

# 1 Diverse interactions and ecosystem engineering can stabilize community assembly

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The complexity of an ecological community can be distilled into a network, where diverse interactions connect species in a web of dependencies. Species interact directly with each other and indirectly through environmental effects, however the role of these ecosystem engineers has not been considered in ecological network models. Here we explore the dynamics of ecosystem assembly, where species colonization and extinction 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 mutualistic interactions. We find that ecosystem engineering has large and nonlinear effects on extinction rates. While small numbers of engineers reduce stability by increasing primary extinctions, larger numbers of engineers increase stability by 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.

15 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>.

20 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. While recent interest in ‘multilayer networks’ comprising multiple interaction types (multi-type interactions) may provide additional insight into these processes<sup>26,27</sup>, there is not yet a well-defined the-

45 ory for the assembly of communities that incorporates multitype interactions and both the biotic/abiotic components from which functioning ecosystems are composed (cf. Ref.<sup>28</sup>).

46 Diverse interactions occur not only between species  
47 but indirectly through the effects that species have  
48 on their environment<sup>29–31</sup>. Elephants root out large  
49 saplings and small trees, enabling the formation and  
50 maintenance of grasslands<sup>32,33</sup> and creating habitat for  
51 smaller vertebrates<sup>34</sup>. Burrowing rodents such as go-  
52 phers and African mole rats create shelter and promote  
53 primary production by aerating the soil<sup>35,36</sup>, salmon  
54 and aquatic invertebrates create freshwater habitats by  
55 changing stream morphology<sup>37</sup>, and leaf-cutter ants al-  
56 ter microclimates, influencing seedling survival and plant  
57 growth<sup>38</sup>. These examples illustrate ecosystem engineer-  
58 ing, where the engineering organism alters the environ-  
59 ment on timescales longer than its own<sup>39</sup>. Engineers are  
60 widely acknowledged to have impacts on both small and  
61 large spatial scales<sup>40</sup>, and likely serve as important key-  
62 stone species in many habitats<sup>41</sup>.

63 Ecosystem engineering not only impacts communities  
64 on ecological timescales, but has profoundly shaped the  
65 evolution of life on Earth<sup>42</sup>. For example, the emergence  
66 of multicellular cyanobacteria fundamentally altered the  
67 atmosphere during the Great Oxidation Event of the  
68 Proterozoic roughly 2.5 Byrs BP<sup>42,43</sup>, paving the way  
69 for the biological invasion of terrestrial habitats. In the  
70 oceans it is thought that rRNA and protein biogenesis of  
71 aquatic photoautotrophs drove the nitrogen:phosphorous

75 ratio (the Redfield Ratio) to ca. 16:1 matching that of 133 data and trophic diversity similar to empirical observa-  
 76 plankton<sup>44</sup>, illustrating that engineering clades can have 134 tions. Second, we show that increasing the frequency  
 77 much larger, sometimes global-scale effects. 135 of mutualistic interactions leads to the assembly of

78 The effect of abiotic environmental conditions on 136 ecological networks that are more nested, a common  
 79 species is commonly included in models of ecological 137 feature of diverse mutualistic systems<sup>50</sup>, but are also  
 80 dynamics<sup>45–47</sup> due to its acknowledged importance and 138 prone to extinction cascades. Our third key result shows  
 81 because it can – to first approximation – be easily sys- 139 that increasing the proportion of ecosystem engineers  
 82 tematized. By comparison the way in which species en- 140 within a community has nonlinear effects on observed  
 83 gineer the environment defies easy systemization due to 141 extinction rates. While we find that a low amount of  
 84 the multitude of mechanisms by which engineering oc- 142 engineering increases extinction rates, a high amount of  
 85 curs. While interactions between species and the abi- 143 engineering has the opposite effect. Finally we show that  
 86 otic environment have been conceptually described<sup>30,48</sup>, 144 redundancies in engineered effects promote community  
 87 the absence of engineered effects in network models was 145 diversity by lowering the barriers to colonization.  
 88 addressed by Odling-Smee et al.<sup>31</sup>, where they outlined  
 89 a conceptual framework that included both species and 146

90 abiotic compartments as nodes of a network, with links 147 **Assembly without ecosystem engineering.** Our  
 91 denoting both biotic and abiotic interactions. 148 framework assumes that communities assemble by ran-  
 92 How does the assembly of species constrained by multi- 149 dom colonization from a source pool. A species from the  
 93 type interactions impact community structure and stabil- 150 source pool can colonize if it finds at least one resource  
 94 ity? How are these processes altered when the presence of 151 that it can consume (one eat interaction is satisfied; cf.  
 95 engineers modifies species' dependencies within the com- 152 Ref.<sup>51</sup>) and all of its non-trophic needs are met (all need  
 96 munity? Here we model the assembly of an ecological 153 interactions are satisfied; see Fig. 1). As such, service  
 97 network where nodes represent ecological entities, includ- 154 interactions are assumed to be obligate, whereas trophic  
 98 ing engineering species, non-engineering species, and the 155 interactions are flexible – except in the case of a consumer  
 99 effects of the former on the environment, which we call 156 with only a single resource. While an abiotic basal re-  
 100 abiotic 'modifiers'. The links of the network that con- 157 source is always assumed to be present (white node in  
 101 nect both species and modifiers represent trophic ('eat' 158 Fig. 1b), following the establishment of an autotrophic  
 102 interactions), service ('need' interactions), and engineer- 159 base, the arrival of mixotrophs (i.e. mixing auto- and  
 103 ing dependencies, respectively (Fig. 1; see Methods for 160 heterotrophy) and lower trophic heterotrophs create op-  
 104 a full description). Trophic interactions represent both 161 portunities for organisms occupying higher trophic levels  
 105 predation as well as parasitism, whereas service interac- 162 to invade. This expanding niche space initially serves as  
 106 tions account for non-trophic interactions associated with 163 an accelerator for community growth.

107 reproductive facilitation such as pollination or seed dis- 164 Following the initial colonization phase, extinctions be-  
 108 persal. In our framework a traditional mutualism (such 165 gin to slow the rate of community growth. Primary ex-  
 109 as a plant-pollinator interaction) consists of a service 166 tinctions occur if a given species is not the strongest  
 110 (need) interaction in one direction and a trophic ('eat') 167 competitor for at least one of its resources. A species' 168 competition strength is determined by its interactions:  
 111 interaction in the other. These multitype interactions be- 169 competition strength is enhanced by the number of need  
 112 tween species and modifiers thus embed multiple depen- 170 interactions (where the number of potential and realized  
 113 dent ecological sub-systems into a single network (Fig. 1). 171 interactions are equivalent) and penalized by the number  
 114 Modifiers in our framework overlap conceptually with the 172 of its realized resources (those present in the local com-  
 115 'abiotic compartments' described in Odling-Smee et al.<sup>31</sup>. 173 munity, thus favoring functional trophic specialists) and  
 116 Following Pillai et al.<sup>49</sup>, we do not track the abundances 174 realized consumers (those present in the local community,  
 117 of biotic or abiotic entities but track only their presence 175 thus favoring species with fewer predators). This encodes  
 118 or absence. We use this framework to explore the dy- 176 three key assumptions: that mutualisms provide a fit-  
 119 namics of ecosystem assembly, where the colonization 177 ness benefit<sup>52</sup>, specialists are stronger competitors than  
 120 and extinction of species within a community depends 178 generalists<sup>53–56</sup>, and many predators entail an energetic  
 121 on the constraints imposed by the trophic, service, and 179 cost<sup>57</sup>. Secondary extinctions occur when a species loses  
 122 engineering dependencies. We then show how observed 180 its last trophic or any of its service requirements. See Fig.  
 123 network structures emerge from the process of assembly, 181 1d,e for an illustration of the assembly process. As the  
 124 compare their attributes with those of empirical systems, 182 colonization and extinction rates converge, the commu-  
 125 and examine the effects of ecosystem engineers. 183 nity reaches a steady state around which it oscillates (Fig.  
 126 Our results offer four key insights into the roles of 184 2a). See Methods and Supplementary Appendix 1 for a  
 127 multitype interactions and ecosystem engineering in 185 complete description of the assembly process. Specific  
 128 driving community assembly. First, we show that the 186 model parameterizations are described in Supplementary  
 129 assembly of communities in the absence of engineering 187 Appendix 2.

130 reproduces many features observed in empirical systems. 188 Assembly of ecological communities in the absence of  
 131 These include changes in the proportion of generalists 189 engineering results in interaction networks with struc-  
 132 over the course of assembly that accord with measured 190 tures consistent with empirical observations. As the com-

133 data and trophic diversity similar to empirical observa-  
 134 tions. Second, we show that increasing the frequency  
 135 of mutualistic interactions leads to the assembly of  
 136 ecological networks that are more nested, a common  
 137 feature of diverse mutualistic systems<sup>50</sup>, but are also  
 138 prone to extinction cascades. Our third key result shows  
 139 that increasing the proportion of ecosystem engineers  
 140 within a community has nonlinear effects on observed  
 141 extinction rates. While we find that a low amount of  
 142 engineering increases extinction rates, a high amount of  
 143 engineering has the opposite effect. Finally we show that  
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147 **Assembly without ecosystem engineering.** Our  
 148 framework assumes that communities assemble by ran-  
 149 dom colonization from a source pool. A species from the  
 150 source pool can colonize if it finds at least one resource  
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 152 Ref.<sup>51</sup>) and all of its non-trophic needs are met (all need  
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 169 interactions (where the number of potential and realized  
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 172 munity, thus favoring functional trophic specialists) and  
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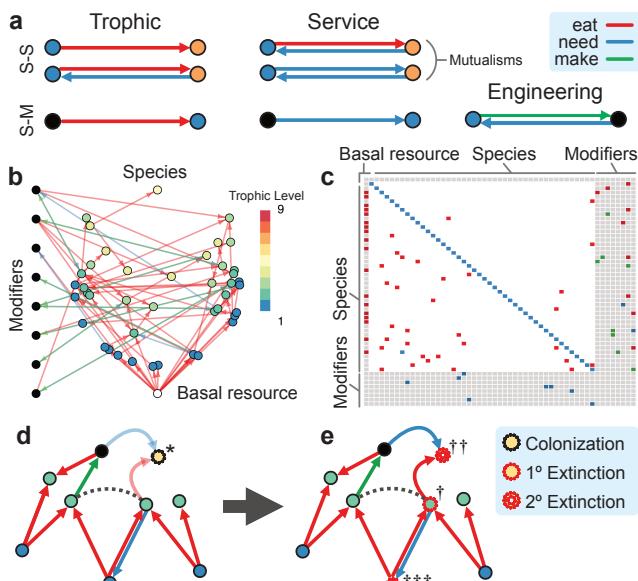


Figure 1. Model framework for communities with multitype interactions and ecosystem engineering. **a**, Multitype interactions between species (colored nodes) and abiotic modifiers (black nodes). Trophic and mutualistic relationships define both species-species (S-S) and species-modifier (S-M) interactions;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

Community reaches steady state (Fig. 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. ??). Decaying connectance followed by stabilization around a constant value has been documented in the assembly of mangrove communities<sup>16</sup> and experimental aquatic mesocosms<sup>17</sup>. 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. In Supplementary Appendix 3 we include a brief comparison of assembly model food webs with those produced by the Niche model<sup>58</sup>. 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.

Recent empirical work has suggested that general-

ist species may dominate early in assembly, whereas specialists colonize after a diverse resource base has accumulated<sup>16,51</sup>. Here the trophic generality of species  $i$  is defined as  $G_i(t) = k_i^{in}(t)/(L^*/S^*)^{58}$ , where  $k_i^{in}(t)$  is the number of resource species linked to consumer  $i$  at time  $t$ , which is scaled by the steady state link density  $L^*/S^*$ , as is typically done in empirical investigations<sup>16</sup>. 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. 2b). As the community grows, more potential interactions become realized, and functional specialists become functional generalists. Moreover, as species assemble the available niche space expands, and the proportion of potential trophic specialists grows (Fig. 2b). This latter observation confirms expectations from the trophic theory of island biogeography<sup>51</sup>, 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 proportion of functional specialists is ca. 56%, which is similar to empirical observations of assembling food webs<sup>16</sup>.

The dominance of functional specialists early in assembly is primarily due to the initial colonization by consumers with few resources. This is evident when we observe that the trophic level (TL) distribution early in assembly ( $t = 5$ ) has an average  $TL = 1.6$ . Four trophic levels are typically established by  $t = 50$ , where colonization is still dominant, and by the time communities reach steady state the interaction networks are characterized by an average  $TL_{max} (\pm \text{standard deviation}) = 11 \pm 2.8$  (Fig. 2c). While the maximum trophic level is higher than that measured in most consumer-resource systems<sup>59</sup>, it is not unreasonable if parasitic interactions (which we do not differentiate from other consumers) are included<sup>60</sup>. Overall, the most common trophic level among species at steady state is ca.  $TL = 4.75$ .

The distribution of trophic levels changes shape over the course of assembly. Early in assembly, we observe a skewed pyramidal structure, where most species feed from the base of the food web. At steady state, we observe that intermediate trophic levels dominate, with frequencies taking on an hourglass structure (purple bars, Fig. 2c). Compellingly, the trophic richness pyramids that we observe at steady state follow closely the hourglass distribution observed for empirical food webs and are less top-heavy than those produced by static food web models<sup>61</sup>.

**Structure and dynamics of mutualisms.** Nested interactions, where specialist interactions are subsets of generalist interactions, are a distinguishing feature of mutualistic networks<sup>50,62-64</sup>. Nestedness has been

shown to maximize the structural stability of mutualistic networks<sup>65</sup>, emerge naturally via adaptive foraging behaviors<sup>24,66</sup> and neutral processes<sup>67</sup>, and promote the influence of indirect effects in driving coevolutionary dynamics<sup>68</sup>. While models and experiments of trophic networks suggest that compartmentalization confers greater stabilizing properties<sup>69,70</sup>, interaction asymmetry among species may promote nestedness in both trophic<sup>64</sup> and mutualistic systems<sup>71</sup>. Processes that operate on different temporal and spatial scales may have a significant influence on these observations<sup>72</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>73</sup>.

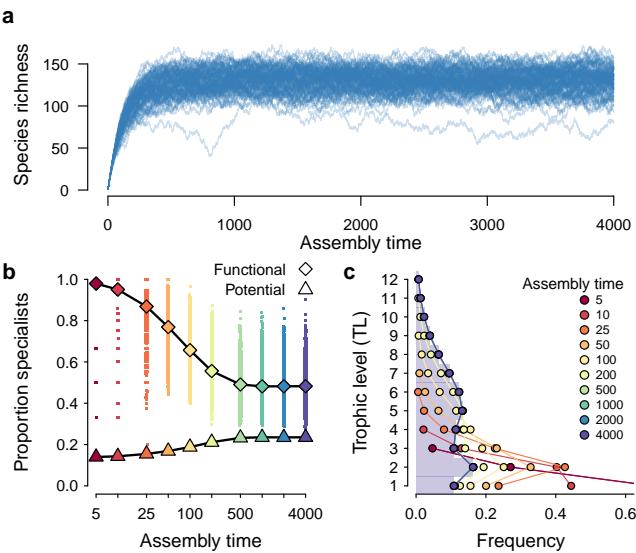


Figure 2. Food web structure over the course of assembly. **a**, Assembling communities over time from a pool of 200 non-engineering species. Steady state species richness is reached by  $t = 250$ . **b**, The proportion of specialists as a function of assembly time (iterations), where a specialist is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

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

generalists are at a competitive disadvantage when they share the same resources with a specialist consumer. Yet we find that as we increase the frequency of service interactions (holding constant trophic interaction frequency; see Supplementary Appendix 2), the assembled community at steady state becomes more nested (Fig. 3a). More service interactions increase a species' competition strength, lowering its primary extinction risk. Participation in a mutualism thus delivers a fitness advantage to the species receiving the service, compensating for the lower competitive strength of generalists and allowing generalists to share subsets of resources with specialists, which promotes nestedness. However increases in mutualisms also increase inter-species dependencies, which raises the potential risk associated with losing mutualistic partners<sup>74,75</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. 3b ??).

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. ??). 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>76</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>23,24,66,78,79</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.

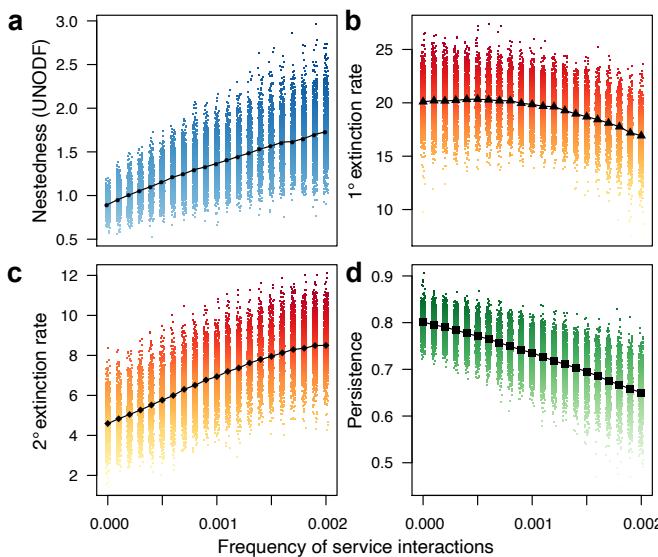


Figure 3. Community structure and stability as a function of the frequency of service interactions. **a**, Structural nestedness of communities, measured as UNODF (Unipartite Nestedness based on Overlap and Decreasing Fill)<sup>77</sup>. The value reported is the mean value taken across the rows and columns of the adjacency matrix accounting for both trophic and service interactions. **b**, Mean rate of primary extinction (where primary extinctions occur from competitive exclusion of consumers over shared resources) and **c**, secondary extinction (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 2 for parameter values.

345

**Assembly with ecosystem engineering.** The concept of ecosystem engineering, or more generally niche construction, has both encouraged an extended evolutionary synthesis<sup>80</sup> while also garnering considerable controversy<sup>81,82</sup>. Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground<sup>31,39</sup>. For example, engineering has been shown to promote invasion<sup>83</sup>, alter primary productivity<sup>84</sup>, and change the selective environment over eco-evolutionary timescales<sup>85,86</sup> which can lead to unexpected outcomes such as the fixation of deleterious alleles<sup>87</sup>. On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities<sup>88</sup>, the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems<sup>89</sup>. The soil is one place where these macro- and microbiotic systems intersect<sup>90</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>91,92</sup>.

We next explore the effects of ecosystem engineering

368 by allowing species to produce abiotic modifiers as additional nodes in the ecological network (Fig. 1). These 369 modifier nodes produced by engineers can serve to fulfill 370 resource or service requirements for other species. The 371 parameter  $\eta$  defines the mean number of modifiers pro- 372 duced per species in the pool, drawn from a Poisson dis- 373 tribution (see Methods and Supplementary Appendix 1 374 for details). If a species makes  $\geq 1$  modifier, we label it 375 an engineer. As the mean number of modifiers/species 376  $\eta$  increases, both the number of engineers in the pool as 377 well as the number of modifiers made per engineer in- 378 creases. As detailed in Supplementary Appendix 1, mul- 379 tiple engineers can make the same modifier, such that 380 engineering redundancies are introduced when  $\eta$  is large. 381 When an engineer colonizes the community, so do its 382 modifiers, which other species in the system may inter- 383 act with. When engineers are lost, their modifiers will 384 also be lost, though can linger in the community for a 385 period of time inversely proportional to the density of 386 disconnected modifiers in the community.

388 While the inclusion of engineering does not signifi- 389 cantly impact the structure of species-species interac- 390 tions within assembling food webs (see Supplementary 391 Appendix 4 and Fig. ??), it does have significant con- 392 sequences for community stability. Importantly, these 393 effects also are sensitive to the frequency of service in- 394 teractions within the community, and we find that their 395 combined influence can be complex.

396 As the number of engineers increases, mean rates of 397 primary extinction are first elevated and then decline 398 (Fig. 4a). At the same time, the mean rates of secondary 399 extinction systematically decline and persistence sys- 400 tematically increases (Fig. 4b-c). When engineered modifiers 401 are rare ( $0 < \eta \leq 0.5$ ), higher rates of primary extinction 402 coupled with lower rates of secondary extinction mean 403 that extinctions are common, but of limited magnitude 404 such that disturbances are compartmentalized. As mod- 405 ifiers become more common both primary and secondary 406 extinction rates decline, which corresponds to increased 407 persistence. We suggest two mechanisms that may pro- 408 duce the observed results. First, when engineers and 409 modifiers are present but rare, they provide additional 410 resources for consumers. This stabilization of consumers 411 ultimately results in increased vulnerability of prey, such 412 that the cumulative effect is increased competitive ex- 413 clusion of prey and higher rates of primary extinction 414 (Fig. 4a). Second, when engineers and their modifiers 415 are common ( $\eta > 0.5$ ) the available niche space expands, 416 lowering competitive overlap and suppressing both pri- 417 mary and secondary extinctions. Notably the presence 418 of even a small number of engineers serves to limit the 419 magnitude of secondary extinction cascades. Assessment 420 of species persistence as a function of trophic in-degree 421 (number of resources) and out-degree (number of con- 422 sumers) generally supports this proposed dynamic (Fig. 423 ??).

424 Increasing the frequency of service interactions pro- 425 motes service interactions between species and engi-

neered 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>93</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 interdependences between and among species. As trophic interactions are replaced by service interactions, previously vulnerable species gain a competitive foothold and persist, lowering rates of primary extinctions (Fig. 4a). The 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.

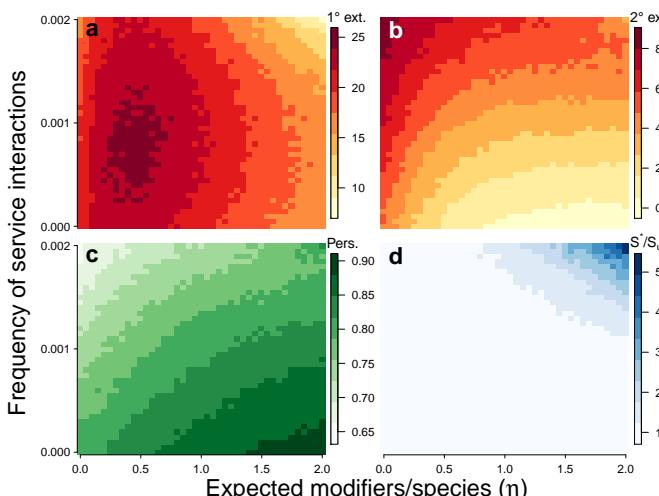


Figure 4. Community stability as a function of the frequency of service interactions and modifiers per species. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade 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>39</sup>, redundant engineering has been assumed to be unimportant<sup>94</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>83</sup> as is generally assumed to be the case with niche construction<sup>86</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>94</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>95</sup>. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic<sup>42,43</sup> among other large-scale engineering events in the history of life<sup>42</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>88,89</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. ??), 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. ??). 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). In contrast, when redundant engineering is not allowed, steady state community richness  $S_u^*$  declines sharply (Figs. 4d, ??b).

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,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>49</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>52</sup>, specialists are stronger competitors than generalists<sup>55</sup>, and many predators entail an energetic cost<sup>57</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>.

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## 951 Author contributions

952 JDY and TG conceived of the model framework. JDY, MMP,  
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 954 JLOD, PRG, DG, and TG analyzed the results and contributed  
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## 956 Competing interests

957 The authors declare no competing interests.