

Diverse interactions and ecosystem engineering can stabilize community assembly

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Abstract

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

Introduction

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

To what extent assembly leaves its fingerprint on the structure and function of ecological communities is a source of considerable debate^{10–12}. There is strong evidence that functional traits constrain assembly^{12–14}, while differences in species' trophic niche^{15,16}, coupled with early establishment of fast/slow energy channels¹⁷, appear to significantly impact long-term community dynamics. There has been growing interest in understanding the combined role of trophic and mutualistic interac-

tions in driving assembly^{18,19}, where the establishment of species from a source pool^{19–21} and the plasticity of species interactions^{22–25} constrain colonization and extinction dynamics. ~~Despite these advances~~ While recent interest in 'multilayer networks' comprising multiple interaction types (multitype interactions) may provide additional insight into these processes ^{26,27}, there is not yet a well-defined theory for the assembly of communities that incorporates ~~multiple interaction types and both biotic/multitype interactions as well as both biotic and abiotic components from which functioning ecosystems are composed (cf. Ref.²⁸).~~

~~Recent interest in 'multilayer networks' comprising multiple interaction types (multitype interactions) may provide additional insight into these processes~~ ^{26,27}. ~~However, interactions where species affect others by altering the abiotic environment in a lasting way have not yet been incorporated into models of ecological networks. These interactions, known as ecosystem engineering~~ ^{31,93} ~~or more generally niche construction~~ ^{12,94}, ~~are quite common in nature and exist in almost every ecosystem.~~

Diverse interactions occur not only between species but indirectly through the effects that species have on ~~their~~ the abiotic environment^{29–31}. Elephants root out

large saplings and small trees, enabling the formation and maintenance of grasslands^{32,33} and creating habitat for smaller vertebrates³⁴. Burrowing rodents such as gophers and African mole rats create shelter and promote primary production by aerating the soil^{35,36}, salmon and aquatic invertebrates create freshwater habitats by changing stream morphology³⁷, and leaf-cutter ants alter microclimates, influencing seedling survival and plant growth³⁸. These examples illustrate ecosystem engineering, where the engineering organism alters the environment on timescales longer than its own³⁹. Engineers are widely acknowledged to have impacts on both small and large spatial scales⁴⁰, and likely serve as important keystone species in many habitats⁴¹.

Ecosystem engineering not only impacts communities on ecological timescales, but has profoundly shaped the evolution of life on Earth⁴². For example, the emergence of multicellular cyanobacteria fundamentally altered the atmosphere during the Great Oxidation Event of the Proterozoic roughly 2.5 Byrs BP^{42,43}, paving the way for the biological invasion of terrestrial habitats. In the oceans it is thought that rRNA and protein biogenesis of aquatic photoautotrophs drove the nitrogen:phosphorous ratio (the Redfield Ratio) to ca. 16:1 matching that of plankton⁴⁴, illustrating that engineering clades can have much larger, sometimes global-scale effects.

The effect of abiotic environmental conditions on species is commonly included in models of ecological dynamics^{45–47} due to its acknowledged importance and because it can – to first approximation – be easily systematized. By comparison the way in which species engineer the environment defies easy systemization due to the multitude of mechanisms by which engineering occurs. While interactions between species and the abiotic environment have been conceptually described^{30,48}, the absence of engineered effects in network models was ~~addressed~~ described by Odling-Smee et al.³¹, where they outlined a conceptual framework that included both species and abiotic compartments as nodes of a network, with links denoting both biotic and abiotic interactions.

How does the assembly of species constrained by multitype interactions impact community structure and stability? How are these processes altered when the presence of engineers modifies species’ dependencies within the community? Here we model the assembly of an ecological network where nodes represent ecological entities, including engineering species, non-engineering species, and the effects of the former on the environment, which we call abiotic ~~modifiers~~ modifiers. The links of the network that connect both species and modifiers represent trophic (~~eat~~ eat interactions), service (~~need~~ need interactions), and engineering dependencies, respectively (Fig-Figure 1; see Methods for a full description). Trophic interactions represent both predation as well as parasitism, whereas service interactions account for non-trophic interactions associated with reproductive facilitation such as pollination or seed dispersal. In our framework a traditional mutualism (such as a plant-pollinator interaction)

consists of a service (need) interaction in one direction and a trophic (eat) interaction in the other. These multitype interactions between species and modifiers thus embed multiple dependent ecological sub-systems into a single network (Fig-Figure 1). Modifiers in our framework overlap conceptually with the ‘abiotic compartments’ described in Odling-Smee et al.³¹. Following Pillai et al.⁴⁹, we do not track the abundances of biotic or abiotic entities but track only their presence or absence. We use this framework to explore the dynamics of ecosystem assembly, where the colonization and extinction of species within a community depends on the constraints imposed by the trophic, service, and engineering dependencies. We then show how observed network structures emerge from the process of assembly, compare their attributes with those of empirical systems, and examine the effects of ecosystem engineers.

Our results offer four key insights into the roles of multitype interactions and ecosystem engineering in driving community assembly. First, we show that the assembly of communities in the absence of engineering reproduces many features observed in empirical systems. These include changes in the proportion of generalists over the course of assembly that accord with measured data and trophic diversity similar to empirical observations. Second, we show that increasing the frequency of mutualistic interactions leads to the assembly of ecological networks that are more nested, a common feature of diverse mutualistic systems⁵⁰, but that are also prone to extinction cascades. Our third key result shows that increasing the proportion of ecosystem engineers within a community has nonlinear effects on observed extinction rates. While we find that a low amount of engineering increases extinction rates, a high amount of engineering has the opposite effect. Finally we show that redundancies in engineered effects promote community diversity by lowering the barriers to colonization.

Results and Discussion

Assembly without ecosystem engineering. Our framework assumes that communities assemble by random colonization from a source pool. A species from the source pool can colonize if it finds at least one resource that it can consume (one ~~eat~~ eat interaction is satisfied; cf. Ref.⁵¹) and all of its non-trophic needs are met (all ~~need~~ need interactions are satisfied; see Fig-Figure 1). As such, service interactions are assumed to be obligate, whereas trophic interactions are flexible – except in the case of a consumer with ~~only~~ just a single resource. While ~~a~~ an abiotic basal resource is always assumed to be present (white node in Fig-Figure 1b), following the establishment of an autotrophic base, the arrival of mixotrophs (i.e. mixing auto- and heterotrophy) and lower trophic heterotrophs create opportunities for organisms occupying higher trophic levels to invade. This expanding niche space initially serves as an accelerator for community growth.

Following the initial colonization phase, extinctions begin to slow the rate of community growth. Primary extinctions occur if a given species is not the strongest competitor for at least one of its resources. A species' competition strength is determined by its interactions: competition strength is enhanced by the number of need interactions (where the number of potential and realized interactions are equivalent) and penalized by the number of its resources (favoring realized resources (i.e. those resources present in the local community, favoring functional trophic specialists) and consumers (favoring species with fewer predators realized predators (i.e. those predators present in the local community)). This encodes three key assumptions: that mutualisms provide a fitness benefit⁵², specialists are stronger competitors than generalists^{53–56}, and many predators entail having many predators entails an energetic cost⁵⁷. Secondary extinctions occur when a species loses its last trophic or any of its service requirements. See Fig. 1d,e for an illustration of the assembly process. As the colonization and extinction rates converge, the community reaches a steady state around which it oscillates (Fig. Figure 2a). See Figure 1d,e for an illustration of the assembly process, and the Methods and Supplementary Appendix Note 1 for a complete description of the assembly process. Specific model parameterizations are described in Supplementary Appendix Note 2.

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.

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

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

Recent empirical work has suggested that generalist species may dominate early in assembly, whereas specialists colonize after a diverse resource base has accumulated^{16,51}. Here the trophic generality of species i is defined as $G_i(t) = k_i^{in}(t)/(L^*/S^*)$, $G_i(t) = k_i^{in}(t)/(L^*/S^*)$ ⁵⁸, where $k_i^{in}(t)$ is the number of species consumed by species i at time t , which is scaled by the steady state link density L^*/S^* , as is typically done performed in empirical investigations¹⁶. Only trophic links between species are considered here, such that we ignore links to the abiotic basal resource in our evaluation of trophic generality. A species is classified as a generalist if $G_i > 1$ and a specialist if $G_i < 1$. If generality is evaluated with respect to the steady state link density, we find that species with many potential trophic interactions realize only a subset of them, thereby functioning as specialists early in the assembly process (Fig. Figure 2b). As the community grows, more potential interactions become realized, and functional specialists become functional generalists. Moreover, as species assemble, the available niche space expands, and the proportion of potential trophic specialists grows (Fig. Figure 2b). This latter observation confirms expectations from the trophic theory of island biogeography⁵¹, where communities with lower richness (i.e. early assembly) are less likely to support specialist consumers than species-rich communities (late assembly). At steady state the proportion of functional specialists is ca. 56.48%, which is similar to empirical observations of assembling mangrove island food webs¹⁶.

The dominance of functional specialists early in assembly is primarily following the initial assembly of autotrophs is due to the initial colonization by autotrophs. This is evident when we observe that the colonization of lower-trophic consumers with few resources, where the observed trophic level (TL) distribution early in assembly ($t = 5$) has an average TL = 1.6 (measured using the NetIndices R package v.1.4.4⁷). Four trophic levels are typically established by $t = 50$, where colonization is still dominant, and by the time communities reach steady state the interaction networks are characterized by an average TL_{max} (\pm standard deviation) = 11 ± 2.8 (Fig. Figure 2c). While the maxi-

326 mum trophic level is higher than that measured in most
 327 consumer-resource systems⁵⁹, it is not unreasonable if
 328 parasitic interactions (which we do not differentiate from
 329 other consumers) are included⁶⁰. Overall, the most com-
 330 mon trophic level among species at steady state is ca.
 331 $TL = 4.75$.

332 The distribution of trophic levels changes shape over
 333 the course of assembly. Early in assembly, we observe
 334 a skewed pyramidal structure, where most species feed
 335 from the base of the food web. At steady state, we
 336 observe that intermediate trophic levels dominate, with
 337 frequencies taking on an hourglass structure (purple
 338 bars, Fig. Figure 2c). Compellingly, the trophic richness
 339 pyramids that we observe at steady state follow closely
 340 the hourglass distribution observed for empirical food
 341 webs and are less top-heavy than those produced by
 342 static food web models⁶¹.

343 **Structure and dynamics of mutualisms.** Nested
 344 interactions, where specialist interactions are subsets
 345 of generalist interactions, are a distinguishing feature
 346 of mutualistic networks^{50,62–64}. Nestedness has been
 347 shown to maximize the structural stability of mutual-
 348 istic networks⁶⁵, emerge naturally via adaptive forag-
 349 ing behaviors^{24,66} and neutral processes⁶⁷, and promote
 350 the influence of indirect effects ~~in driving-on~~ coevolu-
 351 tionary dynamics⁶⁸. While models and experiments of
 352 trophic networks suggest that compartmentalization con-
 353 fers greater stabilizing properties^{69,70}, interaction asym-
 354 metry among species may promote nestedness in both
 355 trophic⁶⁴ and mutualistic systems⁷¹. Processes that op-
 356 erate on different temporal and spatial scales may have a
 357 significant influence on these observations⁷². For exam-
 358 ple, over evolutionary time, coevolution and speciation
 359 may degrade nested structures in favor of modularity²⁵,
 360 and there is some evidence from Pleistocene food webs
 361 that geographic insularity may reinforce this process⁷³.

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

381 Does the assembly of ecological networks favor nest-
 382 edness when mutualistic interactions are frequent? In

383 the absence of mutualisms, the trade-offs in our model
 384 preclude high levels of nestedness because we assume
 385 that generalists are at a competitive disadvantage when
 386 they share the same resources with a specialist consumer.
 387 Yet we find that as we increase the frequency of ser-
 388 vice interactions (holding constant trophic interaction
 389 frequency; see Supplementary Appendix-Note 2), the as-
 390 sembled community at steady state becomes more nested
 391 (Fig. Figure 3a). More service interactions increase a
 392 species' competition strength, lowering its primary ex-
 393 tinction risk. Participation in a mutualism thus deliv-
 394 ers a fitness advantage to the species receiving the ser-
 395 vice, compensating for the lower competitive strength
 396 of generalists and allowing generalists to share subsets
 397 of resources with specialists, ~~which promotes promoting~~
 398 nestedness. However increases in mutualisms also in-
 399 crease inter-species dependencies, which raises the poten-
 400 tial risk associated with losing mutualistic partners^{74,75}.
 401 While this shifting landscape of extinction risks lowers
 402 the steady state species richness of highly mutualistic
 403 communities, we do not observe a direct relationship be-
 404 tween nestedness and richness (Fig. ??).—

405 Supplementary Figure 4).

406 When we examine the dynamics of the community
 407 as a function of service interaction frequency, we ob-
 408 serve that mutualistic interactions have different effects
 409 on primary versus secondary extinction rates. Because
 410 service dependencies bolster the competitive strength of
 411 otherwise susceptible species such as trophic generalists
 412 and species with multiple predators, the rate of primary
 413 extinctions is lowered, though this effect is weak (Fig.
 414 Figure 3b). However, because mutualisms build rigid de-
 415 pendencies between species, more service interactions re-
 416 sult in higher frequencies of secondary extinctions (Fig.
 417 Figure 3c). In communities with many mutualistic inter-
 418 actions, this combined influence yields extinctions that
 419 are less likely to occur, but ~~that~~ lead to larger cascades
 420 when they do.

421 An increased rate of secondary extinctions means that
 422 the network is less robust to perturbation, which may im-
 423 pact community turnover, or persistence. If we measure
 424 persistence in terms of the proportion of time species
 425 are established in the community, we find that higher
 426 frequencies of service interactions lower average persis-
 427 tence (increased species turnover; Fig. Figure 3d). Anal-
 428 ysis of species-specific interactions reveals that it is the
 429 species that require more services that have lower persis-
 430 tence (Fig. ??).—Supplementary Figure 5). Observations
 431 of ~~Some~~ empirical systems appear to support model
 432 predictions. For example, ~~assembling plant-pollinator~~
 433 ~~long-term observations of ant-plant mutualistic~~ systems
 434 have demonstrated high rates of ~~species and interaction~~
 435 ~~turnover~~, both during the assembly process and at the
 436 steady state⁷⁶.—

437 ~~a, Structural nestedness of communities, measured~~
 438 ~~as UNODF (Unipartite Nestedness based on Overlap~~
 439 ~~and Decreasing Fill)⁹⁹. The value reported is the~~
 440 ~~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 10⁴ replicates; see Methods and Supplementary Appendix 2 for parameter values. turnover among service-receivers (plants) relative to service-donors (ants) ⁷⁶.

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^{23,24,66,77,78}. 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.

Assembly with ecosystem engineering. The concept of ecosystem engineering, or more generally niche construction, has both encouraged an extended evolutionary synthesis⁷⁹ while also garnering considerable controversy^{80,81}. Models that explore the effects of ecosystem engineering are relatively few, but have covered important ground^{31,39}. For example, engineering has been shown to promote invasion⁸², alter primary productivity⁸³, and change the selective environment over eco-evolutionary timescales^{84,85} which can lead to unexpected outcomes such as the fixation of deleterious alleles⁸⁶. On smaller scales, microbiota construct shared metabolic resources that have a significant influence on microbial communities⁸⁷, the dynamics of which may even serve as the missing ingredient stabilizing some complex ecological systems⁸⁸. ~~The soil~~ Soil is one place where these macro- and microbiotic systems intersect⁸⁹. 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^{90,91}.

We next explore the effects of ecosystem engineering by allowing species to produce abiotic modifiers as additional nodes in the ecological network (**Fig. Figure 1**). These modifier nodes produced by engineers can serve to fulfill resource or service requirements for other species. The parameter η defines the mean number of modifiers produced per species in the pool, drawn from a Poisson distribution (see Methods and Supplementary **Appendix Note 1** for details). If a species makes ≥ 1 modifier, we label it an engineer. As the mean number of modifiers/species η increases, both the number of engineers in the pool as well as the number of modifiers made per engineer increases. As detailed in Supplementary **Appendix Note 1**, multiple engineers can make the same modifier, such that engineering redundancies are introduced when η is large. When an engineer colonizes the community, so do its modifiers, which other species in the system may interact with. When engineers are lost, their mod-

ifiers will also be lost, though can linger in the community for a period of time inversely proportional to the density of disconnected modifiers in the community (see **Supplementary Note 1**).

While the inclusion of engineering does not significantly impact the structure of species-species interactions within assembling food webs (see Supplementary **Appendix Note 4** and **Fig. ??** **Supplementary Figure 6**), it does have significant consequences for community stability. Importantly, these effects also are sensitive to the frequency of service interactions within the community, and we find that their combined influence can be complex.

As the number of engineers increases, mean rates of primary extinction are first elevated and then decline (**Fig. Figure 4a**). At the same time, the mean rates of secondary extinction systematically decline and persistence systematically increases (**Fig. Figure 4b-c**). When engineered modifiers are rare ($0 < \eta \leq 0.5$), higher rates of primary extinction coupled with lower rates of secondary extinction mean that extinctions are common, but of limited magnitude such that disturbances are compartmentalized. As modifiers become more common both primary and secondary extinction rates decline, which corresponds to increased persistence. We suggest two mechanisms that may produce the observed results. First, when engineers and modifiers are present but rare, they provide additional resources for consumers. This stabilization of consumers ultimately results in increased vulnerability of prey, such that the cumulative effect is increased competitive exclusion of prey and higher rates of primary extinction (**Fig. Figure 4a**). Second, when engineers and their modifiers are common ($\eta > 0.5$) the available niche space expands, lowering competitive overlap and suppressing both primary and secondary extinctions. Notably the presence of even a small number of engineers serves to limit the magnitude of secondary extinction cascades (**Figure 4b**). Assessment of species persistence as a function of trophic in-degree (number of resources) and out-degree (number of consumers) generally supports this proposed dynamic (**Fig. ??** **Supplementary Figure 7**).

Increasing the frequency of service interactions promotes service interactions between species and engineered modifiers (**Fig. Figure 1**). A topical example of the latter is the habitat provided to invertebrates by the recently discovered rock-boring teredinid shipworm (*Lithoredo abatanica*)⁹². 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. Figure 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. Figure 4a). The cost of these added services to the community is an increased rate of secondary extinctions (Fig. Figure 4b) and higher species turnover (Fig. Figure 4c), such that extinctions are less common but lead to larger cascades.

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 previously³⁹, redundant engineering has been assumed to be unimportant⁹³. We argue that redundancy may be an important component of highly engineered systems, and particularly relevant when the effects of engineers increase their own fitness⁸² as is generally assumed to be the case with niche construction⁸⁵. 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 rare⁹³. If we consider longer timescales, diversification of engineering clades may promote redundancy, and in some cases this may feed back to accelerate diversification⁹⁴. Such positive feedback mechanisms likely facilitated the global changes induced by cyanobacteria in the Proterozoic^{42,43} among other large-scale engineering events in the history of life⁴². Engineering redundancies are likely important on shorter timescales as well. For example, diverse sessile epifauna on shelled gravels in shallow marine environments are facilitated by the engineering of their ancestors, such that the engineered effects of the clade determine the future fitness of descendants⁹⁵. In the microbiome, redundant engineering may be very common due to the influence of horizontal gene transfer in structuring metabolite production⁹⁶. In these systems, redundancy in the production of shared metabolic resources may play a key role in community structure and dynamics^{87,88}.

When there are few engineers, each modifier in the community tends to be unique to a particular engineering species. Engineering redundancies increase lin-

early with η (Supplementary Appendix Note 1; Fig. ??Supplementary Figure 8), such that the loss of an engineer will not necessarily lead to the loss of engineered modifiers. We examine the effects of this redundancy by comparing our results to those produced by the same model, but where each modifier is uniquely produced by a single species. Surprisingly, the lack of engineering redundancies does not alter the general relationship between engineering and measures of community stability (Fig. ??). Supplementary Figure 9). However we find that redundancies play a central role in maintaining species diversity. When engineering redundancies are allowed, steady state community richness S^* does not vary considerably with increasing service interactions and engineering (Fig. ??a). Supplementary Figure 10a). In contrast, when redundant engineering is not allowed (each modifier is unique to an engineer, denoted by the subscript 'u'), steady state community richness S_u^* declines sharply (Figs. Figure 4d, ??b). Supplementary Figure 10b).

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

We have shown that simple process-based rules governing the assembly of species with multitype interactions can produce communities with realistic structures and dynamics. Moreover, the inclusion of ecosystem engineering by way of modifier nodes reveals that low levels of engineering may be expected to produce higher rates of extinction while limiting the size of extinction cascades, and that engineering redundancy – whether it is common or rare – serves to promote colonization and by extension community diversity. We suggest that including the effects of engineers, either explicitly as we have done here, or otherwise, is vital for understanding the inter-dependencies that define ecological systems. As past ecosystems have fundamentally altered the landscape on which contemporary communities interact, future ecosystems will be defined by the influence of engineering today. Given the rate and magnitude with which humans are currently engineering environments⁹⁷, understanding the role of ecosystem engineers is thus tantamount to understanding our own effects on the

assembly of natural communities.

Methods

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

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

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

We then consider the assembly of a community which at any time will contain a subset of entities in the pool and always the 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 benefit⁵², specialists are stronger competitors than generalists⁵⁵, and many predators entail an energetic cost⁵⁷. 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 efficiency⁹⁸. 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 and Code availability

The code used to produce simulation data is available for download from <https://github.com/jdyeakel/Lego>.

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

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). 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.

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; measured using the R package UNODF v.1.2)⁹⁹. 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 Note 2 for parameter values.

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 Note 2 for parameter values.

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939

940 **Author contributions**

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

944

945 **Competing interests**

946 The authors declare no competing interests.

SUPPLEMENTARY METHODS

Appendix 1: Building the source pool

Here and henceforth, we refer to the assembly model presented in the main text as the ENigMa model (E:eat, N:need, Ig:ignore, Ma:make). To initiate the ENigMa assembly model, we must first construct the source pool, where each ecological entity (species + modifiers) is defined by their potential interactions. The model is initialized by creating S species and $M = \eta S$ modifiers, such that $N = S + M$ is the expected total number of entities (prior to considering engineering redundancies) and η is the expected number of modifiers made per species in the community, where the expectation 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 trophic and service interactions for both species-species and species-modifier interactions is the same.

Without engineering redundancies (i.e. each modifier that a species makes is unique), the expected number of modifiers is $M = \eta S$ where η is the mean number of modifiers made per species S . 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 $M_i \sim \text{Pois}(\eta)$. 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 modifiers, such that multiple species—with some probability—can make the same modifier, the expected number of modifiers becomes

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

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

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

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

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

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

such that the proportion of redundant modifiers ϕ is

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

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

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 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.

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 in the community that do not have a competition strength that is highest for at least one of their resources: these species are subject to primary extinction; 3) all species in the community that do not meet their eat and/or need dependencies: these species are subject to secondary extinction; 4) all modifiers in the community that no longer have an engineer: these modifiers are subject to elimination. We then select one of the four events with a probability proportional to the number of entities that satisfy the criteria for each event. The rates at which each event occurs change at each step, equal to the number of entities that meet the criteria for each event at that point in time. The species/modifier that colonizes or is eliminated from the community is randomly chosen once the event type is determined.

For example, if the community is empty, and 50 species are able to colonize, the probability of drawing ‘colonization’ is 1, and the colonizer would be randomly drawn from the 50 capable of colonizing. Another example: if 20 species are able to colonize, 10 species are not superior competitors for any one of their resources, and 30 species do not meet their dependencies, $\sum_j r_j = 60$, and $r_{\text{colonize}} = 1/3$, $r_{\text{primary extinction}} = 1/6$, and $r_{\text{secondary extinction}} = 1/2$. In this case, the most probable event is a secondary extinction. After this single event takes place, the community is updated depending on which event occurred, and the simulation proceeds to 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 efficiency⁹⁸.

Appendix 2: Model parameterizations

Simulations described in the main text have default parameterizations of $S = 200$, $p_e = 0.01$, $c_n = \pi$, $c_e = \sqrt{2}$, $c_v = 1$, and 4000 iterations (time-steps).
Assembly without ecosystem engineering Here we set the average number of modifiers made per species $\eta = 0$ and the probability of need interactions in the species pool $p_n = 0.002$.
Structure and dynamics of mutualisms Again we used the default parameterizations but set $\eta = 0$, while varying $p_n \in [0, 0.002]$.
Assembly with ecosystem engineering Here we used the default parameterizations but varied $\eta \in [0, 2]$ and $p_n \in [0, 0.002]$.

Appendix 3: Comparison to Niche Model

We compared certain structural features of ENigMa at steady state to those of the Niche Model⁵⁸. Comparisons were restricted to networks constructed in the absence of engineering because engineers introduce indirect effects that are not considered in static food web models, and may make such comparisons irrelevant. While there are many similarities, there are also some important differences, some of which are highlighted in the main text. While we consider a comparison of our framework with other food web models such as the Niche Model relevant, we emphasize that the motivations underlying both are distinct. Our approach is intended to provide a deeper understanding into how multitype dependencies between species and the environment impact the dynamics of community assembly. While capturing general qualitative features of empirical systems demonstrates that the dynamics we consider are ecologically relevant, the goal of our approach is distinct from that of static food web models, which aim to maximize structural similarities between model and empirical systems^{58?}.
We compared steady state ecological networks that emerge from ENigMa (described in Methods, main text) with food webs constructed from the Niche Model⁵⁸ with similar species richness and connectance. Because species richness and connectance of the Niche Model are often altered by eliminating disconnected species, we compared *i*) species richness, *ii*) connectance, *iii*) mean species degree, *iv*) standard deviation of out-degree distributions, and *v*) standard deviation of in-degree distributions averaged across 1000 replicates for each model.
We found that all measures resulted in fairly similar values between ENigMa and the Niche Model food webs with a some important differences (Figs. ??,??). While similar, ENigMa produces consistently lower values of connectance, mean species degree, as well as standard deviations of the in- and out-degree distributions. This means that the food webs produced by ENigMa are more sparsely connected with less variance between species. These results were expected, as the Niche Model assumes systematically increasing dietary ranges with higher niche values, whereas the trophic interactions assigned to species in the source pool of ENigMa are drawn independently.
An important difference between the Niche Model and ENigMa is that we do not distinguish between traditional consumers and parasites. A different framework known as the Inverse Niche Model[?] has been proposed to address parasitic interactions. The Inverse Niche Model assumes increasing specialization with feeding hierarchies, which would serve to lower the average generality of species (lower degree). In addition, the Inverse Niche model outputs lower standard deviations of in- and out-degree distributions. Together these trends suggest that the qualitative structural differences that we observe for the assembly and Niche model may reflect an important structural distinction between food webs that do and do not include parasitic species.

Appendix 4: The structure of engineered food webs

We examined whether and to what extent the structure of food webs was altered when engineers are introduced into the community. Because trophic links can now exist between species-modifiers as well as species-species, there are different ways of accounting for structure, making direct comparisons with non-engineered food webs somewhat difficult. We note that we exclude service interactions in this case to best match the structural analysis described in the main text and shown in Fig. 2. While the inclusion of engineers ($\eta = 2$) does have an impact on stability in terms of primary versus secondary extinction rates, there is not a strong effect of engineering on steady state species richness (Fig. ??a; species richness is shown in blue, modifier richness is shown in red).
The role of specialists *does* and *does not* change with the introduction of engineering, depending on how specialization is defined. As in the main text, a specialist is defined when its generality index $G_i < 1$ relative to the steady state link density. When engineered modifiers are included, we account for a trophic interaction between a species and another's modifier as an interaction that occurs between those two species indirectly through the modifier intermediary. So if a species B makes a modifier M , and A eats M , then we set A to (indirectly) eat B . This accounting of both direct and indirect trophic interactions between species can then be compared to *i*) the direct trophic link density of the community, or *ii*) the direct + indirect trophic link density of the community, and some insights can be gained from both approaches.
In the first case, where G_i is determined relative to L_{direct}^*/S^* , we find that there are no potential specialists that colonize the community; and (as in the main text) functional specialists colonize first, but (not as in the main text) become functional generalists at steady state (mean proportion specialists at steady state is 0.04; Fig. ??b). This means that the indirect links that define trophic interactions between species and modifiers increase the link density of the network relative to that defined only by direct trophic interactions. In words, modifiers serve to connect otherwise disconnected species, formalizing the otherwise indirect relationships that structure the role of engineers in the community. In the second case, where G_i is determined relative to $L_{\text{indirect}}^*/S^*$, we find that the changes in both functional and potential specialists over the course of assembly (Fig. ??c) follow those observed for non-engineered food webs (Fig. 2b).
Finally, we observe that while the number of trophic levels increase in the presence of species-modifier interactions, the overall trophic structure of the community advances over the course of assembly in much the same way as it does without engineers (Fig. ??d). Trophic levels are calculated with respect to indirect species interactions through modifier intermediaries. Because species at any trophic level can engineer modifiers used as resources by other species, the mean trophic level of the community is systematically elevated.

1060 $\gamma, \& \gamma, ()$.

1061 Left: Assembly of communities over time results in steady state species richness by ca. time-step 250. Right: Trophic connectance early
 1062 in assembly is high because a small number of species interact with each other such that the proportion of realized interactions (out of all
 1063 possible interactions) is closer to unity. Over time, connectance decays as species richness increases, and the density of trophic interactions
 1064 declines.

1065 Comparisons of raw structural measures for the assembly (y-axis) and Niche model (x-axis). If the models produce similar structures;
 1066 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
 1067 deviation of in- and out-degree are all lower for the assembly model relative to those measures for the Niche model.

1068 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
 1069 structural metrics for the assembly and Niche model, respectively. Only the trophic network of the assembly model was used to assess
 1070 metrics.

1071 Nestedness (UNODF) as a function of steady state richness for 1000 replicated communities without service interactions ($p_n = 0$)
 1072 compared to those with a high frequency of service interactions ($p_n = 0.002$). While higher frequencies of service interactions do lower
 1073 steady state species richness (due to increasing secondary extinction rates), there is not a relationship between nestedness and species
 1074 richness across replicates for a given service interaction frequency.

1075 Persistence as a function of trophic and service in/out-degree for communities with higher densities of service interactions
 1076 ($p_e = 0.01$; $p_n = 0.002$). Left column: species-specific persistence as a function of trophic in-degree (the number of prey a species has; top)
 1077 and out-degree (the number of predators a species has; bottom). Right column: species-specific persistence as a function of the mutualism
 1078 in-degree (the number of service receivers a species has; top) and out-degree (the number of service providers a species has; bottom). As
 1079 the trophic in- and out-degree of species increases, competition strength is lowered and persistence decreases. As the mutualism in-degree
 1080 increases, so does the number of service donors that are needed for the receiving species to remain in the community. This introduces
 1081 structural constraints that lowers persistence.

1082 **a**, Assembling communities over time from a pool of 200 non-engineering species. Species richness is blue; modifier richness is red. Steady
 1083 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
 1084 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
 1085 are direct trophic interactions between species. Diamonds represent functional (realized) trophic interactions; triangles represent potential
 1086 trophic interactions. **c**, The proportion of specialists as a function of assembly time, where a specialist is defined as a species with a
 1087 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
 1088 between species and indirect trophic interactions between consumers and those species that produce modifiers as resources. Diamonds
 1089 represent functional (realized) trophic interactions; triangles represent potential trophic interactions. **d**, The frequency distribution of
 1090 trophic levels as a function of assembly time (iterations). Autotrophs occupy $TL = 1$. Measures were evaluated across 10^4 replicates; see
 1091 Methods for parameter values.

1092 Species-specific persistence as a function of **a**, trophic in-degree (number of resources a species has; top) and **b**, out-degree (number of
 1093 consumers that eat the species; bottom) when there are no engineers in the community. Species-specific persistence as a function of **c**,
 1094 trophic in-degree (number of resources a species has; top) and **d**, out-degree (number of consumers that eat the species; bottom) when
 1095 engineers are rare ($\eta = 0.5$). The notion that having a small number of engineers and modifiers in the community increases rates of
 1096 primary extinction (Fig. 4a) by stabilizing consumers at the expense of their prey is supported by *i*) increased persistence of generalist
 1097 consumers, and *ii*) the presence of species with larger number of predators. Species-specific persistence as a function of **e**, trophic in-degree
 1098 (number of resources a species has; top) and **f**, out-degree (number of consumers that eat the species; bottom) when engineers are common
 1099 ($\eta = 2.0$). The notion that a large number of engineers and modifiers in the community decrease rates of primary extinction (Fig. 4a) due to
 1100 expanding niche space (diffusing the effects of competitive exclusion) is supported by the lack of correlation between trophic in/out-degree
 1101 and persistence.

1102 **a**, Number of redundant modifiers in the source pool as a function of the expected number of modifiers made per species η . The red
 1103 dashed line shows the analytical expectation (Eq. ??). **b**, Proportion of redundant modifiers ϕ versus the total number of modifiers in the
 1104 source pool as a function of the expected number of modifiers made per species η . The red dashed line shows the analytical expectation
 1105 of $\phi \approx 0.418$ (Eq. ??).

1106 Measures of community stability as a function of the frequency of service interactions and number of modifiers per species, where
 1107 each modifier is uniquely made by an engineer. **a**, Mean rates of primary extinction, where primary extinctions occur from competitive
 1108 exclusion of consumers over shared resources. **b**, Mean rates of secondary extinction, which cascade from primary extinctions. **c**, Mean
 1109 species persistence, defined as the percent simulation time the community is occupied by a given species, averaged across all species that
 1110 successfully colonize. **d**, The ratio S_u^*/S^* , where S_u^* denotes steady states for systems where all engineered modifiers are unique to each
 1111 engineer, and S^* denote steady states for systems with redundant engineering. Lower values of S_u^*/S^* mean that systems with redundant
 1112 engineers have higher steady states than those without redundancies. Values are averaged over 50 replicates for each parameterization.
 1113 See Methods for default parameter values.

1114 **a**, Steady state community richness with redundant engineering. **b**, Steady state community richness without redundant engineering. **c**,
 1115 Proportion of species in the source pool that colonize the community at least once throughout the simulation (with redundant engineering).
 1116 **d**, Proportion of species in the source pool that colonize the community at least once throughout the simulation (without redundant
 1117 engineering).