus suggest that redundant engineers may play important roles in assembling ecosystems by lowering the barriers to colonization, promoting community diversity.

Discussion

We have shown that simple process-based rules governing the assembly of species with multitype interactions can produce communities with realistic structures and dynamics. Moreover, the inclusion of ecosystem engineering by way of modifier nodes reveals that low levels of engineering may be expected to produce higher rates of extinction while limiting the size of extinction cascades, and that engineering redundancy – whether it is common or rare – serves to promote colonization and by extension **community** diversity. We suggest that including the effects of engineers, either explicitly as we have done here, or otherwise, is vital for understanding the inter-dependencies that define ecological systems. As past ecosystems have fundamentally altered the landscape on which contemporary communities interact, future ecosystems will be defined by the influence of engineering today. Given the rate and magnitude with which humans are currently engineering environments⁹⁸, understanding the role of ecosystem engineers is thus tantamount to understanding our own effects on the assembly of natural communities.

Methods

We model an ecological system with a network where nodes represent 'ecological entities' such as populations of species and/or the presence of abiotic modifiers affecting species. Following Pilai et al.⁴⁹, we do not track the abundances of entities but track only their presence or absence (see also Refs.^{19,20}). The links of the network represent interactions between pairs of entities (x,y). We distinguish three types of such interactions: x eats y, x needs y to be present, x makes modifier y.

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

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

622 basal resource. In time, the entities in the community are updated
 623 following a set of rules. A species from the pool can colonize the
 624 community if the following conditions are met: 1) all entities that
 625 a species needs are present in the community, and 2) at least one
 626 entity that a species eats is present in the community. If a colo-
 627 nization event is possible, it occurs stochastically in time with rate
 628 r_c .

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

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

632 where n_i is the number of entities that species i needs, e_i is the
 633 number of entities from the pool that species i can eat, and v_i is
 634 the number of species in the community that eat species i . This
 635 captures the ecological intuition that mutualisms provide a fitness
 636 benefit⁵², specialists are stronger competitors than generalists⁵⁵,
 637 and many predators entail an energetic cost⁵⁷. The coefficients
 638 c_n , c_e , c_v describe the relative effects of these contributions to
 639 competition strength. In the following, we use the relationship $c_n >$
 640 $c_e > c_v$, such that the competitive benefit of adding an additional
 641 mutualism is greater than the detriment incurred by adding another
 642 resource or predator. A species at risk of extinction leaves the
 643 community stochastically in time at rate r_e .

644 A modifier is present in the community whenever at least one
 645 species that makes the modifier is present. If a species that makes a
 646 modifier colonizes a community, the modifier is introduced as well,

647 however modifiers may persist for some time after the last species
 648 that makes the modifier goes extinct. Any modifier that has lost
 649 all of its makers disappears stochastically in time at rate r_m .

650 The model described here can be simulated efficiently with an
 651 event-driven simulation utilizing a Gillespie algorithm. In these
 652 types of simulations, one computes the rates r_j of all possible events
 653 j in a given step. One then selects the time at which the next
 654 event happens by drawing a random number from an exponential
 655 distribution with mean $1/\sum_j r_j$. At this time, an event occurs
 656 that is randomly selected from the set of possible events such that
 657 the probability of event a is $r_a/\sum_j r_j$. The effect of the event
 658 is then realized and the list of possible events is updated for the
 659 next step. This algorithm is known to offer a much better ap-
 660 proximation to the true stochastic continuous time process than
 661 a simulation in discrete time steps, while providing a much higher
 662 numerical efficiency⁹⁹. Simulations described in the main text have
 663 default parameterizations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$,
 664 $c_v = 1$, and 4000 iterations. Replicates are defined as the indepen-
 665 dent assembly of independently drawn source pools with a given
 666 parameterization.

667 Data availability

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

669

670 Code availability

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

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1040 **Author contributions**

1041 JDY and TG conceived of the model framework. JDY, MMP,
 1042 MAMA, and TG designed the analyses. JDY, MMP, MAMA,
 1043 JLOD, PRG, DG, and TG analyzed the results and contributed
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1045

1046 **Competing interests**

1047 The authors declare no competing interests.

1048

SUPPLEMENTARY METHODS

1049

Appendix 1: Building the source pool

1050 Here and henceforth, we refer to the assembly model presented
 1051 in the main text as the ENIGMa model (E:eat, N:need, Ig:ignore,
 1052 Ma:make). To initiate the ENIGMa assembly model, we must first
 1053 construct the source pool, where each ecological entity (species
 1054 or modifiers) is defined by their potential interactions. The model
 1055 is initialized by creating S species and $M = \eta S$ modifiers, such
 1056 that $N = S + M$ is the expected total number of entities (prior
 1057 to considering engineering redundancies) and η is the expected
 1058 number of modifiers made per species in the community, where
 1059 the expectation is taken across replicates. For each pair of species
 1060 (x, y) there is a probability p_e that x eats y and probability p_n
 1061 that x needs y . For each pair of species x and modifier m ,
 1062 there is a probability q_e that species x eats modifier m and a
 1063 probability q_n that species x needs modifier m . For simplicity we
 1064 assume throughout that $p_e = q_e$ and that $p_n = q_n$, such that the
 1065 probability of drawing trophic and service interactions for both
 1066 species-species and species-modifier interactions is the same.

1067 Without engineering redundancies (i.e. each modifier that a
 1068 species makes is unique), the expected number of modifiers is
 1069 $M = \eta S$ where η is the mean number of modifiers made per species
 1070 S . If we allow for engineering redundancies, the realized number
 1071 of modifiers $M' < M$. To determine the number of modifiers in
 1072 the pool, for each species a set number of modifiers is drawn,
 1073 where $M_i \sim \text{Poiss}(\eta)$. The expected proportion of species that
 1074 are engineers (species that make modifiers) is thus $1 - e^{-\eta}$, where
 1075 e is Euler's number. If a particular modifier is randomly and
 1076 independently drawn for a given engineer from a complete list
 1077 of all possible modifiers, such that multiple species—with some
 1078 probability—can make the same modifier, the expected number of
 1079 modifiers becomes

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

1080 The frequencies of eat and need interactions, p_e and p_n
 1081 respectively, are assigned a priori (see Supplementary Appendix
 1082 2 for different model parameterizations). The frequency of
 1083 engineering (make) interactions can be calculated as

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

1084 The frequency of the null interaction is then calculated
 1085 by $p_\phi = 1 - (p_e + p_n)$ for species-species interactions and
 1086 $p_\phi = 1 - (p_e + p_n + p_m)$ species-modifier interactions,
 1087 respectively. Pairwise interactions are established randomly,
 1088 such that the source pool matrix has no imbued structure apart
 1089 from the number of species, the number of modifiers, and the
 1090 frequency of each directional interaction type. Each source pool is
 1091 provided a basal resource (the first row/column). A species with
 1092 a trophic interaction to this resource is identified as an autotroph
 1093 (or mixotroph depending on its other trophic interactions). If they
 1094 do not have service dependencies with other species/modifiers, it
 1095 is these species that are uniquely able to initiate assembly.

1096 When engineering redundancies are allowed, the expected
 1097 number of unique versus redundant modifiers in the source pool
 1098 can be determined analytically. The total number of modifiers is
 1099 $M' = \eta S(1 - e^{-1})$, and can be subdivided into modifiers that have
 1100 a unique engineer and those that have multiple engineers. The
 1101 number of modifiers with a single engineer is $M'_{\text{unique}} = \eta S e^{-1}$.
 1102 The number of modifiers made by multiple engineers is calculated
 1103 as $M' - M'_{\text{unique}}$, such that

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

1104 such that the proportion of redundant modifiers ϕ is

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

1105 Accordingly, we find that the number of redundant modifiers
 1106 increases linearly with η , while the proportion of modifiers that
 1107 are redundant is fixed. Figure ??a,b shows both analytical
 1108 expectations and numerically-derived measures for $M'_{\text{redundant}}$ and
 1109 ϕ , respectively.

1110 As described in Methods, the assembly process can be simulated
 1111 efficiently with an event-driven simulation utilizing a Gillespie
 1112 algorithm. Generally, one computes the rates r_j of all possible
 1113 events j in a given step. One then selects the time at which the next
 1114 event happens by drawing a random number from an exponential
 1115 distribution with mean $1/\sum_j r_j$. At this time, an event occurs
 1116 that is randomly selected from the set of possible events such that
 1117 the probability of event a is $r_a / \sum_j r_j$. The effect of the event is
 1118 then realized and the list of possible events is updated for the next
 1119 step.

1120 In our framework, at the beginning of each simulation step we
 1121 compute: 1) all species in the pool and absent from the community
 1122 that have trophic and service dependencies met by those species
 1123 in the community: these species are subject to colonization; 2) all
 1124 species in the community that do not have a competition strength
 1125 that is highest for at least one of their resources: these species are
 1126 subject to primary extinction; 3) all species in the community that
 1127 do not meet their eat and/or need dependencies: these species are
 1128 subject to secondary extinction; 4) all modifiers in the community
 1129 that no longer have an engineer: these modifiers are subject to
 1130 elimination. We then select one of the four events with a probability
 1131 proportional to the number of entities that satisfy the criteria for
 1132 each event. The rates at which each event occurs change at each
 1133 step, equal to the number of entities that meet the criteria for each
 1134 event at that point in time. The species/modifier that colonizes
 1135 or is eliminated from the community is randomly chosen once the
 1136 event type is determined.

1137 For example, if the community is empty, and 50 species are
 1138 able to colonize, the probability of drawing ‘colonization’ is 1,
 1139 and the colonizer would be randomly drawn from the 50 capable
 1140 of colonizing. Another example: if 20 species are able to
 1141 colonize, 10 species are not superior competitors for any one of
 1142 their resources, and 30 species do not meet their dependencies,
 1143 $\sum_j r_j = 60$, and $r_{\text{colonize}} = 1/3$, $r_{\text{primary extinction}} = 1/6$, and
 1144 $r_{\text{secondary extinction}} = 1/2$. In this case, the most probable event
 1145 is a secondary extinction. After this single event takes place,
 1146 the community is updated depending on which event occurred,
 1147 and the simulation proceeds to the next step. This algorithm is
 1148 known to offer a much better approximation to the true stochastic
 1149 continuous time process than a simulation in discrete time steps,
 1150 while providing a much higher numerical efficiency ⁹⁹.

Appendix 2: Model parameterizations

1151 Simulations described in the main text have default
 1152 parameterizations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$,
 1153 $c_v = 1$, and 4000 iterations (time-steps).

1154 **Assembly without ecosystem engineering** Here we set
 1155 the average number of modifiers made per species $\eta = 0$ and the
 1156 probability of need interactions in the species pool $p_n = 0.002$.

1157 **Structure and dynamics of mutualisms** Again we used
 1158 the default parameterizations but set $\eta = 0$, while varying
 1159 $p_n \in [0, 0.002]$.

1160 **Assembly with ecosystem engineering** Here we used the
 1161 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 Model⁵⁸. 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 there are many similarities, there are also some important differences, some of which are highlighted in the main text. While we consider a comparison of our framework with other food web models such as the Niche Model relevant, we emphasize that the motivations underlying both are distinct. Our approach is intended to provide a deeper understanding into how multitype dependencies between species and the environment impact the dynamics of community assembly. While capturing general qualitative features of empirical systems demonstrates that the dynamics we consider are ecologically relevant, the goal of our approach is distinct from that of static food web models, which aim to maximize structural similarities between model and empirical systems⁵⁸.

We compared steady state ecological networks that emerge from ENIgMa (described in Methods, main text) with food webs constructed from the Niche Model⁵⁸ with similar species richness and connectance. Because species richness and connectance of the Niche Model are often altered by eliminating disconnected species, we compared i) species richness, ii) connectance, iii) mean species degree, iv) standard deviation of out-degree distributions, and v) standard deviation of in-degree distributions averaged across 1000 replicates for each model.

We found that all measures resulted in fairly similar values between ENIgMa and the Niche Model food webs with a some important differences (Figs. ??, ??). While similar, ENIgMa produces consistently lower values of connectance, mean species degree, as well as standard deviations of the in- and out degree distributions. This means that the food webs produced by ENIgMa are more sparsely connected with less variance between species. These results were expected, as the Niche Model assumes systematically increasing dietary ranges with higher niche values, whereas the trophic interactions assigned to species in the source pool of ENIgMa are drawn independently. An important difference between the Niche Model and ENIgMa is that we do not distinguish between traditional consumers and parasites. A different framework known as the Inverse Niche Model⁷ has been proposed to address parasitic interactions. The Inverse Niche Model assumes increasing specialization with feeding hierarchies, which would serve to lower the average generality of species (lower degree). In addition, the Inverse Niche model outputs lower standard deviations of in- and out degree distributions. Together these trends suggest that the qualitative structural differences that we observe for the assembly and Niche model may reflect an important structural distinction between food webs that do and do not include parasitic species.

Appendix 4: The structure of engineered food webs

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

The role of specialists does and does not change with the

introduction of engineering, depending on how specialization is defined. As in the main text, a specialist is defined when its generality index $G_i < 1$ relative to the steady state link density. When engineered modifiers are included, we account for a trophic interaction between a species and another's modifier as an interaction that occurs between those two species indirectly through the modifier intermediary. So if a species B makes a modifier M , and A eats M , then we set A to (indirectly) eat B . This accounting of both direct and indirect trophic interactions between species can then be compared to i) the direct trophic link density of the community, or ii) the direct + indirect trophic link density of the community, and some insights can be gained from both approaches.

In the first case, where G_i is determined relative to L_{direct}^*/S^* , we find that there are no potential specialists that colonize the community, and (as in the main text) functional specialists colonize first, but (not as in the main text) become functional generalists at steady state (mean proportion specialists at steady state is 0.04; Fig. ??b). This means that the indirect links that define trophic interactions between species and modifiers increase the link density of the network relative to that defined only by direct trophic interactions. In words, modifiers serve to connect otherwise disconnected species, formalizing the otherwise indirect relationships that structure the role of engineers in the community. In the second case, where G_i is determined relative to $L_{\text{indirect}}^*/S^*$, we find that the changes in both functional and potential specialists over the course of assembly (Fig. ??c) follow those observed for non-engineered food webs (Fig. 2b).

Finally, we observe that while the number of trophic levels increase in the presence of species-modifier interactions, the overall trophic structure of the community advances over the course of assembly in much the same way as it does without engineers (Fig. ??d). Trophic levels are calculated with respect to indirect species interactions through modifier intermediaries. Because species at any trophic level can engineer modifiers used as resources by other species, the mean trophic level of the community is systematically elevated.

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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.

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.

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.

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

Persistence as a function of trophic and service in/out degree

for communities with higher densities of service interactions (Fig. 4a). 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.

a. Assembling communities over time from a pool of 200 non-engineering species. Species richness is blue; modifier richness is red. Steady state species richness is reached by $t = 250$. **b.** The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$ relative to the steady state link density. G_i is scaled to the steady state link density where links are direct trophic interactions between species. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **c.** The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index $G_i < 1$. Here G_i is scaled to the steady state link density where links are composed of both direct trophic interactions between species and indirect trophic interactions between consumers and those species that produce modifiers as resources. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **d.** The frequency distribution of trophic levels as a function of assembly time (iterations). Autotrophs occupy TL = 1. Measures were evaluated across 10^4 replicates; see Methods for parameter values.

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.

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. ??). **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. ??).

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.

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).