

# 1 Diverse interactions and ecosystem engineering stabilize community assembly

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

4 <sup>1</sup>*University of California, Merced, Merced, CA 95340, USA*

5 <sup>2</sup>*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA*

6 <sup>3</sup>*Universidade Estadual de Campinas, Campinas - SP, Brazil*

7 <sup>4</sup>*University of Washington, Seattle, WA 98195, USA*

8 <sup>5</sup>*Universidade de São Paulo, São Paulo, Brazil*

9 <sup>6</sup>*Université de Sherbrooke, Sherbrooke, QCJ1K0A5, Canada*

10 <sup>7</sup>*University of California, Davis, Davis, CA 95616, USA*

11 <sup>8</sup>*Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung*

12 <sup>9</sup>*Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB),*

13 *Ammerländer Heerstrasse 231, 26129 Oldenburg, Germany*

14 <sup>10</sup>*University of Oldenburg, ICBM, 26129 Oldenburg, Germany*

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

To unravel nature's secrets we must simplify its abundant complexities and idiosyncrasies. The layers of natural history giving rise to an ecological community can be distilled – among many forms – into a network, where nodes represent species and links represent interactions between them. Networks are generally constructed for one type of interaction, such as food webs capturing predation<sup>1–3</sup> or pollination networks capturing a specific mutualistic interaction<sup>4</sup>, and continues to lead to significant breakthroughs in our understanding of the dynamical consequences of community structure<sup>5–7</sup>. This perspective has also been used to shed light on the generative processes driving the assembly of complex ecological communities<sup>8,9</sup>.

To what extent assembly leaves its fingerprint on the structure and function of ecological communities is a source of considerable debate<sup>10–12</sup>. There is strong evidence that functional traits constrain assembly<sup>12–14</sup>, while differences in species' trophic niche<sup>15,16</sup>, coupled with early establishment of fast/slow energy channels<sup>17</sup>, 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<sup>18,19</sup>, where the establishment of species from a source pool<sup>19–21</sup> and the plasticity of species interactions<sup>22–25</sup> constrain colonization and extinction dynamics. Despite these advances, there is not yet a well-defined theory for the assembly of communities

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

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

53 Diverse interactions occur not only between species  
54 but indirectly through the effects that species have  
55 on their environment<sup>30,32,33</sup>. Elephants root out large  
56 saplings and small trees, enabling the formation and  
57 maintenance of grasslands<sup>34,35</sup> and creating habitat for  
58 smaller vertebrates<sup>36</sup>. Burrowing rodents such as go-  
59 phers and African mole rats create shelter and promote  
60 primary production by aerating the soil<sup>37,38</sup>, salmon  
61 and aquatic invertebrates create freshwater habitats by  
62 changing stream morphology<sup>39</sup>, and leaf-cutter ants al-  
63 ter microclimates, influencing seedling survival and plant  
64 growth<sup>40</sup>. These examples illustrate ecosystem engineer-  
65 ing, where the engineering organism alters the environ-  
66 ment on timescales longer than its own<sup>41</sup>. Engineers are  
67 widely acknowledged to have impacts on both small and  
68 large spatial scales<sup>42</sup>, and likely serve as important key-

71 stone species in many habitats<sup>43</sup>.

72 Ecosystem engineering not only impacts communities  
73 on ecological timescales, but has profoundly shaped the  
74 evolution of life on Earth<sup>44</sup>. For example, the emergence  
75 of multicellular cyanobacteria fundamentally altered the  
76 atmosphere during the Great Oxidation Event of the  
77 Proterozoic roughly 2.5 Byrs BP<sup>44,45</sup>, paving the way  
78 for the biological invasion of terrestrial habitats. In the  
79 oceans it is thought that rRNA and protein biogenesis of  
80 aquatic photoautotrophs drove the nitrogen:phosphorous  
81 ratio (the Redfield Ratio) to ca. 16:1 matching that of  
82 plankton<sup>46</sup>, illustrating that engineering clades can have  
83 much larger, sometimes global-scale effects.

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

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

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

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

132 Our results offer four key insights into the roles of  
133 multitype interactions and ecosystem engineering in  
134 driving community assembly. First, we show that the  
135 assembly of communities in the absence of engineering  
136 reproduces many features observed in empirical systems.  
137 These include changes in the proportion of generalists  
138 over the course of assembly that accord with measured  
139 data and trophic diversity similar to empirical observa-  
140 tions. Second, we show that increasing the frequency  
141 of mutualistic interactions leads to the assembly of  
142 ecological networks that are more nested, a common  
143 feature of diverse mutualistic systems<sup>52</sup>, but are also  
144 prone to extinction cascades. Our third key result shows  
145 that increasing the proportion of ecosystem engineers  
146 within a community has nonlinear effects on observed  
147 extinction rates. While we find that a low amount of  
148 engineering increases extinction rates, a high amount of  
149 engineering has the opposite effect. Finally we show that  
150 redundancies in engineered effects promote community  
151 diversity by lowering the barriers to colonization.

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

169 Following the initial colonization phase, extinctions be-  
170 gin to slow the rate of community growth. Primary ex-  
171 tinctions occur if a given species is not the strongest  
172 competitor for at least one of its resources. A species'  
173 competition strength is determined by its interactions:  
174 competition strength is enhanced by the number of need  
175 interactions and penalized by the number of its resources  
176 (favoring trophic specialists) and consumers (favoring  
177 species with fewer predators). This encodes three key as-  
178 sumptions: that mutualisms provide a fitness benefit<sup>54</sup>,  
179 specialists are stronger competitors than generalists<sup>55–58</sup>,  
180 and many predators entail an energetic cost<sup>59</sup>. Secondary  
181 extinctions occur when a species loses its last trophic  
182 or any of its service requirements. See Fig. 1d,e for  
183 an illustration of the assembly process. As the colo-  
184 nization and extinction rates converge, the community  
185 reaches a steady state around which it oscillates (Fig.  
186

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

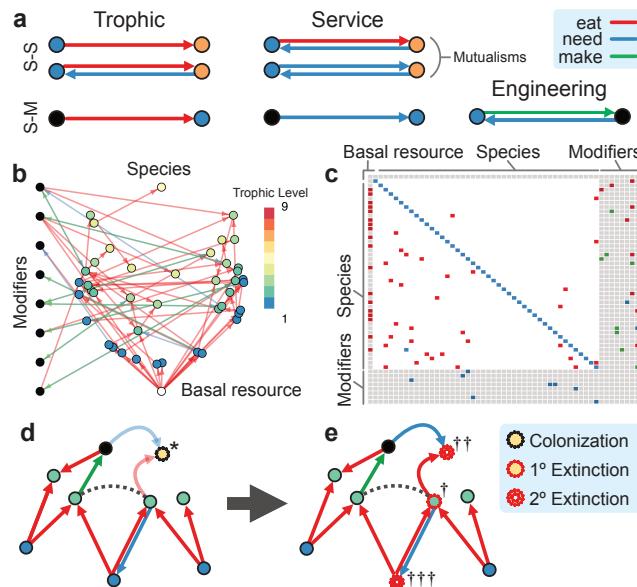


Figure 1. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mu-  
 tualistic relationships define both species-species (S-S) and  
 species-modifier (S-M) interactions; an engineering interac-  
 tion is denoted by an engineer that makes a modifier, such  
 that the modifier needs the engineer to persist. **b**, An as-  
 sembling food web with species (color denotes trophic level)  
 and modifiers. The basal resource is the white node at the bottom  
 of the network. **c**, The corresponding adjacency matrix with  
 colors denoting interactions between species and modifiers.  
**d**, A species (\*) can colonize a community when a single trophic  
 and all service requirements are met. **e**, Greater vulnerability  
 increases the risk of primary extinction via competitive exclu-  
 sion (competition denoted by dashed line) to species (†). The  
 extinction of species (†) will cascade to affect those connected  
 by trophic (††) and service (†††) dependencies.

191 Assembly of ecological communities in the absence of  
 192 engineering results in interaction networks with struc-  
 193 tures consistent with empirical observations. As the com-  
 194 munity reaches steady state (Fig. 2a), we find that the  
 195 connectance of trophic interactions ( $C(t) = L(t)/S(t)^2$ ,  
 196 where  $S(t)$  is species richness and  $L(t)$  is the number  
 197 of links at time  $t$ ) decays to a constant value (Fig. S1).  
 198 Decaying connectance followed by stabilization around  
 199 a constant value has been documented in the assem-  
 200 bly of mangrove communities<sup>16</sup> and experimental aquatic  
 201 mesocosms<sup>17</sup>. The initial decay is likely inevitable in  
 202 sparse webs as early in the assembly process the small set  
 203 of tightly interacting species will have a high link density  
 204 from which it will decline as the number of species in-  
 205 creases. Compared to trophic networks constructed using  
 206 the Niche model<sup>60</sup> given similar species richness and con-  
 207 nection, our framework results in networks with degree

236 The dominance of functional specialists early in as-  
 237 sembly is primarily due to the initial colonization by  
 238 autotrophs. This is evident when we observe that the  
 239 trophic level (TL) distribution early in assembly ( $t = 5$ )  
 240 has an average  $TL = 1.6$ . Four trophic levels are typ-  
 241 ically established by  $t = 50$ , where colonization is still  
 242 dominant, and by the time communities reach steady  
 243 state the interaction networks are characterized by an  
 244 average  $TL_{max} (\pm \text{standard deviation}) = 11 \pm 2.8$  (Fig.  
 245 2c). While the maximum trophic level is higher than  
 246 that measured in most consumer-resource systems<sup>61</sup>, it  
 247 is not unreasonable if parasitic interactions (which we do  
 248 not differentiate from other consumers) are included<sup>62</sup>.  
 249 Overall, the most common trophic level among species  
 250 at steady state is ca.  $TL = 4.75$ .

251 The distribution of trophic levels changes shape over  
 252 the course of assembly. Early in assembly, we observe  
 253 a skewed pyramidal structure, where most species feed  
 254 from the base of the food web. At steady state, we  
 255 observe that intermediate trophic levels dominate, with  
 256 frequencies taking on an hourglass structure (purple  
 257 bars, Fig. 2c). Compellingly, the trophic richness  
 258 pyramids that we observe at steady state follow closely  
 259 the hourglass distribution observed for empirical food  
 260 webs and are less top-heavy than those produced by  
 261 static food web models<sup>63</sup>.

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

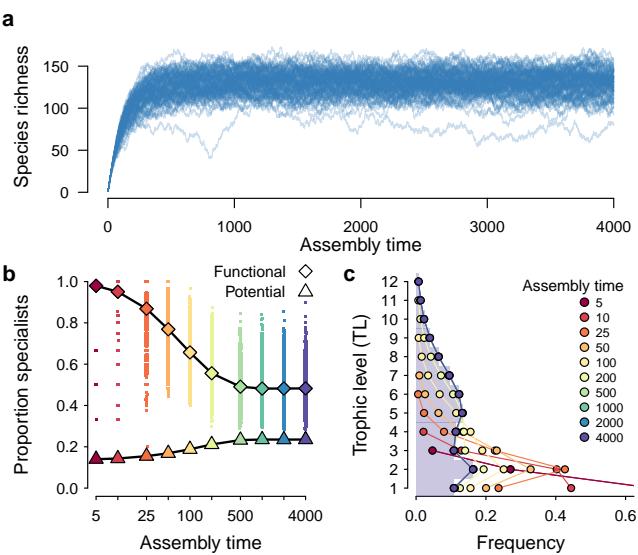
of mutualistic networks<sup>52,64–66</sup>. Nestedness has been shown to maximize the structural stability of mutualistic networks<sup>67</sup>, emerge naturally via adaptive foraging behaviors<sup>24,68</sup> and neutral processes<sup>69</sup>, and promote the influence of indirect effects in driving coevolutionary dynamics<sup>70</sup>. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties<sup>71,72</sup>, interaction asymmetry among species may promote nestedness in both trophic<sup>66</sup> and mutualistic systems<sup>73</sup>. Processes that operate on different temporal and spatial scales may have a significant influence on these observations<sup>74</sup>. For example, over evolutionary time, coevolution and speciation may degrade nested structures in favor of modularity<sup>25</sup>, and there is some evidence from Pleistocene food webs that geographic insularity may reinforce this process<sup>75</sup>.

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

When we examine the dynamics of the community as a function of service interaction frequency, we observe that mutualistic interactions have different effects on primary versus secondary extinction rates. Because service dependencies bolster the competitive strength of otherwise susceptible species such as trophic generalists and species with multiple predators, the rate of primary extinctions is lowered, though this effect is weak (Fig. 3b). However, because mutualisms build rigid dependencies between species, more service interactions result in higher frequencies of secondary extinctions (Fig. 3c). In communities with many mutualistic interactions, this combined influence yields extinctions that are less likely to occur, but lead to larger cascades when they do.

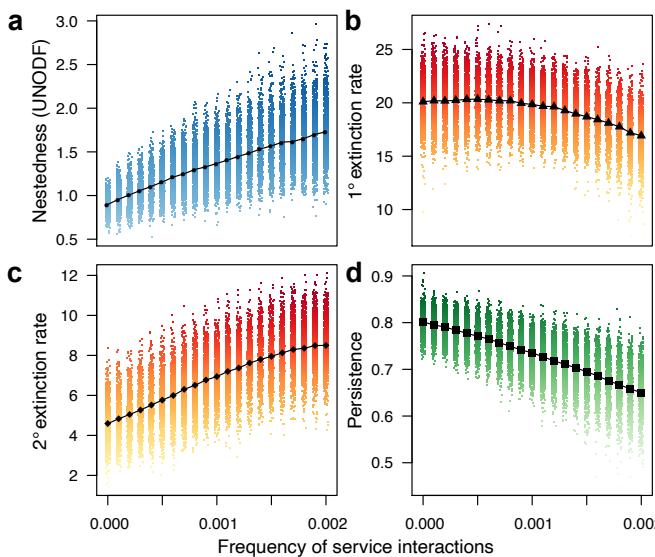
An increased rate of secondary extinctions means that the network is less robust to perturbation, which may impact community turnover, or persistence. If we measure persistence in terms of the proportion of time species are established in the community, we find that higher frequencies of service interactions lower average persistence (increased species turnover; Fig. 3d). Analysis of species-specific interactions reveals that it is the species that require more services that have lower persistence (Fig. S5). Observations of empirical systems appear to support model predictions. For example, assembling plant-pollinator systems have demonstrated high rates of species and interaction turnover, both during the assembly process and at the steady state<sup>78</sup>.

We emphasize that we have restricted ourselves to examining the effects of obligate mutualisms, although the importance of non-obligate mutualisms has long been recognized<sup>23,24,68,80,81</sup>. We expect that the increased rate of secondary extinctions attributable to the loss of obligate mutualistic partners to have greater impact on system stability than the potential loss of non-obligate mutualistic partners. As such, we do not expect inclusion of non-obligate mutualisms to alter the qualitative nature of our findings.



**Figure 2.** **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by  $t = 250$ . **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is defined as a species with a generality index  $G_i < 1$ . All measures of  $G_i$  are scaled by the average number of links per species where  $L$  and  $S$  are measured at steady state. Diamonds denote expected values for functional (realized) trophic interactions at each point in time, and triangles denote expected values for potential trophic interactions (as if all trophic interactions with all species in the pool were realized), where the expectation is taken across replicates. Individual replicate results are shown for functional trophic interactions (small points). **c**, The frequency distribution of trophic levels as a function of assembly time (iterations). Autotrophs occupy  $TL = 1$ . Measures were evaluated across  $10^4$  replicates; see Methods for parameter values.

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



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

344

**Assembly with ecosystem engineering.** The concept of ecosystem engineering, or more generally niche construction, has both encouraged an extended evolutionary synthesis<sup>82</sup> while also garnering considerable controversy<sup>83,84</sup>. Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground<sup>30,41</sup>. For example, engineering has been shown to promote invasion<sup>85</sup>, alter primary productivity<sup>86</sup>, and change the selective environment over eco-evolutionary timescales<sup>87,88</sup> which can lead to unexpected outcomes such as the fixation of deleterious alleles<sup>89</sup>. On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities<sup>90</sup>, the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems<sup>91</sup>. The soil is one place where these macro- and microbiotic systems intersect<sup>92</sup>. Many microbes and detritivores transform and deliver organic matter into the macrobiotic food web, themselves hosting a complex network of trophic and service dependencies between species and abiotic entities<sup>93,94</sup>.

We next explore the effects of ecosystem engineering by allowing species to produce abiotic modifiers as additional nodes in the ecological network (Fig. 1). These modifier nodes produced by engineers can serve to fulfill resource or service requirements for other species. The parameter  $\eta$  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  $\geq 1$  modifier, we label it an engineer. As the mean number of modifiers/species  $\eta$  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  $\eta$  is large. When an engineer colonizes the community, so do its modifiers, which other species in the system may interact with. When engineers are lost, their modifiers will also be lost, though can linger in the community for a period of time inversely proportional to the density of disconnected modifiers in the community.

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

As the number of engineers increases, mean rates of primary extinction are first elevated and then decline (Fig. 4a). At the same time, the mean rates of secondary extinction systematically decline and persistence systematically increases (Fig. 4b-c). When engineered modifiers are rare ( $0 < \eta \leq 0.5$ ), higher rates of primary extinction coupled with lower rates of secondary extinction mean that extinctions are common, but of limited magnitude such that disturbances are compartmentalized. As modifiers become more common both primary and secondary extinction rates decline, which corresponds to increased persistence. We suggest two mechanisms that may produce the observed results. First, when engineers and modifiers are present but rare, they provide additional resources for consumers. This stabilization of consumers ultimately results in increased vulnerability of prey, such that the cumulative effect is increased competitive exclusion of prey and higher rates of primary extinction (Fig. 4a). Second, when engineers and their modifiers are common ( $\eta > 0.5$ ) the available niche space expands, lowering competitive overlap and suppressing both primary and secondary extinctions. Notably the presence of even a small number of engineers serves to limit the magnitude of secondary extinction cascades. Assessment of species persistence as a function of trophic in-degree (number of resources) and out-degree (number of consumers) generally supports this proposed dynamic (Fig. S7).

Increasing the frequency of service interactions promotes service interactions between species and engineered modifiers (Fig. 1). A topical example of the latter is the habitat provided to invertebrates by the recently discovered rock-boring teredinid shipworm (*Lithoredo abatanica*)<sup>95</sup>. Here, freshwater invertebrates are serviced by the habitat modifications engineered by the shipworm, linking species indirectly via an abiotic effect (in our framework via a modifier node). As the frequency of

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

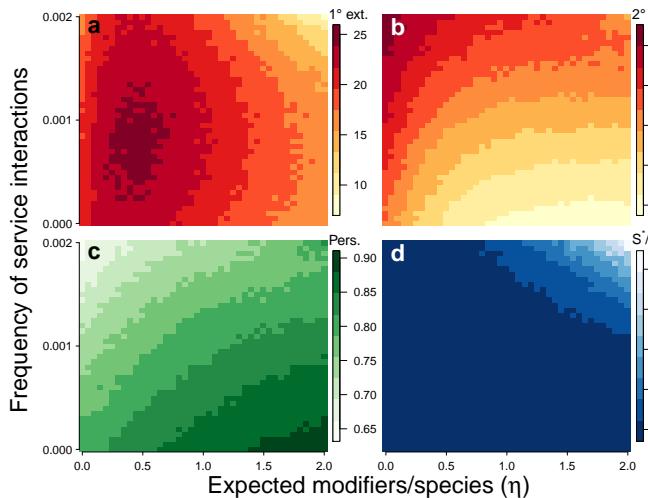


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade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

While the importance of engineering timescales has been emphasized previously<sup>41</sup>, redundant engineering has been assumed to be unimportant<sup>29</sup>. We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when the effects of engineers increase their own fitness<sup>85</sup> as is generally assumed to be the case with niche construction<sup>88</sup>. If ecosystem engineering also includes, for example, biogeochemical processes such as nitrogen-fixing among plants and mycorrhizal fungi, redundancy may be perceived as the rule rather than the exception. Moreover, the vast

majority of contemporary ecosystem engineering case studies focus on single taxa, such that redundant engineers appear rare<sup>29</sup>. If we consider longer timescales, diversification of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification<sup>31</sup>. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic<sup>44,45</sup> among other large-scale engineering events in the history of life<sup>44</sup>. 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 descendants<sup>96</sup>.

In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production<sup>97</sup>. In these systems, redundancy in the production of shared metabolic resources may play a key role in community structure and dynamics<sup>90,91</sup>.

When there are few engineers, each modifier in the community tends to be unique to a particular engineering species. Engineering redundancies increase linearly with  $\eta$  (Supplementary Appendix 1; Fig. S8), such that the loss of an engineer will not necessarily lead to the loss of engineered modifiers. We examine the effects of this redundancy by comparing our results to those produced by the same model, but where each modifier is uniquely produced by a single species. Surprisingly, the lack of engineering redundancies does not alter the general relationship between engineering and measures of community stability (Fig. S9). However we find that redundancies play a central role in maintaining species diversity. When engineering redundancies are allowed, steady state community richness  $S^*$  does not vary considerably with increasing service interactions and engineering (Fig. S10a). In contrast, when redundant engineering is not allowed, steady state community richness  $S_u^*$  declines sharply (Figs. 4d, S10b).

Communities lacking redundant engineering have lower species richness because species' trophic and service dependencies are unlikely to be fulfilled within a given assemblage (Fig. S10c,d). Colonization occurs only when trophic and service dependencies are fulfilled. A species requiring multiple engineered modifiers, each uniquely produced, means that each required entity must precede colonization. This magnifies the role of priority effects in constraining assembly order<sup>12</sup>, precluding many species from colonizing. In contrast, redundant engineering increases the temporal stability of species' niches while minimizing priority effects by allowing multiple engineers to fulfill the dependencies of a particular species. Our results thus suggest that redundant engineers may play important roles in assembling ecosystems by lowering the barriers to colonization, promoting community diversity.

We have shown that simple process-based rules governing the assembly of species with multitype interactions can produce communities with realistic

structures and dynamics. Moreover, the inclusion of ecosystem engineering by way of modifier nodes reveals that low levels of engineering may be expected to produce higher rates of extinction while limiting the size of extinction cascades, and that engineering redundancy – whether it is common or rare – serves to promote colonization and by extension diversity. We suggest that including the effects of engineers, either explicitly as we have done here, or otherwise, is vital for understanding the inter-dependencies that define ecological systems. As past ecosystems have fundamentally altered the landscape on which contemporary communities interact, future ecosystems will be defined by the influence of engineering today. Given the rate and magnitude with which humans are currently engineering environments<sup>98</sup>, 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.<sup>51</sup>, we do not track the abundances of entities but track only their presence or absence (see also Refs.<sup>19,20</sup>). 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  $\eta$  is the expected number of modifiers made per species in the community, where the expectation is taken across independent replicates. For each pair of species (x,y) there is a probability  $p_e$  that x eats y and probability  $p_n$  that x needs y. For each pair of species x and modifier m, there is a probability  $q_e$  that species x eats modifier m and a probability  $q_n$  that species x needs modifier m. Throughout we assume that  $p_e = q_e$  and  $p_n = q_n$  for simplicity. Each species  $i$  makes a number of modifiers  $M_i \sim \text{Poiss}(\eta)$ . If engineering redundancies are allowed, once the number of modifiers per species is determined each modifier is assigned to a species independently to match its assigned number of modifiers. This means that multiple species may make the same modifier, and that there may be some modifiers that are not assigned to any species, which are eliminated from the pool. Accounting for engineering redundancies, the number of modifiers in the pool becomes  $M' = \eta S(e-1)/e$  where e is Euler's number. If engineering redundancies are not allowed, each modifier is made by a single engineer and  $M' = M$ .

In addition to interactions with ecosystem entities, there can be interactions with a basal resource, which is always present. The first species always eats this resource, such that there is always a primary producer in the pool. Other species eat the basal resource

with probability  $p_e$ . Species with zero assigned trophic interactions are assumed to be primary producers. See Supplementary Appendix 1 for additional details on defining the source pool.

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

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

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

where  $n_i$  is the number of entities that species  $i$  needs,  $e_i$  is the number of entities from the pool that species  $i$  can eat, and  $v_i$  is the number of species in the community that eat species  $i$ . This captures the ecological intuition that mutualisms provide a fitness benefit<sup>54</sup>, specialists are stronger competitors than generalists<sup>57</sup>, and many predators entail an energetic cost<sup>59</sup>. The coefficients  $c_n$ ,  $c_e$ ,  $c_v$  describe the relative effects of these contributions to competition strength. In the following, we use the relationship  $c_n > c_e > c_v$ , such that the competitive benefit of adding an additional mutualism is greater than the detriment incurred by adding another resource or predator. A species at risk of extinction leaves the community stochastically in time at rate  $r_e$ .

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

The model described here can be simulated efficiently with an event-driven simulation utilizing a Gillespie algorithm. In these types of simulations, one computes the rates  $r_j$  of all possible events  $j$  in a given step. One then selects the time at which the next event happens by drawing a random number from an exponential distribution with mean  $1/\sum_j r_j$ . At this time, an event occurs that is randomly selected from the set of possible events such that the probability of event  $a$  is  $r_a / \sum_j r_j$ . The effect of the event is then realized and the list of possible events is updated for the next step. This algorithm is known to offer a much better approximation to the true stochastic continuous time process than a simulation in discrete time steps, while providing a much higher numerical efficiency<sup>99</sup>. Simulations described in the main text have default parameterizations of  $S = 200$ ,  $p_e = 0.01$ ,  $c_n = \pi$ ,  $c_e = \sqrt{2}$ ,  $c_v = 1$ , and 4000 iterations. Replicates are defined as the independent assembly of independently drawn source pools with a given parameterization.

## Data availability

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

## Code availability

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

- 
- [1] Paine, R. T. Food web complexity and species diversity. *Am. Nat.* **100**, 65–75 (1966).
- [2] Dunne, J. A., Williams, R. J. & Martinez, N. D. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. USA* **99**, 12917–12922 (2002).
- [3] Pascual, M. & Dunne, J. *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Oxford University Press, Oxford, UK, 2006).
- [4] Bascompte, J. & Jordano, P. *Mutualistic Networks*. Monographs in Population Biology (Princeton University Press,

- Princeton, NJ, 2013).
- [5] May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).
- [6] Gross, T., Levin, S. A. & Dieckmann, U. Generalized models reveal stabilizing factors in food webs. *Science* **325**, 747–750 (2009).
- [7] Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
- [8] Montoya, J. M. & Solé, R. V. Topological properties of food webs: from real data to community assembly models. *Oikos* **102**, 614–622 (2003).
- [9] Bascompte, J. & Stouffer, D. The assembly and disassembly of ecological networks. *Philos. T. Roy. Soc. B* **364**, 1781 (2009).
- [10] Hubbell, S. *The unified neutral theory of biodiversity and biogeography* (Princeton Univ Press, Princeton, USA, 2001).
- [11] Tilman, D. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. USA* **101**, 10854–10861 (2004).
- [12] Fukami, T. Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23 (2015).
- [13] Kraft, N. J. B., Valencia, R. & Ackerly, D. D. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science* **322**, 580–582 (2008).
- [14] O'Dwyer, J. P., Lake, J., Ostling, A., Savage, V. M. & Green, J. An integrative framework for stochastic, size-structured community assembly. *Proc. Natl. Acad. Sci. USA* **106**, 6170 (2009).
- [15] Brown, J. H., Kelt, D. A. & Fox, B. J. Assembly Rules and Competition in Desert Rodents. *Am. Nat.* **160**, 815–818 (2002).
- [16] Piechnik, D. A., Lawler, S. P. & Martinez, N. D. Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos* **117**, 665–674 (2008).
- [17] Fahimipour, A. K. & Hein, A. M. The dynamics of assembling food webs. *Ecol. Lett.* **17**, 606–613 (2014).
- [18] Barbier, M., Arnoldi, J.-F., Bunin, G. & Loreau, M. Generic assembly patterns in complex ecological communities. *Proc. Natl. Acad. Sci. USA* **115**, 2156–2161 (2018).
- [19] Campbell, C., Yang, S., Albert, R. & Shea, K. A network model for plant-pollinator community assembly. *Proc. Natl. Acad. Sci. USA* **108**, 197–202 (2011).
- [20] Hang-Kwang, L. & Pimm, S. L. The assembly of ecological communities: A minimalist approach. *J. Anim. Ecol.* **62**, 749–765 (1993).
- [21] Law, R. & Morton, R. D. Permanence and the Assembly of Ecological Communities. *Ecology* **77**, 762–775 (1996).
- [22] Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J. A. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.* **13**, 1546–1559 (2010).
- [23] Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de Espinés, P. & Flores, J. D. Topological plasticity increases robustness of mutualistic networks. *J. Anim. Ecol.* **81**, 896–904 (2012).
- [24] Valdovinos, F. S. *et al.* Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecol. Lett.* **19**, 1277–1286 (2016).
- [25] Ponisio, L. C. *et al.* A network perspective for community assembly. *Front. Ecol. Evol.* **7**, 103 (2019).
- [26] Odum, E. P. The strategy of ecosystem development. *Science* **164**, 262–270 (1969).
- [27] Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A. & Berlow, E. L. How structured is the entangled bank? the surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. *PLoS Biol* **14**, e1002527 (2016).
- [28] Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The multilayer nature of ecological networks. *Nat. Ecol. Evol.* **1**, 1–9 (2017).
- [29] Lawton, J. H. What do species do in ecosystems? *Oikos* **71**, 367–374 (1994).
- [30] Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W. & Laland, K. N. Niche construction theory: a practical guide for ecologists. *Q. Rev. Biol.* **88**, 4–28 (2013).
- [31] Odling-Smee, F., Laland, K. & Feldman, M. *Niche Construction: The Neglected Process in Evolution*. Monographs in Population Biology (Princeton University Press, Princeton, NJ, 2013).
- [32] Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
- [33] Olff, H. *et al.* Parallel ecological networks in ecosystems. *Philos. T. Roy. Soc. B* **364**, 1755–1779 (2009).
- [34] Leuthold, W. Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–94. *Afr. J. Ecol.* **34**, 101–112 (1996).
- [35] Haynes, G. Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology* **157–158**, 99 – 107 (2012).
- [36] Pringle, R. M. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* **89**, 26–33 (2008).
- [37] Reichman, O. & Seabloom, E. W. The role of pocket gophers as subterranean ecosystem engineers. *Trends Ecol. Evol.* **17**, 44 – 49 (2002).
- [38] Hagenah, N. & Bennett, N. C. Mole rats act as ecosystem engineers within a biodiversity hotspot, the cape fynbos. *J. Zool.* **289**, 19–26 (2013).
- [39] Moore, J. W. Animal ecosystem engineers in streams. *BioScience* **56**, 237–246 (2006).
- [40] Meyer, S. T., Leal, I. R., Tabarelli, M. & Wirth, R. Ecosystem engineering by leaf-cutting ants: nests of atta cephalotes drastically alter forest structure and microclimate. *Ecol. Entomol.* **36**, 14–24 (2011).
- [41] Hastings, A. *et al.* Ecosystem engineering in space and time. *Ecol. Lett.* **10**, 153–164 (2007).
- [42] Wright, J. P., Jones, C. G., Boeken, B. & Shachak, M. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *J. Ecol.* **94**, 815–824 (2006).
- [43] Jones, C. & Lawton, J. *Linking Species & Ecosystems* (Springer, New York City, USA, 2012).
- [44] Erwin, D. H. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends Ecol. Evol.* **23**, 304 – 310 (2008).
- [45] Schirrmeyer, B. E., de Vos, J. M., Antonelli, A. & Bagheri, H. C. Evolution of multicellularity coincided with increased diversification of cyanobacteria and the great oxidation event. *Proc. Natl. Acad. Sci. USA* **110**, 1791–1796 (2013).
- [46] Loladze, I. & Elser, J. J. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homoeostatic

- 764 protein-to-rRNA ratio. *Ecol. Lett.* **14**, 244–250 (2011). 828  
 765 [47] Woodward, G., Perkins, D. M. & Brown, L. E. Climate 829  
 766 change and freshwater ecosystems: impacts across multi- 830  
 767 ple levels of organization. *Philos. T. Roy. Soc. B* **365**, 831  
 768 2093–2106 (2010). 832  
 769 [48] Brose, U. *et al.* Climate change in size-structured ecosys- 833  
 770 tems. *Philos. T. Roy. Soc. B* **367**, 2903–2912 (2012). 834  
 771 [49] Gilbert, J. P. Temperature directly and indirectly influ- 835  
 772 ences food web structure. *Sci. Rep.-UK* **9**, 5312 (2019). 836  
 773 [50] Getz, W. M. Biomass transformation webs provide a 837  
 774 unified approach to consumer-resource modelling. *Ecol. 838  
 775 Lett.* **14**, 113–124 (2011). 839  
 776 [51] Pillai, P., Gonzalez, A. & Loreau, M. Metacommunity 840  
 777 theory explains the emergence of food web complexity. 841  
 778 *Proc. Natl. Acad. Sci. USA* **108**, 19293–19298 (2011). 842  
 779 [52] Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. 843  
 780 The nested assembly of plant-animal mutualistic networks. 844  
 781 *Proc. Natl. Acad. Sci. USA* **100**, 9383–9387 (2003). 845  
 782 [53] Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mou- 846  
 783 quet, N. Trophic theory of island biogeography. *Ecol. Lett.* 847  
 784 **14**, 1010–1016 (2011). 848  
 785 [54] Bronstein, J. L. Conditional outcomes in mutualistic in- 849  
 786 teractions. *Trends Ecol. Evol.* **9**, 214–217 (1994). 850  
 787 [55] MacArthur, R. & Levins, R. Competition, habitat selec- 851  
 788 tion, and character displacement in a patchy environment. 852  
 789 *Proc. Natl. Acad. Sci. USA* **51**, 1207 (1964). 853  
 790 [56] Dykhuizen, D. & Davies, M. An experimental 854  
 791 model: bacterial specialists and generalists competing in 855  
 792 chemostats. *Ecology* **61**, 1213–1227 (1980). 856  
 793 [57] Futuyma, D. J. & Moreno, G. The evolution of ecological 857  
 794 specialization. *Annu. Rev. Ecol. Syst.* **19**, 207–233 (1988). 858  
 795 [58] Costa, A. *et al.* Generalisation within specialization: 859  
 796 inter-individual diet variation in the only specialized sala- 860  
 797 mander in the world. *Sci. Rep.* **5**, 1–10 (2015). 861  
 798 [59] Brown, J. S., Kotler, B. P. & Valone, T. J. Foraging under 862  
 799 predation - a comparison of energetic and predation costs 863  
 800 in rodent communities of the negev and sonoran deserts. 864  
 801 *Aust. J. Zool.* **42**, 435–448 (1994). 865  
 802 [60] Williams, R. J. & Martinez, N. D. Simple rules yield 866  
 803 complex food webs. *Nature* **404**, 180–183 (2000). 867  
 804 [61] Williams, R. & Martinez, N. Limits to trophic levels and 868  
 805 omnivory in complex food webs: Theory and data. *Am. 869  
 806 Nat.* **163**, 458–468 (2004). 870  
 807 [62] Lafferty, K. D., Dobson, A. P. & Kuris, A. M. Parasites 871  
 808 dominate food web links. *Proc. Natl. Acad. Sci. USA* **103**, 872  
 809 11211–11216 (2006). 873  
 810 [63] Turney, S. & Buddle, C. M. Pyramids of species rich- 874  
 811 ness: the determinants and distribution of species diver- 875  
 812 sity across trophic levels. *Oikos* **125**, 1224–1232 (2016). 876  
 813 [64] Bascompte, J., Jordano, P. & Olesen, J. M. Asymmetric 877  
 814 Coevolutionary Networks Facilitate Biodiversity Mainte- 878  
 815 nance. *Science* **312**, 431–433 (2006). 879  
 816 [65] Guimarães Jr, P. R., Rico-Gray, V., Furtado dos Reis, 880  
 817 S. & Thompson, J. N. Asymmetries in specialization in 881  
 818 ant-plant mutualistic networks. *Proc. Roy. Soc. B* **273**, 882  
 819 2041 (2006). 883  
 820 [66] Araújo, M. S. *et al.* Nested diets: a novel pattern of 884  
 821 individual-level resource use. *Oikos* **119**, 81–88 (2010). 885  
 822 [67] Rohr, R. P., Saavedra, S. & Bascompte, J. On the 886  
 823 structural stability of mutualistic systems. *Science* **345**, 887  
 824 1253497–1253497 (2014). 888  
 825 [68] Valdovinos, F. S. Mutualistic networks: moving closer to 889  
 826 a predictive theory. *Ecol. Lett.* **0** (2019). 890  
 827 [69] Krishna, A., Guimarães Jr, P. R., Jordano, P. & Bas- 891  
 828 compté, J. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* **117**, 1609–1618 (2008).  
 829 [70] Guimarães Jr, P. R., Pires, M. M., Jordano, P., Bas-  
 830 compté, J. & Thompson, J. N. Indirect effects drive co-  
 831 evolution in mutualistic networks. *Nature* **18**, 586 (2017).  
 832 [71] Stouffer, D. B. Compartmentalization increases food-web  
 833 persistence. *Proc. Natl. Acad. Sci. USA* **108**, 3648–3652  
 834 (2011).  
 835 [72] Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bas-  
 836 compté, J. & González, A. Effects of network modular-  
 837 ity on the spread of perturbation impact in experimental  
 838 metapopulations. *Science* **357**, 199–201 (2017).  
 839 [73] Pires, M. M., Prado, P. I. & Guimarães Jr, P. R. Do  
 840 food web models reproduce the structure of mutualistic  
 841 networks? *PLoS ONE* **6**, e27280 (2011).  
 842 [74] Massol, F. *et al.* Linking community and ecosystem dy-  
 843 namics through spatial ecology. *Ecol. Lett.* **14**, 313–323  
 844 (2011).  
 845 [75] Yeakel, J. D., Guimarães Jr, P. R., Bocherens, H. &  
 846 Koch, P. L. The impact of climate change on the struc-  
 847 ture of Pleistocene food webs across the mammoth steppe.  
 848 *Proc. Roy. Soc. B* **280**, 20130239 (2013).  
 849 [76] Bond, W. J., Lawton, J. H. & May, R. M. Do mutualisms  
 850 matter? Assessing the impact of pollinator and disperser  
 851 disruption on plant extinction. *Phil. Trans. Roy. Soc. B*  
 852 **344**, 83–90 (1994).  
 853 [77] Colwell, R. K., Dunn, R. R. & Harris, N. C. Coextinction  
 854 and persistence of dependent species in a changing world.  
 855 *Ann. Rev. Ecol. Evol. Syst.* **43**, 183–203 (2012).  
 856 [78] Díaz-Castelazo, C., Sánchez-Galván, I. R., Guimarães,  
 857 J., Paulo R., Raimundo, R. L. G. & Rico-Gray, V. Long-  
 858 term temporal variation in the organization of an ant-plant  
 859 network. *Ann. Bot.-London* **111**, 1285–1293 (2013).  
 860 [79] Cantor, M. *et al.* Nestedness across biological scales. *PloS  
 861 one* **12** (2017).  
 862 [80] Vieira, M. C. & Almeida Neto, M. A simple stochastic  
 863 model for complex coextinctions in mutualistic networks:  
 864 robustness decreases with connectance. *Ecol. Lett.* **18**,  
 865 144–152 (2015).  
 866 [81] Ponisio, L. C., Gaiarsa, M. P. & Kremen, C. Opportunis-  
 867 tic attachment assembles plant-pollinator networks. *Ecol.  
 868 Lett.* **20**, 1261–1272 (2017).  
 869 [82] Laland, K. N. *et al.* The extended evolutionary synthesis:  
 870 its structure, assumptions and predictions. *Proc. Roy. Soc.  
 871 B* **282**, 20151019 (2015).  
 872 [83] Gupta, M., Prasad, N., Dey, S., Joshi, A. & Vidya, T.  
 873 Niche construction in evolutionary theory: the construc-  
 874 tion of an academic niche? *J. Gen.* **96**, 491–504 (2017).  
 875 [84] Feldman, M. W., Odling-Smee, J. & Laland, K. N. Why  
 876 Gupta et al.'s critique of niche construction theory is off  
 877 target. *J. Gen.* **96**, 505–508 (2017).  
 878 [85] Cuddington, K. Invasive engineers. *Ecol. Model.* **178**,  
 879 335–347 (2004).  
 880 [86] Wright, J. P. & Jones, C. G. Predicting effects of ecosys-  
 881 tem engineers on patch-scale species richness from primary  
 882 productivity. *Ecology* **85**, 2071–2081 (2004).  
 883 [87] Kylafis, G. & Loreau, M. Ecological and evolutionary  
 884 consequences of niche construction for its agent. *Ecol.  
 885 Lett.* **11**, 1072–1081 (2008).  
 886 [88] Krakauer, D. C., Page, K. M. & Erwin, D. H. Diversity,  
 887 dilemmas, and monopolies of niche construction. *Am. Nat.*  
 888 **173**, 26–40 (2009).  
 889 [89] Laland, K. N., Odling-Smee, F. J. & Feldman, M. W.  
 890 Evolutionary consequences of niche construction and their

- 892 implications for ecology. *Proc. Natl. Acad. Sci. USA* **96**,  
 893 10242–10247 (1999).
- 894 [90] Kallus, Y., Miller, J. H. & Libby, E. Paradoxes in leaky  
 895 microbial trade. *Nat. Commun.* **8**, 1361 (2017).
- 896 [91] Butler, S. & O'Dwyer, J. P. Stability criteria for complex  
 897 microbial communities. *Nat. Comm.* **9**, 2970 (2018).
- 898 [92] Amundson, R. *et al.* Soil and human security in the 21st  
 899 century. *Science* **348** (2015).
- 900 [93] Gutiérrez, J. L. & Jones, C. G. Physical ecosystem en-  
 901 gineers as agents of biogeochemical heterogeneity. *Bio-*  
 902 *Science* **56**, 227–236 (2006).
- 903 [94] Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. & Lep-  
 904 age, M. Soil invertebrates as ecosystem engineers: In-  
 905 tended and accidental effects on soil and feedback loops.  
 906 *Appl. Soil Ecol.* **32**, 153 – 164 (2006).
- 907 [95] Shipway, J. R. *et al.* A rock-boring and rock-ingesting  
 908 freshwater bivalve (shipworm) from the Philippines. *Proc.*  
 909 *Roy. Soc. B* **286**, 20190434 (2019).
- 910 [96] Kidwell, S. M. Taphonomic feedback in Miocene assem-  
 911 blages: testing the role of dead hardparts in benthic com-  
 912 munities. *Palaios* **1**, 239–255 (1986).
- 913 [97] Polz, M. F., Alm, E. J. & Hanage, W. P. Horizontal  
 914 gene transfer and the evolution of bacterial and archaeal  
 915 population structure. *Trends Genet.* **29**, 170 – 175 (2013).
- 916 [98] Corlett, R. T. The anthropocene concept in ecology and  
 917 conservation. *Trends Ecol. Evol.* **30**, 36 – 41 (2015).
- 918 [99] Gillespie, D. T. Exact stochastic simulation of coupled  
 919 chemical reactions. *J. Phys. Chem.* **81**, 2340–2361 (1977).

## 920 Acknowledgements

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

942

943

## 944 Author contributions

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

949

## 950 Competing interests

951 The authors declare no competing interests.

952

## SUPPLEMENTARY METHODS

953

### Appendix 1: Building the source pool

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

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

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

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

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

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

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

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

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

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

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

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

963 such that the proportion of redundant modifiers  $\phi$  is

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

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

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

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

967

968

969

970

971

972

973

974

975

976

977

978

979

980

981

982

983

984

985

986

987

988

989

990

991

992

993

994

995

996

997

998

999

1000

1001

1002

1003

1004

1005

1006

1007

1008

1009

1010

1011

1012

1013

1014

1015

1016

1017

1018

1019

1020

1021

1022

1023

1024

1025

1026

1027

1028

1029

1030

1031

1032

1033

1034

1035

1036

1037

1038

1039

1040

1041

1042

1043

1044

1045

1046

1047

1048

1049

1050

1051

1052

1053

1054

1055

1056

1057

1058

1059

1060

1061

1062

1063

1064

1065

1066

1067

1068

1069

1070

1071

1072

1073

1074

1075

1076

1077

1078

1079

1080

1081

1082

1083

1084

1085

1086

1087

1088

1089

1090

1091

1092

1093

1094

1095

1096

1097

1098

1099

1100

1101

1102

1103

1104

1105

1106

1107

1108

1109

1110

1111

1112

1113

1114

1115

1116

1117

1118

1119

1120

1121

1122

1123

1124

1125

1126

1127

1128

1129

1130

1131

1132

1133

1134

1135

1136

1137

1138

1139

1140

1141

1142

1143

1144

1145

1146

1147

1148

1149

1150

1151

1152

1153

1154

1155

1156

1157

1158

1159

1160

1161

1162

1163

1164

1165

1166

1167

1168

1169

1170

1171

1172

1173

1174

1175

1176

1177

1178

1179

1180

1181

1182

1183

1184

1185

1186

1187

1188

1189

1190

1191

</

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

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

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

1082 We compared steady state ecological networks that emerge from  
 1083 ENIgMa (described in Methods, main text) with food webs con-  
 1084 structed from the Niche Model<sup>2</sup> with similar species richness and  
 1085 connectance. Because species richness and connectance of the  
 1086 Niche Model are often altered by eliminating disconnected species,  
 1087 we compared *i*) species richness, *ii*) connectance, *iii*) mean species  
 1088 degree, *iv*) standard deviation of out-degree distributions, and *v*)  
 1089 standard deviation of in-degree distributions averaged across 1000  
 1090 replicates for each model.

1129 We found that all measures resulted in fairly similar values be- 1141 In the first case, where  $G_i$  is determined relative to  $L_{\text{direct}}^*/S^*$ ,  
 1142 tween ENIgMa and the Niche Model food webs with a some im- 1143 we find that there are no potential specialists that colonize the  
 1144 portant differences (Figs. S2,S3). While similar, ENIgMa pro- 1145 community, and (as in the main text) functional specialists colonize  
 1146 duces consistently lower values of connectance, mean species de- 1147 at steady state (mean proportion specialists at steady state is 0.04;  
 1147 gree, as well as standard deviations of the in- and out-degree dis- 1148 Fig. S6b). This means that the indirect links that define trophic in-  
 1149 tributions. This means that the food webs produced by ENIgMa 1149 teractions between species and modifiers increase the link-density of  
 1150 are more sparsely connected with less variance between species. 1150 the network relative to that defined only by direct trophic inter-  
 1151 These results were expected, as the Niche Model assumes system- 1151 actions. In words, modifiers serve to connect otherwise disconnected  
 1152 atically increasing dietary ranges with higher niche values, whereas 1152 species, formalizing the otherwise indirect relationships that struc-  
 1153 the trophic interactions assigned to species in the source pool of 1153 ture the role of engineers in the community. In the second case,  
 1154 ENIgMa are drawn independently. An important difference be- 1154 where  $G_i$  is determined relative to  $L_{\text{indirect}}^*/S^*$ , we find that the  
 1155 tween the Niche Model and ENIgMa is that we do not distinguish 1155 changes in both functional and potential specialists over the course  
 1156 between traditional consumers and parasites. A different frame- 1156 of assembly (Fig. S6c) follow those observed for non-engineered  
 1157 work known as the Inverse Niche Model<sup>4</sup> has been proposed to ad- 1157 food webs (Fig. 2b).

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

- 
- 1164 [1] Gillespie, D. T. Exact stochastic simulation of coupled 1170 of empirical food webs. *Ecology* **92**, 1849–1857 (2011).  
 1165 chemical reactions. *J. Phys. Chem.* **81**, 2340–2361 (1977). 1171 [4] Warren, C. P., Pascual, M., Lafferty, K. D. & Kuris, A. M.  
 1166 [2] Williams, R. J. & Martinez, N. D. Simple rules yield 1172 The inverse niche model for food webs with parasites.  
 1167 complex food webs. *Nature* **404**, 180–183 (2000). 1173 *Theor. Ecol.* **3**, 285–294 (2010).  
 1168 [3] Williams, R. J. & Purves, D. W. The probabilistic niche 1174  
 1169 model reveals substantial variation in the niche structure

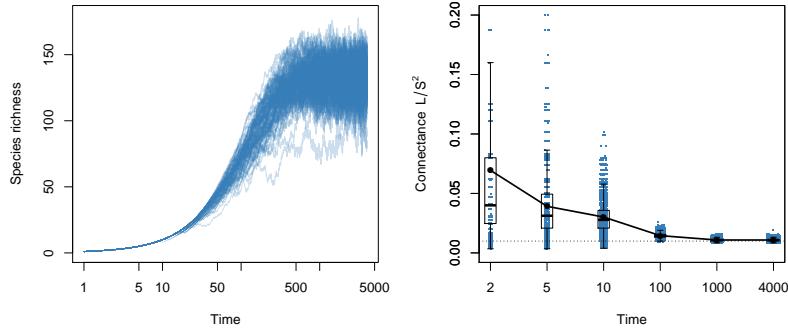


Figure S1. Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early in assembly is high because a small number of species interact with each other such that the proportion of realized interactions (out of all possible interactions)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

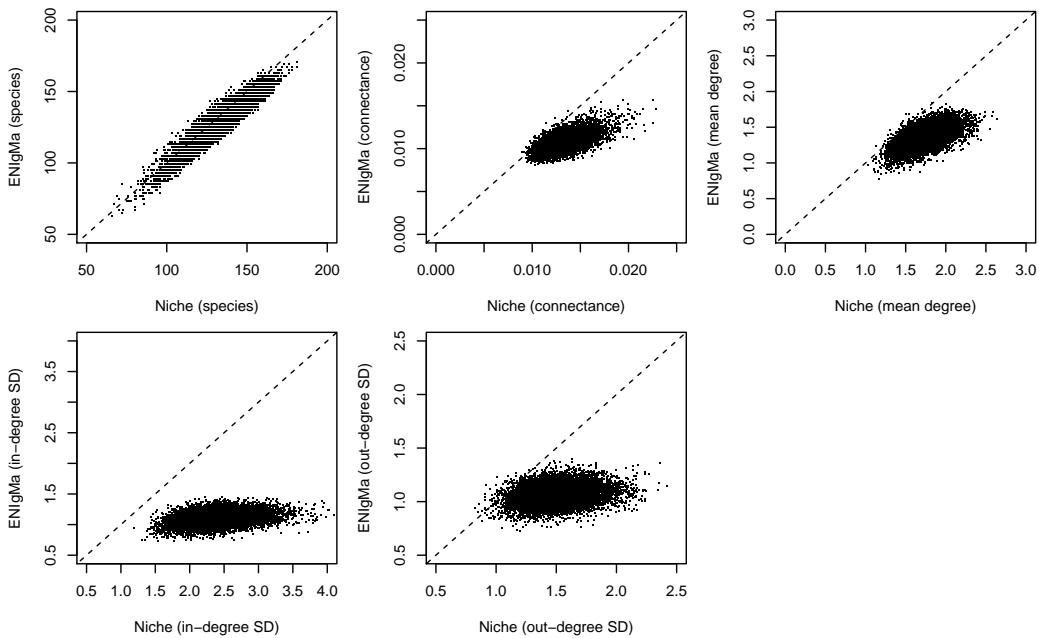


Figure S2. Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures, metrics will tend to fall on the 1:1 line (drawn). While the values for both models are similar, connectance, mean degree, and the standard deviation of in-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

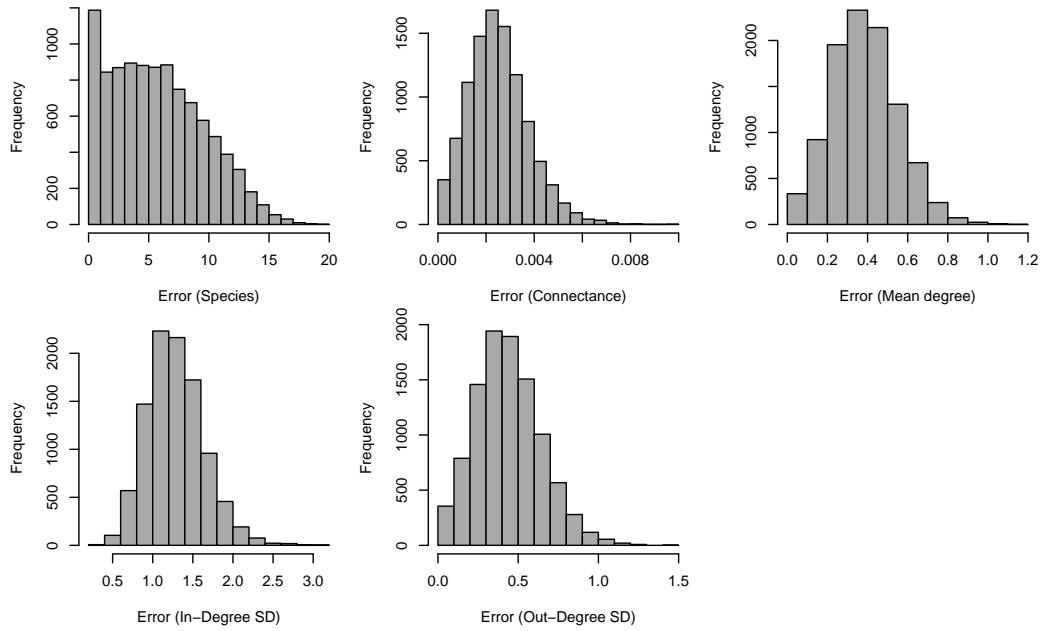


Figure S3. Error between structural measures of the assembly and Niche models. Error is measured as  $\sqrt{(m_i - m_j)^2}$ , where  $m_i$  and  $m_j$  are structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model was used to assess metrics.

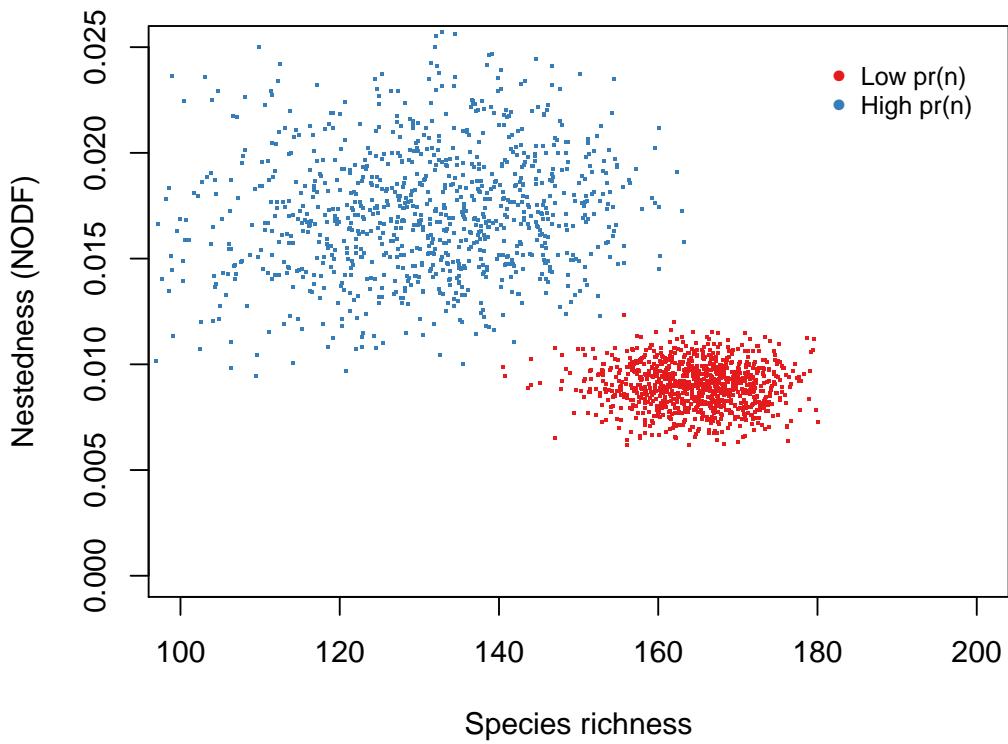


Figure S4. Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities without service interactions ( $p_n = 0$ ) compared to those with a high frequency of service interactions ( $p_n = 0.002$ ). While higher frequencies of service interactions do lower steady state species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

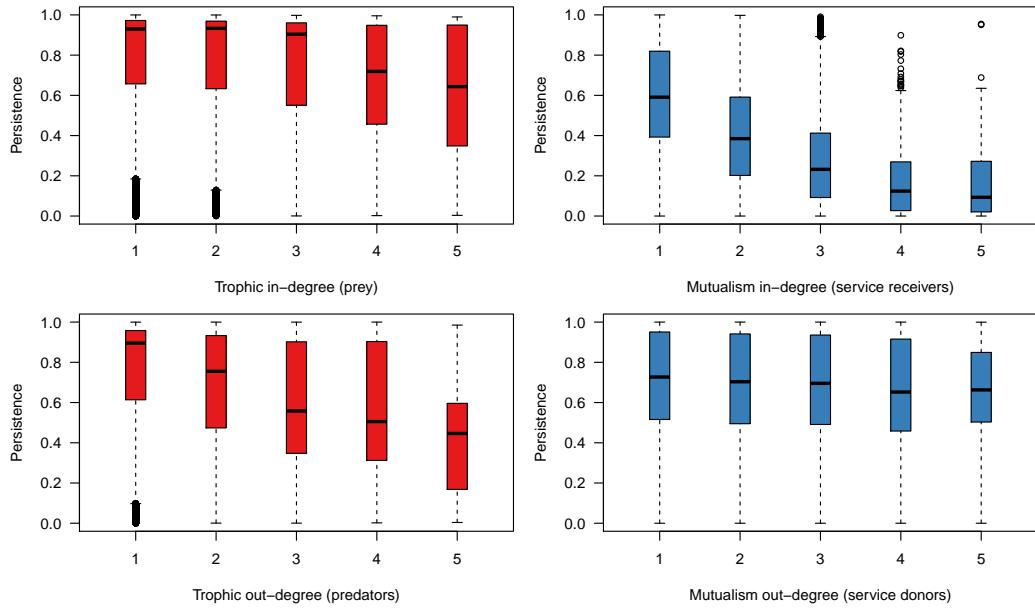


Figure S5. Persistence as a function of trophic and service in/out-degree for communities with higher densities of service interactions ( $p_e = 0.01$ ;  $p_n = 0.002$ ). Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top) and out-degree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

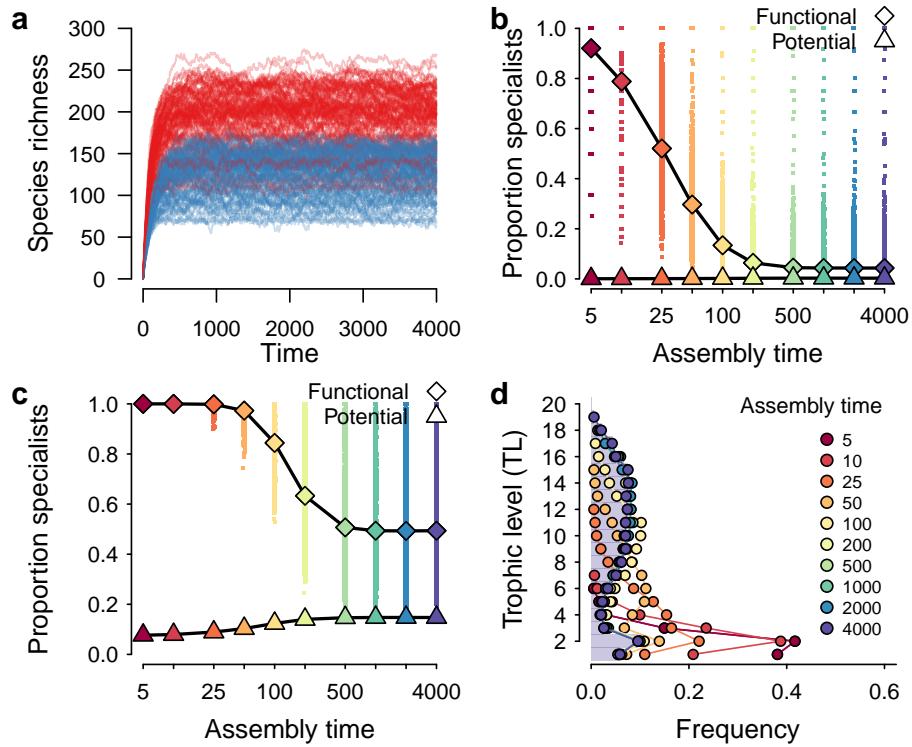


Figure S6. **a**, Assembling communities over time from a pool of 200 non-engineering species. Species richness is blue; modifier richness is red. Steady state species richness is reached by  $t = 250$ . **b**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index  $G_i < 1$  relative to the steady state link density.  $G_i$  is scaled to the steady state link density where links are direct trophic interactions between species. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **c**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a generality index  $G_i < 1$ . Here  $G_i$  is scaled to the steady state link density where links are composed of *both* direct trophic interactions between species and indirect trophic interactions between consumers and those species that produce modifiers as resources. Diamonds represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **d**, The frequency distribution of trophic levels as a function of assembly time (iterations). Autotrophs occupy  $TL = 1$ . Measures were evaluated across  $10^4$  replicates; see Methods for parameter values.

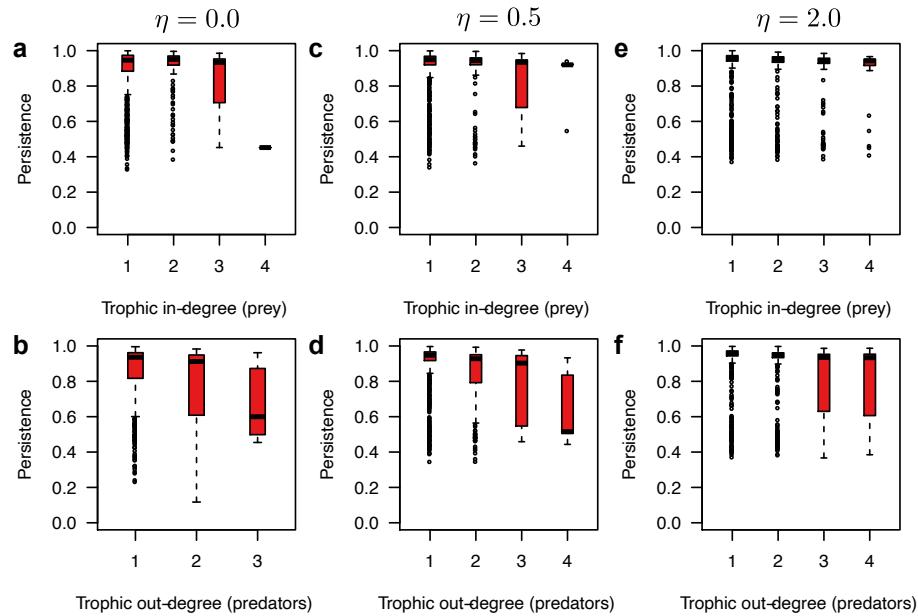


Figure S7. Species-specific persistence as a function of **a**, trophic in-degree (number of resources a species has; top) and **b**, out-degree (number of consumers that eat the species; bottom) when there are no engineers in the community. Species-specific persistence as a function of **c**, trophic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

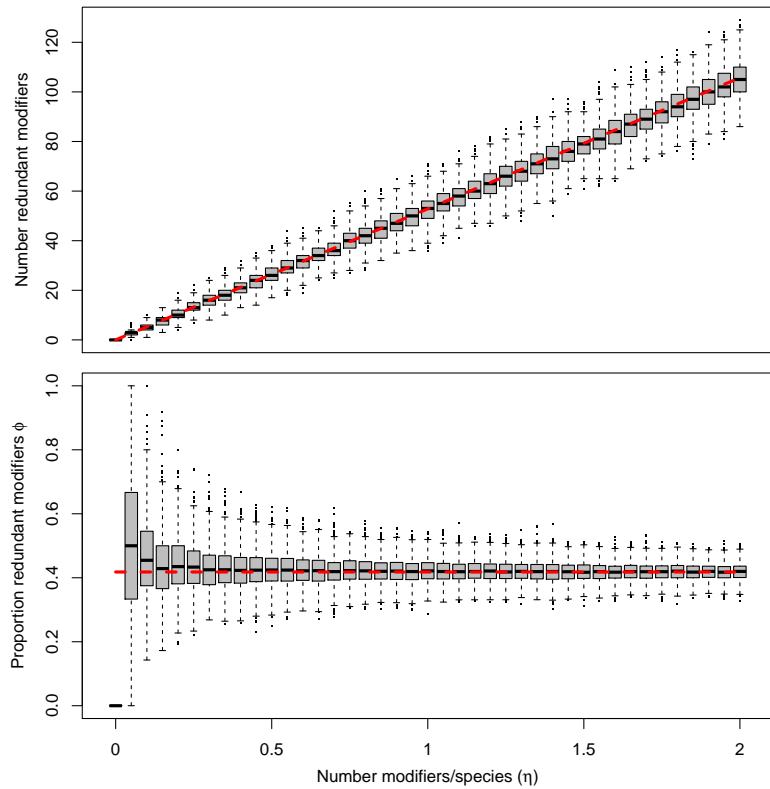


Figure S8. **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species  $\eta$ . The red dashed line shows the analytical expectation (Eq. S3). **b**, Proportion of redundant modifiers  $\phi$  versus the total number of modifiers in the source pool as a function of the expected number of modifiers made per species  $\eta$ . The red dashed line shows the analytical expectation of  $\phi \approx 0.418$  (Eq. S4).

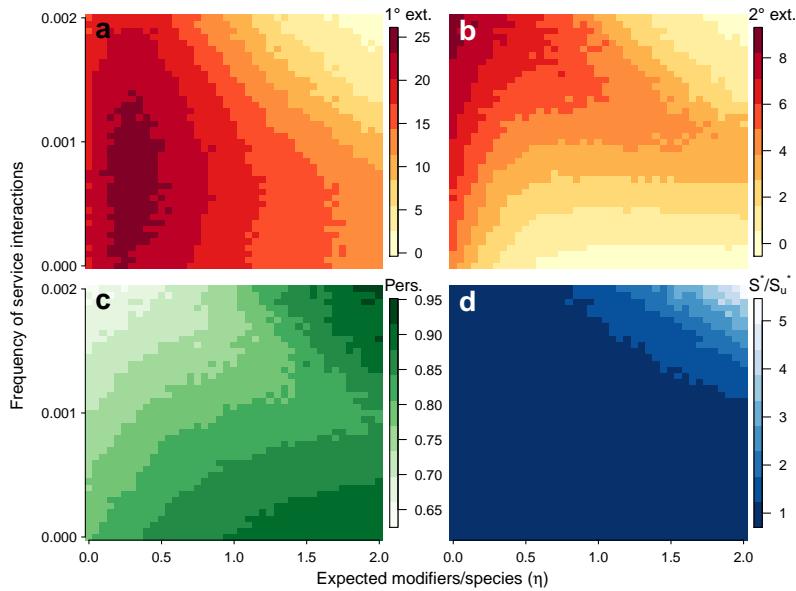


Figure S9. Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean species persistence, defined as the percent simulation time the community is occupied by a given species, averaged across all species that successfully colonize. **d**, The ratio  $S_u^*/S^*$ , where  $S_u^*$  denotes steady states for systems where all engineered modifiers are unique to each engineer, and  $S^*$  denote steady states for systems with redundant engineering. Lower values of  $S_u^*/S^*$  mean that systems with redundant engineers have higher steady states than those without redundancies. Values are averaged over 50 replicates for each parameterization. See Methods for default parameter values.

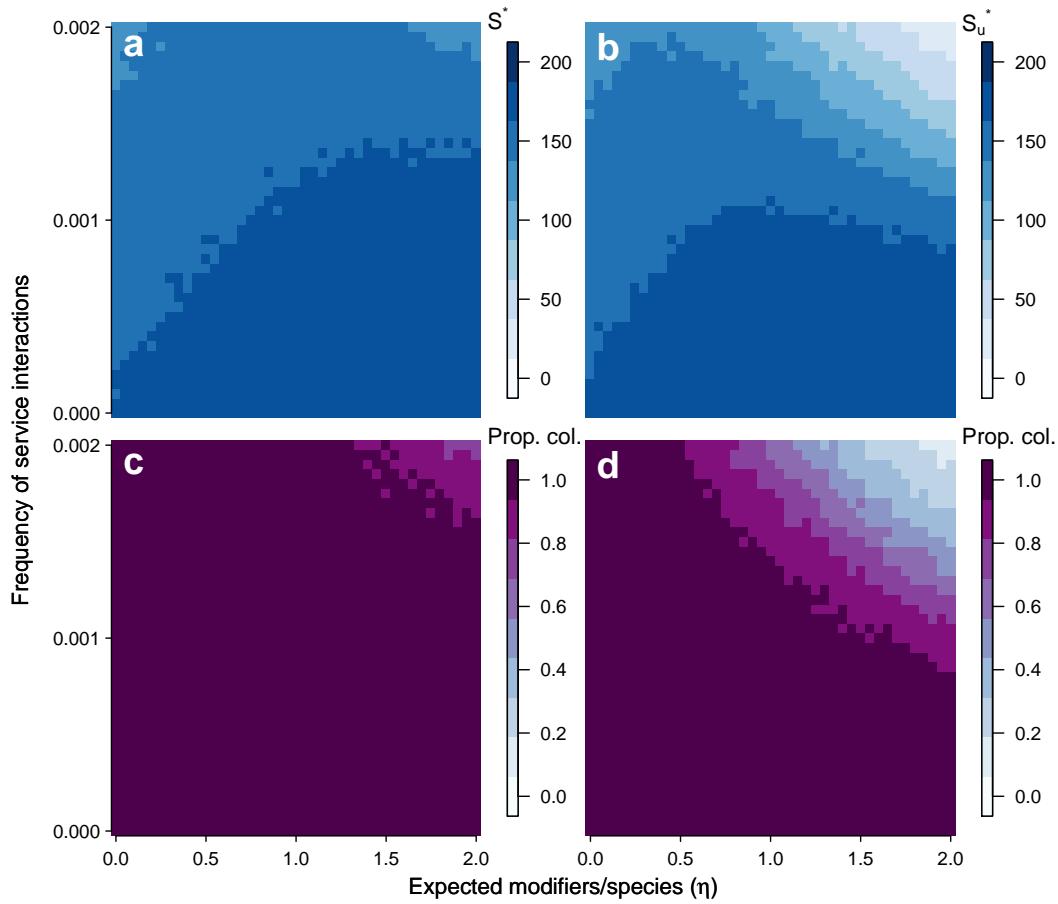


Figure S10. **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering). **d**,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