Pollinators in food webs: Mutualistic interactions increase diversity, stability, and function in multiplex networks

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Keywords: food webs, pollination, ecological networks, dynamics, diversity, stability, ecosystem function

ABSTRACT

Ecosystems are composed of complex networks of many species interacting in different ways. While ecologists have long studied food webs of feeding interactions, recent studies increasingly focus on mutualistic networks including plants that exchange food for reproductive services provided by animals such as pollinators. Here, we synthesize both types of consumer-resource interactions to better understand the controversial effects of mutualism on ecosystems at the species, guild, and whole-community levels. We find that consumer-resource mechanisms underlying plant-pollinator mutualisms can increase the persistence, productivity, abundance, and temporal stability of both mutualists and non-mutualists in food webs. These effects strongly increase with floral reward productivity and are qualitatively robust to variation in the prevalence of mutualism and pollinators feeding upon resources in addition to rewards. This work advances the ability of mechanistic network theory to synthesize different types of interactions and illustrates how mutualism can enhance the diversity, stability, and function of complex ecosystems.

INTRODUCTION

As elegantly illustrated by Darwin's "tangled bank," [1] ecosystems are complex, composed of many different types of interactions among many different species. However, theory has classically predicted that complexity in terms of the number and strength of interspecific interactions destabilizes ecological systems [2]. Mutualistic interactions like those between plants and their pollinators are thought to be particularly destabilizing [3,4]. Robert May famously emphasized this point by calling mutualism an "orgy of mutual benefaction" (pg. 95) [5] whose instability due to positive feedback loops helps explain why mutualism is infrequent and unimportant in natural systems [3]. Yet, mutualisms appear to be not only frequent but key to maintaining much of the biodiversity that drives ecosystems [6,7], especially agricultural ecosystems essential to human wellbeing [8,9]. Here, we address such disparities between theory and observation by developing and applying consumer-resource theory of feeding and reproductive mechanisms that integrates food webs and mutualistic networks into "multiplex" networks containing different types of interactions. We use our multiplex model to study how mutualism affects the diversity, stability, and function of complex ecosystems.

The integration pursued here benefits from long but largely separate traditions of research on feeding and mutualistic interactions [8,10]. For example, "mutualistic" feeding interactions between species with positive effects on each other (+,+), e.g. pollinators foraging on the nectar of flowering plants, are often excluded from food web data (e.g., ref [11]), while "antagonistic" feeding interactions (+, –), e.g. herbivory and predation, are typically excluded from mutualistic networks [12]. Additionally, food web research has focused more on aquatic systems [13] where feeding interactions are strongly structured by

body mass or gape size [13,14], while mutualism research has focused more on terrestrial systems where feeding interactions may be more strongly structured by other organismal traits like chemical defense and shape of mouth parts [13–15]. Within aquatic ecosystems, the allometric trophic network theory [16,17] of food webs has leveraged body-size considerations to successfully simulate the seasonal dynamics of many interacting species [18,19] and predict the quantitative effects of experimental species manipulations [20–22]. However, the failure of these predictions in the presence of facilitation (+, 0), e.g. habitat provisioning for mussels by barnacles, highlights the need for food-web theory to better address interactions with positive effects beyond nutrition [20]. Mutualistic network theory has focused on animal-mediated pollination, an interaction involving trophic and reproductive effects [12,23], motivated in part by large agricultural and evolutionary significance [9,24,25]. Merging these distinct traditions requires a more unified approach that addresses several problems.

One significant problem is that classifying interactions based on positive and/or negative effects ignores logical inconsistencies such as when "antagonistic" herbivory or predation respectively increase plant fitness [26] or prey abundance [27] and when "mutualistic" pollinators parasitize plants by robbing their floral rewards without transferring pollen [24]. We resolve such conflicts by modelling mechanisms by which organisms interact and allowing effects to emerge from the interactions rather than asserting such effects *a priori*. We do this by developing consumer-resource theory that has long been applied to food web theory [16,28] and more recently applied to mutualistic interactions [29,30] with success predicting pollinators' foraging preferences in the field [31]. Both feeding and mutualistic interactions typically involve food consumption while mutualistic interactions also often involve reproductive services provided by animals such as pollinators and seed dispersers

[27,29,30]. Positive, negative, and neutral interspecific effects dynamically emerge from the benefits and costs of participating in these interactions, which often both involve the same organisms and jointly determine much of the stability and function of ecosystems [8,10,32–36]. For example, feeding interactions such as parasitism and predation on pollinators, herbivory on animal-pollinated plants, and feeding by pollinators on animals and plant vegetation in addition to floral rewards such as nectar and pollen profoundly affect pollination dynamics, crop yields [37], and long-term sustainability of agroecosystems [38].

Another outstanding problem with understanding the joint effects of feeding and mutualistic interactions concerns contradictory conclusions of previous theoretical work. Classic "effects-based" theory has long held that mutualistic interactions are generally *destabilizing* (Table 1) especially at high complexity [3,4]. However, more recent theory finds that mutualisms *stabilize* ecological systems under conditions such as high levels of complexity of mutualism relative to antagonism in "merged" plant-pollinator and plant-herbivore networks [35,39], low levels of complexity in hierarchical networks of all types of interactions [40], or intermediate levels of mutualism when mutualistic links are randomly assigned and animals allocate effort to feeding and mutualistic interactions separately [41–43]. Contradictions among these findings may arise from different definitions of stability (i.e. local stability or persistence, Table 1) and network architectures [4,41] that often misrepresent empirically-observed structure [40]. A broader problem is that narrowly focusing on stability develops inefficient theory [44] that ignores how mutualisms alter the diversity, population dynamics, and overall functioning of complex ecosystems.

To more broadly understand the ecology of mutualistic interactions, here, we follow repeated calls to synthesize different types of interactions within networks [8,10,32–36,45] by

developing and applying mechanistic consumer-resource theory to "multiplex" ecological networks (Table 1) [34,36]. Our model based on this theory integrates the structure and dynamics of feeding and reproductive mechanisms from which effects of interspecific interactions emerge including predation (+, –), mutualism (+, +), and resource and apparent competition (–, –) [46,47]. We simulate network *dynamics* by extending Brose *et al.*'s allometric trophic network theory [16] to incorporate Valdovinos *et al.*'s theory of the exchange of food for reproductive services between plants and their pollinators (Fig. 1) [30,31]. We simulate network *structures* by integrating Williams and Martinez' "niche model" of food webs [48] with Thébault and Fontaine's model of mutualistic networks [49] (Fig. 2). Using this multiplex model, we investigate how the presence, prevalence, and intensity of mutualism affect multiple dimensions of ecological stability [50] by assessing diversity, persistence, dynamics, and function at the species, guild, and ecosystem levels.

RESULTS

The multiplex model.

We synthesize the *structure* and *dynamics* of feeding and reproductive interactions by integrating food webs and mutualistic networks and extending Allometric Trophic Network (ATN) theory [16-18,20,51] to include the consumption of floral rewards produced by plants and reproductive services produced by pollinators (Fig. 1, Methods). In addition to ATN theory's logistically growing "plants without pollinators," "plants with pollinators" in our multiplex model must consume reproductive services produced by their pollinators to vegetatively grow. This involves partitioning the biomass of plants with pollinators into coupled pools of vegetation and floral rewards [30] that plants produce at an energetic cost [33,52,53]. The vegetative growth rate of plants with pollinators is a saturating function of

129 reproductive services consumed by the plants [53] determined by the quantity (consumption
130 rate) and quality (fidelity) of pollinator visits [30] limited by community-wide carrying
131 capacity [18,51]. The foraging rates and metabolic maintenance costs of all animals including
132 pollinators scale allometrically with body size [16].

133 We integrated realistic food-web and mutualistic-network structures into multiplex
134 networks by generating 102 niche-model food webs [48] of $S_f = 50$ species including exactly
135 20 plant species (Fig. 2a, Methods) and 238 plant-pollinator networks [49] (Fig. 2b) of
136 varying species diversity ($S_p = A + P = 9, 12, ..., 57$) and empirically-observed pollinator-
137 to-plant ratio ($A/P = 2$) and ranges of connectance and nestedness (S1). We pair each food
138 web with each plant-pollinator network ($N = 102 * 238 = 24{,}276$ pairs) and add the
139 pollinators of each plant within the plant-pollinator network to its paired food web by
140 linking the pollinators to a randomly selected plant species in the food web (Fig. 2c). Our
141 Rewards Only (RO) treatment links only floral rewards to the pollinators (Fig. 2d). Our
142 Rewards Plus (RP) treatment links floral rewards, vegetative biomass, and prey (Fig. 2e) to
143 the pollinators. Pollinators are preyed upon by predators of herbivores in RO networks or
144 predators of herbivores and low trophic-level omnivores in RP networks (Fig. 2d-e). As
145 such, RO and RP treatments generate two different topological classes of multiplex
146 networks for which we generate two groups of topologically-comparable food webs (RO
147 FW and RP FW), described below.

148 Sensitivity and uncertainty analyses (S2) revealed a pivotal role of floral rewards in
149 determining ecological effects of mutualism (Tables S1-S3, Fig. S5). We illustrate this role
150 by presenting results from networks with High ($\beta = 1.0$), Low ($\beta = 0.2$), and no rewards
151 productivity (Eqn. 4). High and Low productivities apply to both RO and RP multiplex

152 networks (High RO, Low RO, High RP, Low RP) containing both feeding and reproductive
153 interactions. Treatments with no rewards productivity convert all feeding on rewards to
154 feeding on the same plants' vegetative biomass and eliminate reproductive interactions
155 resulting in networks with only traditional Food Web (FW) interactions where comparable
156 plants with pollinators in multiplex networks instead grow as plants without pollinators and
157 their former pollinators graze only on their plant partners' vegetation instead of floral
158 rewards. This conversion transforms the added pollinators in multiplex networks into
159 "added animals": herbivores in RO FW networks or herbivores and omnivores in RP FW
160 networks (Fig. 2d, 2e). These two Food Web treatments (RO FW, RP FW) control for
161 network structure, including the varying numbers and trophic levels of species and links in
162 RO and RP networks, to help elucidate the effects of mutualism in multiplex networks.

163 By integrating food webs of fixed size with plant-pollinator networks of varying
164 size, the initial diversity (S = 50 + added animals = 56, 58, ..., 88) of our 24,276 networks
165 corresponds to prevalence of herbivory in our FW treatments or prevalence of mutualism in
166 our multiplex treatments via the fraction of plants that are animal-pollinated and the
167 fraction and number of species and links directly involved in mutualistic interactions (Fig.
168 5a). This allows us to analyze our results in terms of increasing initial diversity (S) for all
169 treatments and increasing *prevalence* of mutualism for multiplex treatments. The *intensity*
170 of mutualism in our treatments varies with rewards productivity (Table 1) from high (High
171 RO, High RP) to low (Low RO, Low RP) to none (RO FW, RP FW). We simulate the
172 24,276 networks subjected to these six treatments by initializing each species and pool of
173 rewards with a biomass of 10 and recording results after 5000 timesteps when species have
174 persisted or gone extinct and system dynamics are at, or close to, steady-state (Table 1, Fig.

175 3). We use these results to compare multiple measures of stability and function among
176 treatments averaged over all initial diversity classes (Fig. 4) or within initial diversity
177 classes (Figs. 5-6) at the species, guild, and ecosystem levels (Table 1). Below, we
178 describe the effects of the presence, prevalence, and intensity of mutualism first on
179 biodiversity, then on ecosystem function, and finally on temporal stability.

180 **Diversity.**

181 Multiplex networks with High rewards productivity (High RO, High RP) had higher
182 average diversity (Fig. 4a) and persistence (Fig. 4b) than their counterparts with less (Low
183 RO, Low RP) and no rewards productivity (RO FW, RP FW). Diversity and persistence
184 were also slightly elevated in the Low RP compared to the corresponding RP FW
185 treatment. Persistence decreased with increasing initial diversity and prevalence of
186 mutualism in all treatments except High RO (Fig. 5c). However, these decreases were not
187 strong enough to prevent overall increased final diversity (Fig. 5b) with increased initial
188 diversity and mutualism (Fig. 5a) in all treatments. These results indicate that effects of
189 mutualisms on biodiversity depend both on the prevalence and intensity of mutualism
190 expressed as rewards productivity.

191 Since all 20 plant species nearly always persisted in all treatments (Fig. S1),
192 differences in animal persistence among treatments underlie the overall patterns in
193 diversity. Most notably, relatively high and increasing persistence of omnivores with
194 mutualism (Fig. 5e) and consistently high persistence of added pollinators (Fig. 5f-g)
195 doubled animal diversity in High RO and High RP treatments over that in FW, Low RO,
196 and Low RP treatments (Fig. 5b). The few carnivores (~3 initial species) made smaller
197 contributions to elevated diversity in High rewards treatments via substantial increases in

198 persistence with increasing mutualism (Fig. 5d). In contrast, FW and Low rewards
199 treatments had much lower persistence of carnivores (Fig.5d), omnivores (Fig. 5e), and
200 added animals (Fig. 5f-g) that, except for carnivores, decreased with increasing mutualism.
201 In the High RO treatment, the few herbivores (~5 initial species) achieved higher
202 persistence than in the corresponding FW (Fig. 5h). However, in the other multiplex
203 treatments (Low RO, Low RP, High RP), herbivore persistence was lower and declined
204 dramatically with increasing mutualism.

205 **Function.**

206 Similar to final diversity, the total biomass (Fig. 4c), productivity (Fig. 4d), and
207 consumption in all multiplex treatments were comparatively higher than in FW treatments
208 with some exceptions in the Low RO treatment. Specifically, biomass was up to twice as
209 high while productivity and consumption were up to an order of magnitude higher in
210 multiplex compared to FW treatments. The Low RO treatment also had higher biomass,
211 but lower diversity, productivity, and consumption than the corresponding RO FW
212 treatment (Fig. 4). Overall, this indicates that both the presence and intensity of pollination
213 mutualisms increase key measures of ecosystem function.

214 In all treatments, total biomass (Fig. 6b), productivity (Fig. 6c), and consumption
215 (Fig. 6d) increased with initial diversity and prevalence of mutualism, with the strongest
216 increases occurring in the High rewards treatments. Plant biomass substantially decreased
217 below carrying capacity (Fig. 6b) with increasing initial diversity in all but Low RO
218 treatments, but these decreases were strongly compensated for by increases in the biomass
219 of animals and floral rewards. As might be expected, biomass and productivity of
220 pollinators, plants with pollinators, and rewards increased with increasing mutualism in

multiplex treatments. Concurrently, plant productivity increased with initial diversity and mutualism in all but Low RO treatments. Total consumption (Fig. 6d) in all treatments very closely matched total production (Fig. 6c) and was distributed similarly to that of animal species' biomass (Fig. 6b).

The higher biomass of multiplex compared to FW treatments was primarily due to increases in animal biomass (Fig. 6b), while differences in productivity were due to decreases in vegetative productivity coupled with strong increases in productivity of rewards and smaller increases in animals (Fig. 6c). These differences emerge primarily due to the interactive dynamics of rewards in which growth potential, unlike all other stocks of biomass, depends not on its own abundance but on the abundance of another component, i.e., the vegetative biomass of plants with pollinators (Methods, Eqn. 6). This allows rewards to be highly productive even when very rare whereas other network components would be unproductive or could even go extinct. In FW treatments, the overall weak increases in ecosystem biomass and strong increases in total productivity with increasing initial diversity emerge from increasing herbivore biomass that reduces plant vegetation below carrying capacity (Fig. 6b), freeing plants from competition. This increases plant productivity (Fig. 6c) and animal biomass enough to lead to small net increases in total biomass with initial diversity (Fig. 6b). Multiplex treatments experience similar decreases of plant biomass and corresponding increases in vegetative plant productivity (Fig. 6b-c), but rewards productivity dramatically increases as does animal biomass. These increases are mostly due to increases in pollinator abundance that stimulate rewards productivity by depleting rewards below their self-limitation threshold. Then, animal biomass and productivity are further elevated by increases in the biomass of omnivores and carnivores

that feed on the increasingly abundant pollinators. These patterns in production, consumption, and increased animal biomass are greatly enhanced in High rewards treatments.

Stability.

We evaluated the temporal stability of our networks by analyzing coefficients of variation (CV = standard deviation / mean) of biomass during our simulations' final 1000 timesteps for each species, for the sum of each species within each guild (Fig. 6f), and for the sum of each species within the ecosystem. We calculated a species-level CV for each guild by summing each species' CV within the guild and dividing by the number of species in the guild (Fig. 6e) and a species-level CV for each ecosystem by doing the same thing for all species within the network (Fig. 4e). We calculated a guild-level CV for each guild as the CV for the total biomass in each guild (Fig. 6f), and a guild-level CV for each ecosystem by summing all guilds' CVs and dividing by the number of guilds (standardized across treatments, Fig. 4f). Finally, we calculated an ecosystem-level CV as the CV of the total biomass of the ecosystem.

At the ecosystem level, all treatments were exceedingly stable (CV < 0.001). In contrast, species on average were much more variable (Fig. 4e), especially in Low rewards treatments where plants with pollinators and their rewards contributed large amounts of variability (Fig. 6e). Large variability in plant and reward biomass in multiplex treatments was caused by the very low biomass of a few plant with pollinators species whose biomass decreased throughout the end of the simulations (e.g. Fig. 3). This low and decreasing biomass yields large CVs at the species level but contributes very little to guild-level variation (Fig. 6e-f) due to the tiny fraction of their guild's biomass comprised by these

very rare species. In FW treatments, where extinctions occur relatively early (Fig. S2), species-level and guild-level variation are comparable (Fig. 4e-f). In contrast, average guild-level variation (Fig. 4f) is only a fraction of the species-level variation (Fig. 4e) in multiplex treatments. Variation at both the species and guild levels decrease with initial diversity and mutualism in all treatments except for species-level variation in High RP networks where large decreases in animal variability only partly compensate for larger increases in rewards variability (Fig. 6e-f). High RP networks are by far the most stable at the guild level however, both on average (Fig. 4f) and with increasing mutualism (Fig. 6f). Overall, mutualism broadly stabilizes the dynamics of multiplex networks by reducing variability of animal populations compared to those in FWs.

Overall effects of mutualism.

Excepting Low RO networks, multiplex treatments had higher average diversity, persistence, biomass, productivity, and consumption than their FW counterparts (Fig. 4). Multiplex treatments were also more temporally stable than FW treatments at the guild level and, for animal populations, at the species and guild levels. Interestingly, though Low RO networks displayed lower average diversity, persistence, productivity, and overall species-level stability than FW treatments, these effects were ameliorated in Low RP networks, in which pollinators had additional food available to them in the form of plant and animal resources. This suggests that the positive effects of mutualism are reasonably restricted to systems that provide sufficient food for mutualistic animals to survive (also see S2) and that the low persistence of the many added pollinators in Low RO networks (Fig. 5g) throttles the positive effects of mutualisms from more generally increasing ecosystem diversity, function, and stability beyond that of FW treatments. These observations indicate

290 that intensity of pollination mutualisms in terms of rewards productivity is critical to
291 positive effects of mutualism on ecosystems.

292 **Mutualistic feedbacks.**

293 We studied the degree to which mutualistic feedbacks affect ecosystems beyond
294 broadly providing food for animals by developing "feedback controls." At steady-state of
295 the multiplex simulations, plants' production of rewards interacts with their vegetative
296 production and their pollinators' consumption. These interactions emerge from the
297 dynamic feedbacks between plants and pollinators whereby plants produce rewards, which
298 pollinators consume while providing reproductive services, which increase vegetative
299 growth rate, which affects vegetative biomass, which affects rewards productivity, etc. (see
300 Fig. 1). Our feedback controls are non-mutualistic systems initialized with rewards and
301 forced to produce rewards at rates seen in a steady-state mutualistic system, but without the
302 mutualistic feedbacks (blue arrows in Fig. 1 removed). This allows us to test whether the
303 additional biomass produced by plants with pollinators is the sole cause of diversity,
304 stability, and function in our multiplex networks or whether sustained plant-pollinator
305 feedbacks are required for these effects (Methods, S3).

306 The overall ecosystem diversity, persistence, biomass, and productivity in our
307 feedback controls equilibrate to similar values as in the multiplex simulations (Fig. S7).
308 However, ecosystem *composition* in controls differed from that of multiplex treatments.
309 Eliminating dynamic feedbacks increased vegetative biomass of plants with pollinators,
310 decreased biomass of plants without pollinators, and decreased persistence and biomass of
311 omnivores and herbivores (Fig. S8). These guild-level differences were tiny in the High RP
312 treatment but much larger in the RO and Low RP treatments. This pattern suggests that the

313 combination of sufficient rewards productivity and increased trophic connectedness of
314 mutualists in High RP networks dampen mutualistic feedback effects.

315 Overall, our results suggest that the added productivity of mutualistic rewards drive
316 our observations of ecosystem stability and function in the multiplex treatments (see S2).
317 However, our results also suggest that the *dynamics* of mutualistic feedbacks alter the
318 composition of ecosystems by increasing biomass and persistence of consumers,
319 particularly omnivores, and decreasing biomass of plants with pollinators.

320 DISCUSSION

321 Our investigation of the effects of mutualism on the diversity, stability, and
322 ecosystem function of realistically complex ecological networks used six treatments that
323 varied the intensity (no, low, and high productivity of floral rewards) and prevalence
324 (number and fraction of species directly involved in mutualisms) of mutualistic interactions
325 between plants and their pollinators that either ate only floral rewards (rewards only, RO)
326 or other sources of biomass in addition to floral rewards (rewards plus, RP). We found that
327 adding more intense mutualisms strongly increases diversity, persistence, productivity,
328 consumption, biomass, network complexity (number of species and interactions), and the
329 temporal stability of biomass over that in networks with weaker or no mutualisms (Fig. 4).
330 With a few exceptions, these effects increased with the prevalence of both strong and weak
331 mutualisms (Fig. 5-6). Perhaps most strikingly, overall persistence increased with the
332 prevalence of strong mutualisms involving RO pollinators (Fig. 5c, High RO). Temporal
333 stability more generally increased in all six treatments with diversity and prevalence of
334 mutualism at the levels of species (Fig. 6e) and guilds (Fig. 6f) except for the slightly
335 negative relationship at the species-level in networks with strong mutualisms involving RP

336 pollinators (Fig. 6e, High RP). With one exception (Low RO productivity), networks with
337 the most prevalent mutualistic interactions had higher abundance (Fig. 6b), productivity
338 (Fig. 6c), and guild-level stability (Fig. 6d) than in corresponding networks with no
339 mutualism.

340 These increases of stability and function due to increases in mutualism are broadly
341 consistent with empirical observations of the effects of increased pollinator diversity in
342 blueberry, watermelon, and other agroecosystems [54–57]. Though consistent with empirical
343 observations, our results are unexpected in light of classic theory that mutualism decreases
344 stability to small perturbations around assumed equilibria [2–4], which we did not asses.
345 Instead, we more comprehensively addressed both stability in terms of diversity,
346 persistence, and biomass variability and also function in terms of productivity,
347 consumption, and biomass abundance at species, guild, and ecosystem levels of
348 organization (Table 1) [50]. Mutualism tends to increase stability and ecosystem function
349 according to *all* of our measures in treatments with stronger mutualistic interactions and by
350 several metrics in treatments with weaker mutualisms (Fig. 4).

351 Examining our results in more detail indicates that these strong positive effects of
352 mutualism on ecosystems emerge because mutualistic rewards at Low and even more so at
353 High productivity levels stabilize ecological networks by increasing persistence of
354 omnivores (Fig. 5e), omnivorous pollinators (Fig. 5f), and carnivores (Fig. 5d) above that
355 of comparable species in food webs of only feeding interactions (FW treatments). In
356 contrast, pollinators that only consume rewards (RO treatments) exceed the persistence of
357 comparable herbivores in FW treatments at High rewards productivity only. Our feedback
358 controls show that these positive effects of mutualism are not fully reproduced by

traditional food web dynamics when supplementing food webs with rewards productivity similar to that in multiplex networks. The removal of dynamic feedbacks between pollinators and animal-pollinated plants alters species composition and abundance by reducing persistence and abundance of omnivores but increasing abundance of plants formerly dynamically partnered with pollinators (Fig. S7-8). Thus, the combination of dynamic feedbacks and mutualistic interaction strength, in terms of rewards productivity, lead to the increased stability and function we observed in our multiplex ecological networks.

Our theory embraces Levin's assertion that "The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns" (p.1943) [58] by using trophic and reproductive mechanisms underlying the observed structure and dynamics of multiplex networks to understand and predict how mutualism affects complex ecosystems. Previous theory obscures key dynamics of such mechanisms by assuming their effects [23,47,59]. For example, the few studies of ecological networks involving both feeding and mutualistic interactions assert species have constant per-capita direct effects on each other's fitness or abundance [36,45]. Such effects can rarely be reproducibly measured due to, e.g., context-dependence and temporal variability [59,60]. We instead focused on mechanisms such as more reproducibly observed rates of production and consumption of food in terms of biomass [18,61] and reproductive services in terms of pollinator visits [36]. We also focused on more realistic (i.e., empirically-corroborated) network architectures – as have others with results similar to ours. For example, García-Callejas *et al*. [40] found that mutualism increases or leaves unaffected persistence of ecological networks containing different types of interactions structured according to realistic species abundance

distributions among different trophic levels. Several studies of near-equilibrium stability similarly find that destabilizing effects of mutualism may be overstated in models of fewer species [32] and interaction types [41] compared to more realistic ecological networks. However, unlike studies that require the "peculiar" constraint that animals' interaction efforts are allocated separately between mutualistic and non-mutualistic interactions [41–43], we find that mutualism is stabilizing according to empirically-relevant metrics (Table 1) when unpartitioned effort is allocated to both types of interactions.

Our multiplex treatments may bound the diet breadth of pollinators in the field by providing pollinators unrealistically few resources in RO networks and unrealistically many resources in RP networks. This suggests results intermediate between RO and RP networks may best predict empirical observations. For example, in both RO and RP treatments, High rewards productivity increases the persistence, biomass, and productivity on average of all consumer guilds over that in Low rewards networks (Figs. 5d-h, 6b-c) excepting the decrease in herbivore persistence in RP networks (Fig. 5h). This suggests that, in natural systems, we may expect the weakest increases in persistence, biomass, and productivity due to increased mutualism to occur among herbivores. The different effects of our treatments on herbivores may be due to RP pollinators' additional herbivorous and carnivorous feeding links compared to RO pollinators. These additional links increase competition and predation pressure on herbivores by pollinators, omnivores, and carnivores. More broadly, our results suggest that, as the prevalence of pollination mutualisms increase, the diversity and biomass of upper trophic-level consumers will increase while our predictions for the effects on herbivores are less certain.

404 Key limitations of our work concern how the network architecture and bioenergetic
405 parameters in our models match those seen in nature. While the multi-trophic and
406 mutualistic components of our multiplex network structures correspond to empirical
407 patterns, we lack observations of their interconnection into multiplex networks with which
408 to test against our simulated networks [8,45], though recent multiplex networks for rocky
409 intertidal systems that include facilitation suggest progress in this direction [36]. Regarding
410 dynamics, the metabolic rates of animals should be better related to the intrinsic
411 productivities of plants. Most such estimates come from aquatic ecosystems that often
412 differ from those in aboveground terrestrial systems [13,14]. The cryptic yet critically
413 important rates determining reward availability are also only rarely estimated. For
414 example, Baude *et al.* [62] suggest that nectar productivity of meadows in the UK can be up
415 to ~5-10% of net primary productivity and Adgabe *et al.* [63] estimate nearly 1000 kg/ha of
416 floral sugar is produced in a 5-month flowering season by a single tree species. Pollen
417 production may significantly increase such estimates and accounting for seasonality of
418 reward production and pollinator activity could greatly decrease estimates of resource
419 demand needed to sustain pollinators. This highlights the need for improved theory of
420 seasonal effects on both food webs [18] and mutualistic networks [64]. Bioenergetic costs of
421 reward production compared to vegetation production should also be considered.
422 Accounting for such anabolic efficiencies greatly increased the ability of allometric trophic
423 network theory [16,18,20] to predict realistic stocks and flows of carbon and energy in complex
424 food webs [18,65]. Compared to the relatively complex compounds that comprise vegetative
425 biomass, efficiencies of synthesizing simple sugars that provide nearly all the usable energy
426 in nectar may be much higher. Such efficiencies are suggested by estimates for animals
427 that indicate, for example, the energetic efficiency of producing milk is almost six times

428 than that of beef [66]. Attending to these less studied aspects of the structure and function of
429 multiplex networks may advance research on networks including plants and pollinators as
430 well as those involving coral, mycorrhizal fungi, and frugivores that disperse seeds, all of
431 which involve the exchange of autotrophic food for increased growth of primary producers.
432 More broadly, our theoretical development shows how non-trophic effects can more
433 generally include effects that directly depend on interaction *dynamics*, such as quality and
434 quantity of pollinator visits, in addition to depending on the abundance of interactors as in
435 previous work [10,40,41,67].

436 We have advanced theory on multiplex networks in order to explore the effects of
437 mutualism on ecological systems. Our focus on reproductive interactions follows previous
438 extensions of allometric trophic network theory involving plant nutrients [20], detritus [18],
439 ontogenetic niche shifts [68], environmental stochasticity [69], fishing [51,68], economics [51] and
440 other non-trophic effects [67] integrated into food webs comprised of feeding interactions
441 distinguished by their relative body sizes [16] such as diseases [11], parasites [11,70], parasitoids [11],
442 and predators [13]. Such integration of multiple interaction types into multiplex networks is
443 increasingly recognized as an effective means of accommodating different mechanisms
444 responsible for ecosystem structure and function [8,10,36,67]. Our application to mutualistic
445 mechanisms finds a striking ability of mutualism to enhance ecosystems including their
446 diversity, stability, and function when mutualistic rewards suffice to sustain mutualistic
447 partners. Further work incorporating mutualism into multiplex network theory (e.g.
448 mutualisms between zooxanthellae and coral polyps or plants and mycorrhizal fungi) may
449 illuminate whether mutualisms more generally enhance other systems. Such research
450 would help compensate for ecologists' emphasis on competition by elucidating the much

451 less studied roles of mutualistic and other facilitative interactions [24] in biodiversity
452 maintenance [6], ecosystem function [7], and evolution [25].

453 METHODS

454 **Network architecture.**

455 We created multiplex networks (Fig. 2) by generating food webs using the "niche
456 model" (Fig. 2a) parameterized with 50 species ($S_f = 50$) and 10% directed connectance (C_f
457 $= L_f / S_f^2 = 0.1$ where L_f is the number of feeding links) [48]. The niche model stochastically
458 assigns each species i three traits: (1) a niche value (n_i) drawn randomly from a uniform
459 distribution between 0 and 1, (2) a feeding range (r_i) where $r_i = xn_i$ and x is drawn from
460 randomly from a beta distribution with expected value $2C_f$, and (3) a feeding centre (c_i)
461 drawn randomly from a uniform distribution between $r_i/2$ and $min(n_i, 1 - r_i/2)$. Species i
462 feeds on j if n_j falls within i's feeding interval $[c_i - r_i, c_i + r_i]$. We selected niche-model
463 food webs with $0.0976 < C_f < 0.1024$ that were comprised of 50 species ($S_f = 50$), of which
464 exactly 20 were plants and five were herbivores that only feed on plants (i.e. have trophic
465 level [TL] = 2), yielding 102 food webs. We also generated plant-pollinator networks
466 using a stochastic model [49] with 3 to 19 plant-with-pollinator species (P) and exactly twice
467 as many animal-pollinator species ($A = 2 * P$) to maintain pollinators' average resource
468 availability in networks of increasing diversity. This yielded approximately 14 networks
469 within each of 17 diversity classes ranging from 9 to 57 species ($S_p = P + A = 9, 12, \ldots, 57$)
470 for a total of 14 * 17 = 238 plant-pollinator networks that covered the empirically observed
471 range of nestedness (Fig. 2b, see S1 for more details). We constrained the number of
472 pollination links (L_p) to ensure that pollination connectance ($C_p = L_p / PA$) broadly
473 decreased as S_p increased in an empirically realistic manner (Fig. S4a). We integrated each

474 of the 238 plant-pollinator networks with one of the 102 food webs yielding $N = 238*102 =$
475 24,276 networks of increasing species diversity ($S = S_f + A = 56, 58, \ldots, 88$). We did this
476 by randomly choosing P of the 20 plant species already in the food web and assigning the A
477 pollinators to those P plant species as determined by the plant-pollinator network (Fig. 2c).
478 This leaves $20 - P$ plant species without pollinators.

479 We linked pollinators to consumers in the food web in Rewards Only (RO)
480 treatments by setting each pollinator's n_i to +/– 5% of the n_i of a randomly selected (i.e.,
481 non-omnivorous) strict herbivore (TL = 2) from the food web (Fig. 2d). Pollinators' r_i and
482 c_i were set to zero. This causes pollinators to be preyed upon by predators similar to
483 predators of herbivores and to consume only floral rewards as determined by the plant-
484 pollinator network. Because the connectance (C_p) of our simulated plant-pollinator
485 networks decreases with increasing diversity (S_p) and pollinators have no other resources in
486 RO networks, connectance ($C = L/S^2$, where L is the total number of links) decreases on
487 average from 0.091 to 0.06 as initial species diversity (S) increases from 56 to 88 in the RO
488 multiplex and corresponding Food Web (FW) treatments (Fig. S3). The Rewards Plus (RP)
489 treatments link herbivorous and omnivorous pollinators to food webs (Fig. 2e) by setting
490 each pollinator's n_i, r_i and c_i to +/-5% of the corresponding n_i, r_i and c_i of a randomly
491 selected herbivore or omnivore that eats plants ($2 \leq \text{TL} \leq 2.3$). This procedure maintains a
492 constant average connectance ($C = 0.102$) with increasing S (Fig. S3) among RP networks.
493 Feeding on both vegetation and floral rewards of the same plant species allows two links
494 between plants and pollinators in RP networks. The corresponding FW treatment has
495 slightly less C than the RP multiplex network because the FW eliminates the link to

496 rewards and maintains only the herbivory link (Fig. 2d, Fig. S3). We ignore this issue to
497 simplify comparisons between all treatments.

498 Overall, as initial species diversity (*S*) increases, plants with pollinators in the
499 multiplex networks increase from 3 to 19 of the 20 total plant species and mutualistic
500 interactions increase from directly involving 16% to 65% of species in the networks.
501 Correspondingly, initial herbivory in Food Web (FW) treatments increases from directly
502 involving approximately half to three quarters of the species in the networks. We thus
503 analyze how networks vary with *increasing initial diversity*, which corresponds to
504 *increasing prevalence of mutualism* in multiplex treatments or *increasing herbivory* in FW
505 treatments.

506 **Network dynamics.**

507 To model multiplex dynamics, we extended Allometric Trophic Network (ATN)
508 theory [16,18,20,51] by integrating a consumer-resource approach to pollination mutualisms in
509 which pollinators feed on floral rewards (*R*) and plants consume reproductive services
510 produced by plants [30,31]. Plants benefit from pollinators depending upon on the quantity
511 and quality of pollinators' visits in terms of the rate at which pollinators consume plants'
512 rewards and the fidelity of pollinators' visits to conspecific plants [30,31]. Pollinators in RP
513 treatments also feed on species' biomass according to ATN theory.

514 More specifically, ATN theory models the change in biomass B_i over time t for
515 consumer i as

516 $$\frac{dB_i}{dt} = \sum_{j \in resources} C_{ij}(B_j) - x_i B_i - \sum_{j \in consumers} C_{ji}(B_i)/e_{ji} \qquad (1)$$

where x_i is the allometrically-scaled mass-specific metabolic rate of species i and e_{ji} is the assimilation efficiency of species j eating i. C_{ij} is the rate of species i assimilating B_j, the biomass of species j:

$$C_{ij}(B_j) = x_i y_{ij} B_i F_{ij}(B_j) \quad (2)$$

where y_{ij} is the maximum consumption rate per metabolic rate. $F_{ij}(B_j)$ is the functional response of i eating j:

$$F_{ij}(B_j) = \frac{\omega_{ij} B_j^h}{B_{0ij}^h + \sum_{k \in resources} \omega_{ik} B_k^h} \quad (3)$$

where ω_{ij} is i's relative preference for j, h is the Hill coefficient [71], and B_{0ij} is the "half-saturation" density of resource j at which i's consumption rate is half y_{ij} [18]. The form of the preference term, ω_{ij}, determines if a trophic generalist (i) is treated either as a "strong generalist" ($\omega_{ij} = 1$) or "weak generalist" ($\omega_{ij} = 1/$(# of species in i's diet) [72]. Here, we present results only for weak generalists that search for each of their resources equally even if one or more of their resources are extinct. Eqn. 3 is a Type II functional response when $h = 1$ and a Type III response when $h = 2$. We use $h = 1.5$ for a weak Type III response [71].

We use ATN theory's logistic growth model [18] to simulate biomass dynamics of plants without pollinators as:

$$\frac{dB_i}{dt} = \left(1 - \frac{1}{K}\sum_{j \in plants} B_j\right) r_i B_i - \sum_{j \in consumers} C_{ji}(B_i)/e_{ji} \quad (4)$$

where r_i is the maximum mass-specific growth rate of plant i, and K is the carrying capacity of the plant community. For plant with pollinators i (Fig. 1), we model its vegetative biomass dynamics as:

537 $$\frac{dB_i}{dt} = \left(1 - \frac{1}{K}\sum_{j\in plants} B_j\right) r_i B_i P(R_i) - \sum_{j\in consumers} C_{ji}(B_i)/e_{ji} - \kappa_i(\beta_i B_i - s_i R_i) \quad (5)$$

538 and the dynamics of its floral rewards biomass as:

539 $$\frac{dR_i}{dt} = \beta_i B_i - s_i R_i - \sum_{j\in pollinators} C_{ji}(R_i)/e_{ji} \quad (6)$$

540 where β_i is the production rate of floral rewards, s_i is the self-limitation rate of floral reward
541 production, and κ_i is the cost of producing rewards in terms of total vegetative growth.
542 $P(R_i)$ is the functional response describing how benefit to i accrues due to reproductive
543 services provided by i's pollinators:

544 $$P(R_i) = f\overbrace{\left(\sum_{j\in pollinators} \overbrace{C_{ji}(R_i)}^{quantity} \overbrace{\frac{C_{ji}(R_i)}{\sum_{k\in resources} C_{jk}(B_k \text{ or } R_k)}}^{quality}\right)}^{reproductive\ services} \quad (7)$$

545 which is a function of the quantity and quality of pollination visits by pollinator j. Quantity
546 is j's consumption rate on i's floral rewards. Quality is j's consumption of i's rewards as
547 compared to j's consumption of all the resources it consumes. Quality is therefore j's
548 relative consumption rate of i's floral rewards, a measure of j's fidelity that ensures more
549 specialist pollinators typically provide higher quality services than generalist pollinators by,
550 for example, depositing higher concentrations of conspecific pollen [30]. The form of the
551 functional response describing benefit accrual due to pollination (f) reflects the assertion
552 that reproductive services saturate [53] at 1 according to: *reproductive services* / (0.05 +
553 *reproductive services*). As $P(R_i)$ approaches 1, the realized growth rate of plant with
554 pollinators i's vegetative component approaches r_i, its maximum growth rate.

555 Pollinators follow the dynamics typical of ATN consumers (Eqn. 1) with the
556 exception that they access rewards biomass R_i instead of B_i in RO treatments (Eqn. 1-1) or
557 in addition to the biomass of other resource species (Eqn. 1-2) in RP treatments:

558 $$\frac{dB_i}{dt} = \sum_{j \in resources} C_{ij}(R_j) - x_i B_i - \sum_{j \in consumers} C_{ji}(B_i)/e_{ji} \quad (1\text{-}1)$$

559 $$\frac{dB_i}{dt} = \sum_{j \in resources} C_{ij}(R_j \; and \; B_j) - x_i B_i - \sum_{j \in consumers} C_{ji}(B_i)/e_{ji} \quad (1\text{-}2)$$

560 **Parameterization.**

561 Vital rates for consumers follow previously described allometric scaling for
562 invertebrates [51]. Specifically, we set plant species' "body mass" to a reference value (m_i =
563 1) [16] and calculated consumers' body mass as $m_i = Z_i^{swTLi-1}$, where $swTL_i$ is i's short-
564 weighted trophic level [73] and Z_i is i's average consumer-resource body size ratio sampled
565 from a lognormal distribution with mean = 10 and standard deviation = 100. Then, for i
566 eating j, i's mass-specific metabolic rate (x_i) is $0.314m_i^{-0.25}$, its maximum consumption rate
567 per metabolic rate (y_{ij}) is 10, and its assimilation efficiency (e_{ij}) is 0.85 if j is an animal or
568 0.66 if j is plant vegetation. We set the maximum mass-specific growth rate (r_i) of plant i
569 to be 0.8 for plants without pollinators or 1.0 for plants with pollinators, so that when
570 sufficient reproductive services are provisioned by pollinators, the mass-specific growth
571 rate of plants with pollinators is comparable or can even exceed that of the plants without
572 pollinators.

573 The remaining parameters are not allometrically constrained. We assigned a "half-
574 saturation" density for consumers of species' biomass or rewards of B_0 = 60 or 30,
575 respectively. This reflects the decreased "handling time" for rewards compared to typically
576 more defended vegetation. We also assigned a Hill coefficient of h = 1.5, a community-

wide carrying capacity for plant vegetative biomass of $K = 480$, and an assimilation efficiency of $e_{ij} = 1.0$ for pollinator species i consuming the floral rewards of j. For plants with pollinators, we used a rewards production rate of $\beta_i = 0.2$ or 1.0 (Low or High rewards productivity treatments, respectively), a self-limitation rate of $s_i = 0.4$, and a vegetative cost of rewards production of $\kappa_i = 0.1$. In FW treatments, rewards are zeroed out ($R_i = \beta_i = 0$) and all plants are parameterized so that they behave as plants without pollinators while pollinators are parameterized as "added animals" (herbivores or omnivores) that consume vegetation with the associated lower assimilation efficiency ($e_{ij} = 0.66$) but have otherwise unchanged vital rates. See Table S4 for a summary of model parameters and values.

Simulations.

We simulated each of our $N = 24{,}276$ networks subjected to each six treatments (High RO, Low RO, RO FW, High RP, Low RP, and RP FW) for a total of 145,656 simulations. We used MATLAB's [74] differential equation solvers (ode15s for the multiplex treatments and ode45 for FWs) to simulate these networks for 5000 timesteps (Fig. 3). By 2000 timesteps, the simulations were approximately at dynamical steady-state, which we assessed through small changes in persistence with increased simulation length. More specifically, persistence decreased by 5% on average between 2,000 and 500,000 timesteps in a sample of 90 networks from each treatment (Fig. S2). We initialized all biomasses (B_i and R_i) to 10 and used an extinction threshold of $B_i < 10^{-6}$. Statistical analyses were performed in JMP 14 [75]. Our results are qualitatively robust to simulation length (Fig. S2). Sensitivity of our results to parameter variation are reported in the Supplementary Information (Tables S1-S3) and qualitative effects of each parameter are summarized in Table S2.

Outputs.

We quantified ecosystem stability and function using species persistence, biomass, productivity, consumption, and variability at or near the end of the simulations, when the dynamics were approximately at steady state (Table 1). We calculated these metrics for the whole ecosystem (Fig. 4) and for seven guilds of species (Figs. 5-6). Two guilds are self-evidently described as species of plants without pollinators and plants with pollinators. Herbivores, omnivores, and carnivores refer only to species present in the niche-model food webs prior to integrating animals from plant-pollinator networks in Fig. 2c. Herbivores eat only vegetative biomass. Omnivores eat vegetation and animals. Carnivores eat only animals. The meanings of the two remaining guilds (collectively referred to as the "added animals") depend on the treatment that adds them to the food web. Added herbivores/pollinators refer to herbivores added by the FW treatments, pollinators added by the RO or RP multiplex treatments that consume only rewards, and pollinators added by the RP multiplex treatment that consume rewards and vegetation. Added omnivores/pollinators refer to omnivores added by the RP FW treatment and analogous pollinators added by the RP multiplex treatment that consume rewards, other animals, and potentially vegetation. When relevant (e.g. in Fig. 6), we considered the rewards biomass of all plants with pollinators as an eighth guild.

We calculated all outputs at the end of the simulations (timestep 5000) except for biomass variability, which we calculated over the last 1000 timesteps. Final diversity and persistence are the *number* and the *fraction*, respectively, of the initial species whose biomass stayed above the extinction threshold throughout the simulation. Biomass abundance, productivity, and consumption are calculated as summed totals for the whole

ecosystem and/or each guild of species. Plant productivity is the rate of biomass increase due to growth minus loss due to rewards production. Rewards productivity is the rate rewards production minus self-limitation. Animal productivity is the rate of biomass increase due to assimilation minus losses due to metabolic maintenance. Consumption is the rate of biomass assimilated by consumers divided by assimilation efficiency. Species-level variability for the whole ecosystem (Fig. 4e) is the averaged coefficients of variation of biomasses (CV = standard deviation / mean) of all surviving species in the ecosystem. Species-level variability for each guild (Fig. 6e) is the averaged CVs of all surviving species within that guild. Guild-level variability for each guild (Fig. 6f) is the CV of the summed biomass of all species in that guild. Guild-level variability of the whole ecosystem (Fig. 4f) is the averaged CVs for five guilds (all plants, herbivores, all added animals, omnivores, and carnivores), which standardizes the grouping of species into guilds across treatments. Ecosystem-level variability (not shown) is the CV of the summed biomass of all species in the ecosystem.

Feedback control.

To disentangle effects of mutualistic feedbacks from effects of floral rewards, we ran multiplex simulations with mutualism "turned off" ("feedback control"), in which all feedbacks (blue arrows in Fig. 1) between vegetation, rewards, and pollinators are severed. This control transforms plants with pollinators into two *independent* biomass pools: a plant-without-pollinators (vegetation) pool and a rewards pool, both with constant production rates. In this way, rewards production is forced to match that of the multiplex model in the absence of mutualistic feedbacks even though these feedbacks also generated the

645 production rate through dynamics over the course of the multiplex simulations. All feeding
646 interactions (gray arrows) remain the same.

647 Specifically, we modified the dynamics of each former plant with pollinators *i* so
648 that its vegetative biomass follows the dynamics and parametrization of plants without
649 pollinators (Eqn. 4, $r_i = 0.8$) and its rewards biomass follows:

650 $$\frac{dR_i}{dt} = (\overline{\beta_i B_i - s_i R_i}) - \sum_{j \in pollinators} C_{ji}(R_i)/e_{ji} \qquad (6\text{-}1)$$

651 with fixed production rate ($\overline{\beta_\iota B_\iota - s_\iota R_\iota}$) equal to *i*'s average net rewards production during
652 the last 1000 timesteps of the multiplex simulations. In this manner, vegetation is not
653 dependent upon pollinator consumption of rewards nor on rewards production, and rewards
654 production is fixed and not dependent upon vegetation. All other species followed the
655 same dynamic equations and parameterization as in the multiplex simulations.

656 We applied these feedback controls to the four multiplex treatments (RO Low, RO
657 High, RP Low, RP High) and initialized all species at biomass $B_i = 10$ and rewards nodes at
658 $R_i = \overline{R}_\iota$, the average rewards biomass for each plant with pollinator species *i* during the last
659 1000 timesteps of the multiplex simulations. Simulations were run for 5000 timesteps to
660 approximate steady state. We compared the results of these simulations with those of the
661 original multiplex simulations by measuring absolute differences in persistence and total
662 biomass at timestep 5000, where the *effect of feedback = multiplex – control*. To assess
663 differences in these ecosystem metrics due to guilds, we calculated absolute differences in
664 the fraction of persisting species composed by each guild:

665 $$\frac{multipex\ final\ guild\ diversity}{multiplex\ final\ diversity} - \frac{control\ final\ guild\ diversity}{control\ final\ diversity} \qquad (8)$$

and the fraction of ecosystem biomass composed by each guild:

$$\frac{multipex\ guild\ biomass}{multiplex\ total\ biomass} - \frac{control\ guild\ biomass}{control\ total\ biomass}. \quad (9)$$

If these *effects of feedbacks* evaluate to positive numbers, feedbacks in multiplex simulations have a positive effect, i.e. they increase persistence or biomass of the ecosystem or guild. If *effects of feedbacks* are negative, feedbacks decrease persistence or biomass. If, instead, *effects of feedbacks* are approximately zero, stability and function in our multiplex treatments can be attributed to the overall rates of plant (vegetative and rewards) productivity that emerge during those simulations.

Data availability.

Network structures and simulation outputs are available in the online repository at https://github.com/kayla-hale/Multiplex-Dynamics/.

Code availability.

Simulation and analysis code are available in the online repository at https://github.com/kayla-hale/Multiplex-Dynamics/.

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868 **Table 1. Definitions of terms.**

Ecosystem "Stability" and "Function"	We use a range of complementary metrics to assess ecosystem "stability" and "function" in a broad sense [50]. We apply the metrics both to the whole **ecosystem** (all species in the network) and to individual **guilds** in the network at **steady-state dynamics** of our simulations.
Biomass Variability (CVs)	**Coefficient of Variation** (CV = standard deviation / mean) of species' or guilds' biomass evaluated over the last 1000 timesteps of the simulations when their dynamics are approximately at **steady state**. Increased **temporal stability** corresponds to decreased biomass variability.
Consumption Rate	Total rates of biomass extracted by consumers.
Diversity	Number of species within a network. Networks of **initial diversity** *S* are subjected to the dynamical simulations, during which species may go extinct or persist. The resulting number of species is the **final diversity**, or simply **diversity**.
Guilds	Guilds are groups of "species" with similar consumer-resource interactions: **plants without pollinators**; **plants with pollinators**; **floral rewards** of plants with pollinators (when relevant to analyze their biomass and flows separately from vegetation, Fig. 1); **herbivores**: species that only eat plant vegetation in the original niche-model food web (Fig. 2a); **omnivores**: species that eat vegetation and animals in the original niche-model food web (Fig. 2a); **carnivores**: species that eat only animals; **added (+) herbivores/pollinators**: herbivores or herbivorous pollinators added by the RO or RP treatments that consume rewards (multiplex treatments) and/or vegetation (FW treatments; Fig. 2, yellow-green nodes); **added (+) omnivores/pollinators**: omnivores or omnivorous pollinators added by the RP treatment that consume rewards (multiplex treatment), animals, and/or vegetation (Fig. 2e, orange nodes). "**Added animals**" include both +herbivores/pollinators and +omnivores/pollinators.
Local Stability	Categorizes the behavior of a system around an equilibrium point as "locally stable" if the system tends to return to that equilibrium after a very small perturbation [4].
Persistence	Fraction of species that survive to the end of simulations (= initial diversity / final diversity).
Productivity	Total rates of biomass increase due to plant growth and food assimilated by animals minus loss due to animals' metabolic maintenance costs and plants' costs of producing rewards.
Steady-State Dynamics	Formally, dynamics in which all species have constant abundance ($dB_i/dt = dR_i/dt = 0$ for all i). At the end of 5000 timesteps, our systems *approximate* steady-state dynamics (Fig. 3) as quantified by very small variability in total ecosystem biomass over the last 1000 timesteps of the simulations (CVs < 0.0001).

Multiplex Networks	Ecological networks that include more than one type of species interaction. Here, we focus on multiplex networks that combine food webs (including carnivory and herbivory, Fig. 2a) and pollination networks (Fig. 2b).
Rewards Only (RO) Treatment	Network construction treatment in which pollinators can access floral rewards of plants w/ pollinators as their only resource (Fig. 2d). These networks are subjected to multiplex dynamics, which include pollination in addition to traditional food web dynamics.
Rewards Plus (RP) Treatment	Network construction treatment in which pollinators can access floral rewards plus plant vegetation and/or animal biomass resources (Fig. 2e). These networks are subjected to multiplex dynamics, which include pollination in addition to traditional food web dynamics.
Pollination Link *or* Mutualistic Interaction	A pollination link or mutualistic interaction between pollinator i and plant w/ pollinator j describes both the consumption of j's floral rewards by i and the reproductive services provisioning to the vegetative growth rate of j by i (Fig. 1). In the FW treatments, pollination links are switched to links in which i consumes the vegetative biomass of j, i.e. to herbivory links.
Food Web (FW) Treatments	Ecological networks with the same structure as multiplex networks, but with all **pollination links** switched to herbivory (also corresponding to zero rewards productivity). In the Rewards Only Food Web (RO FW) construction, animal i is strictly an herbivore (Fig. 2d), while in the Rewards Plus Food Web (RP FW) construction, animal i could be an omnivore or herbivore (Fig. 2e). These networks are subjected to traditional food web dynamics.
Rewards Productivity (β)	Parameter in our multiplex model specifying the rate of rewards biomass produced by plants w/ pollinators per unit of their vegetative biomass. "Low" ($\beta = 0.2$) and "High" ($\beta = 1.0$) are arbitrary values chosen to illustrate two behaviors of the multiplex model compared to traditional food web dynamics. "None" corresponds to Food Web treatments. We interpret rewards productivity as a proxy for the **intensity** of pollination interactions. See Fig. S5 for persistence results across a range of β values.
Feedback Control	To test whether transient mutualistic feedbacks isolated from rewards availability lead to the differences between our multiplex and Food Web treatments, we initialized simulations forced with rewards availability from multiplex simulations but with feedbacks (blue arrows in Fig. 1) turned "off." We then observed potential changes in steady-state ecosystem stability and function.

869

870 **Figure Legends**

871 **Figure 1. Interaction mechanisms in the multiplex model.** Interspecific and
872 intraspecific mechanisms of feeding and reproduction combine to describe pollination
873 mutualisms and traditional trophic interactions. Biomass of plants with pollinators is
874 partitioned into two pools, vegetation (blue node) and floral rewards (purple node), coupled
875 by intraspecific dynamic feedbacks (dotted arrows). Rewards production is proportional to
876 vegetative biomass but subject to self-limitation such that its productivity per unit biomass
877 decreases with increasing rewards abundance. Producing rewards incurs costs (reduced
878 vegetative productivity), which create tradeoffs between producing rewards to attract
879 pollinators and benefiting from the *quantity* (number of visits measured as feeding rate on
880 rewards) and *quality* (conspecific feeding / total feeding) of pollinators' reproductive
881 services (blue arrow) that are required for vegetative production. At saturation,
882 reproductive services allow plants with pollinators to potentially achieve a 25% higher per-
883 biomass growth rate than that of plants without pollinators whose intrinsic growth rate is
884 independent of consumers' behavior. All plants are also subjected to competition from the
885 plant community in the form of a community-level carrying capacity, which reduces per-
886 biomass vegetative growth rate as the plant community approaches its carrying capacity.
887 Gray arrows show herbivores feeding on vegetation and pollinators feeding on rewards.

888 **Figure 2. Steps for constructing food-web and multiplex-network treatments.** Nodes
889 are vertically arranged by trophic level with plant species at the bottom and carnivores at
890 the top. All (grey, red, orange) links represent feeding by the consumer above the resource
891 except the bi-directional pollination links (blue, simplified from Fig. 1) that represent
892 pollinators consuming plants' floral rewards (e.g., nectar) and plants consuming

893 pollinators' reproductive services. **Steps: a)** Generate food web with diversity S_f and
894 connectance C_f [48]. **b)** Generate plant-pollinator network with diversity S_p and connectance
895 C_p [49]. **c)** Integrate the food web and plant-pollinator network by adding pollinators and
896 their links from b) to the food web in a) by randomly assigning plant species in a) to
897 become the animal-pollinated plants in b). **d) Rewards Only (RO) treatments:** following
898 a), b), and c), construct the RO multiplex treatment by stochastically linking predators of
899 herbivores in c) to pollinators and then, for the RO FW treatment, transform pollinators into
900 herbivores and plants with pollinators into plants without pollinators. **e) Rewards Plus**
901 **(RP) treatments:** following a), b), and c), construct the RP multiplex treatment by
902 stochastically linking predators and diets of herbivores and herbivorous omnivores in c) to
903 pollinators and then, for the RP FW treatment, transform omnivorous and herbivorous
904 pollinators and plants with pollinators into omnivores, herbivores, and plants without
905 pollinators, respectively. Resulting diversity (S) and connectance (C) is shown under each
906 network treatment (d–e). See Methods.

907 **Figure 3. Timeseries of a 72-species ecological network subjected to six treatments.**
908 This example uses a 50-species niche-model food web integrated with a 33-species plant-
909 pollinator network according to the Rewards Only (RO, top row) and Rewards Plus (RP,
910 bottom row) network treatments subjected to traditional Food Web (FW) dynamics (left) or
911 multiplex dynamics with Low (center) or High (right) rewards productivity. Note that 11
912 plant species in the food web are chosen to represent the 11 plant species in the pollination
913 network. Simulations last 5000 timesteps and are presented on log-log axes. Each line
914 (colored by guild following Fig. 2) is the trajectory of a species' biomass over time.
915 Species that fall below a biomass of 10^{-4} continue to extinction (10^{-6}). Resulting overall

916 persistence is labeled in the upper right corner of each panel. Plants with pollinators are
917 considered extinct when their vegetative biomass (light blue) drops below 10^{-6}; their
918 rewards biomass (purple) is strongly coupled and declines accordingly. The vast majority
919 of species' biomasses achieve steady state by 2000 timesteps with nearly all animal
920 extinctions occurring before then, while several low-abundance plants with pollinators
921 continue slow declines well past 2000 timesteps.

922 **Figure 4. Overall effects of mutualism on stability and function in complex**
923 **ecosystems.** Column headings label the treatments described in Fig. 3. Gray bars and
924 associated μ's are means over all levels of initial diversity for all networks or "ecosystems"
925 within each treatment at the end of $N = 24{,}276$ simulations. Shown are the total a) diversity,
926 b) persistence, c) biomass, d) productivity and consumption rates, and the mean CVs of
927 biomass of all e) species within each ecosystem and f) guilds within each ecosystem
928 averaged over all the ecosystems within each treatment. Black error bars show 95%
929 confidence intervals. Mutualism is absent in Food Web (FW) treatments and present in
930 corresponding multiplex treatments. Mutualisms are less intense in Low than in High
931 rewards productivity treatments. Total rates of productivity and consumption were
932 approximately equal (i.e. at steady-state, all production is being consumed) so they are
933 shown in one row (d).

934 **Figure 5. Effects of increasing mutualism on diversity and persistence in complex**
935 **ecosystems.** Colors represent guilds of species described in Fig. 2 and Table 1. Initial
936 diversity (S) on the x-axis and in a) describes the initial number of species in food webs
937 plus added herbivores and omnivores in the Food Web (FW) treatments or pollinators in
938 the multiplex treatments. Increasing S corresponds to both to an increasing *number* of

added (+) animals and to an increasing *fraction* of the 20 plants without pollinators that are assigned to be plants with pollinators, and thus to *increasing prevalence of mutualism* in multiplex treatments. Bars show mean values for networks of a given initial *S* in increments of 2 species. Stacked bar graphs show the mean number of species in each guild (colors) that contribute to a) initial or b) final ecosystem diversity. Persistence, the fraction of the initial diversity that persists to the end of the simulations, is shown for c) the entire ecosystem (i.e. network of species) and d-h) for each guild of animals. c) Error bars show standard deviations. d-h) μ is the mean guild persistence over all $N = 24{,}276$ simulations in each treatment. Plants nearly always persist in our treatments (Fig. S1), so their persistence is not shown.

Figure 6. Effects of increasing mutualism on diversity, abundance, function, and temporal stability in complex ecosystems. Formatting follows Fig. 5 with the addition of floral rewards shown in purple. a) Final diversity from Fig. 5 is shown again for reference. Stacked bar graphs show the contribution of each guild (colors) to total ecosystem b) abundance, c) productivity, d) consumption, and average variability over time of e) species and f) guilds, with colors representing the average variability of the guild in f) or species within the guild in e). b) The community-wide carrying capacity for plant vegetative biomass (*K*) is marked on the y-axis; total plant vegetative biomass (summed vegetation of plants with and without pollinators) does not exceed this value.

Figure 1.

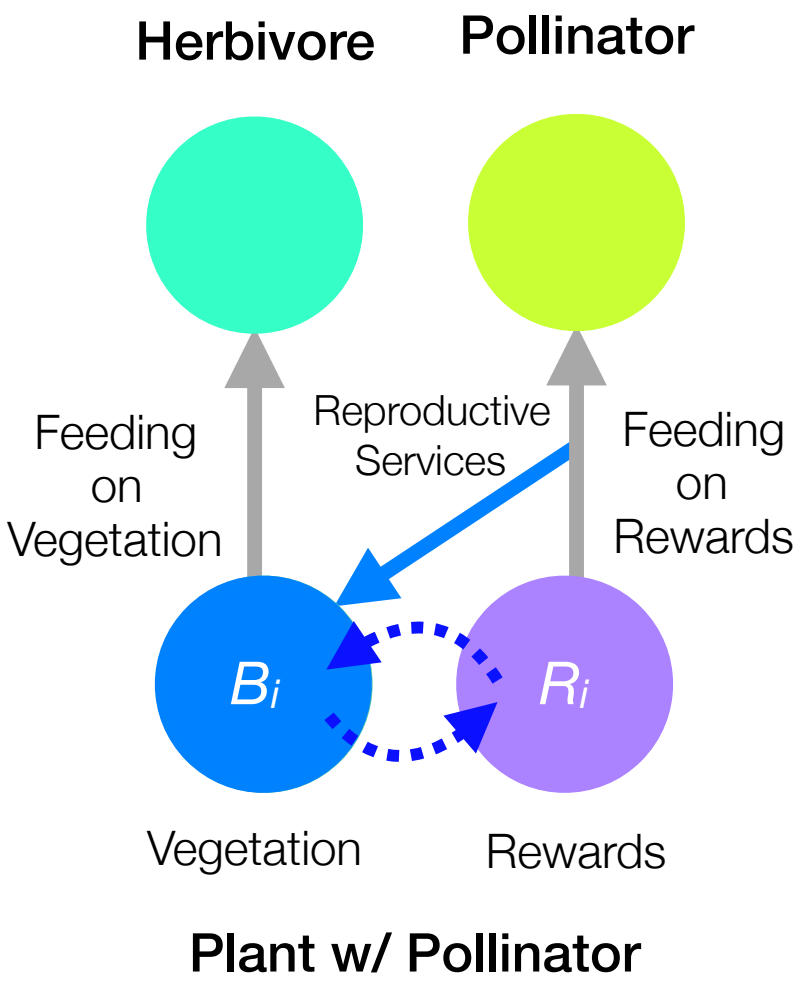

Herbivore
Pollinator
Feeding on Vegetation
Reproductive Services
Feeding on Rewards
B_i
R_i
Vegetation
Rewards
Plant w/ Pollinator

Figure 2.

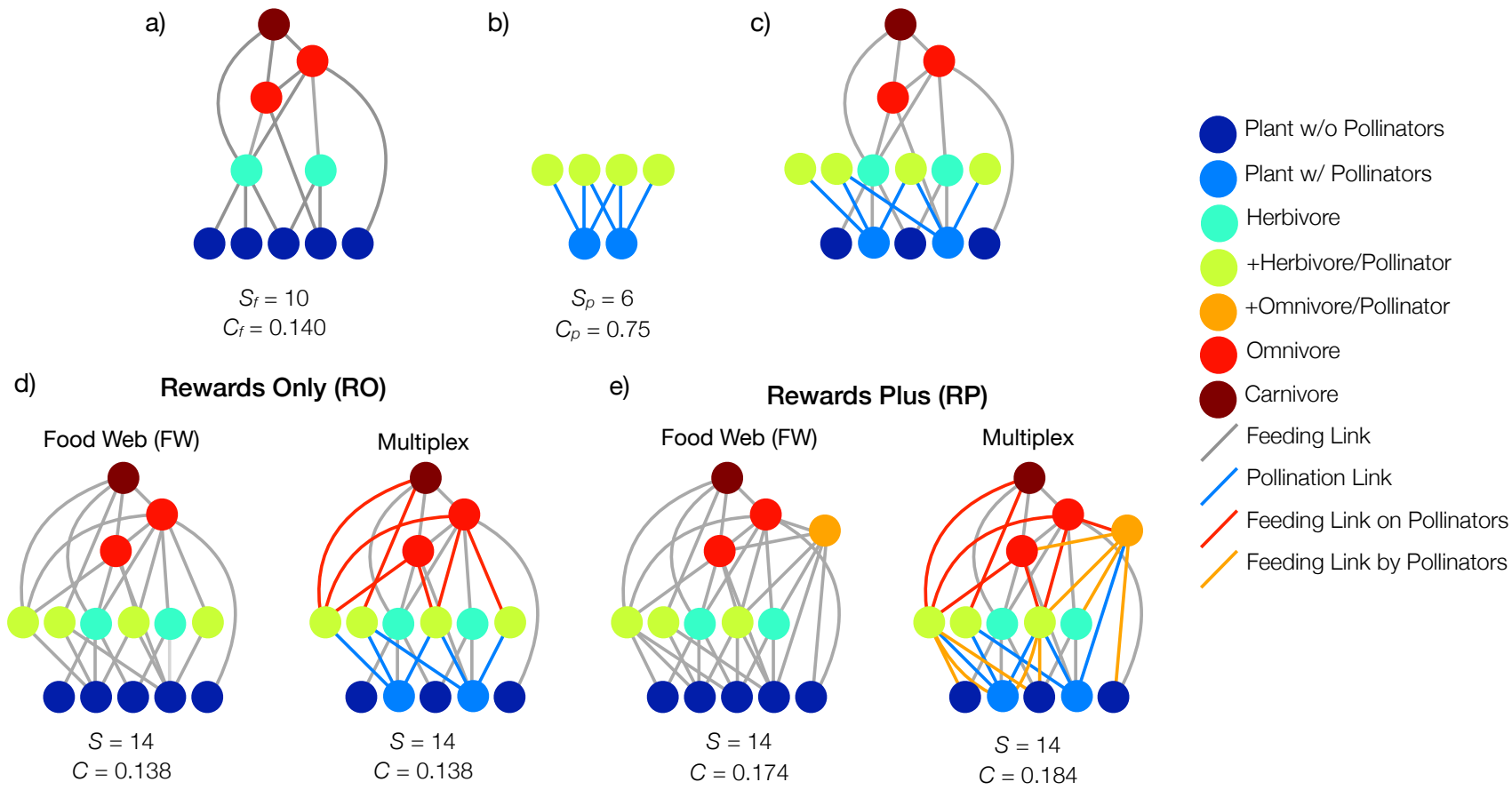

a)
S_f = 10
C_f = 0.140
b)
S_p = 6
C_p = 0.75
c)
Plant w/o Pollinators
Plant w/ Pollinators
Herbivore
+Herbivore/Pollinator
+Omnivore/Pollinator
Omnivore
Carnivore
Feeding Link
Pollination Link
Feeding Link on Pollinators
Feeding Link by Pollinators
d)
Rewards Only (RO)
Food Web (FW)
S = 14
C = 0.138
Multiplex
S = 14
C = 0.138
e)
Rewards Plus (RP)
Food Web (FW)
S = 14
C = 0.174
Multiplex
S = 14
C = 0.184

Figure 3.

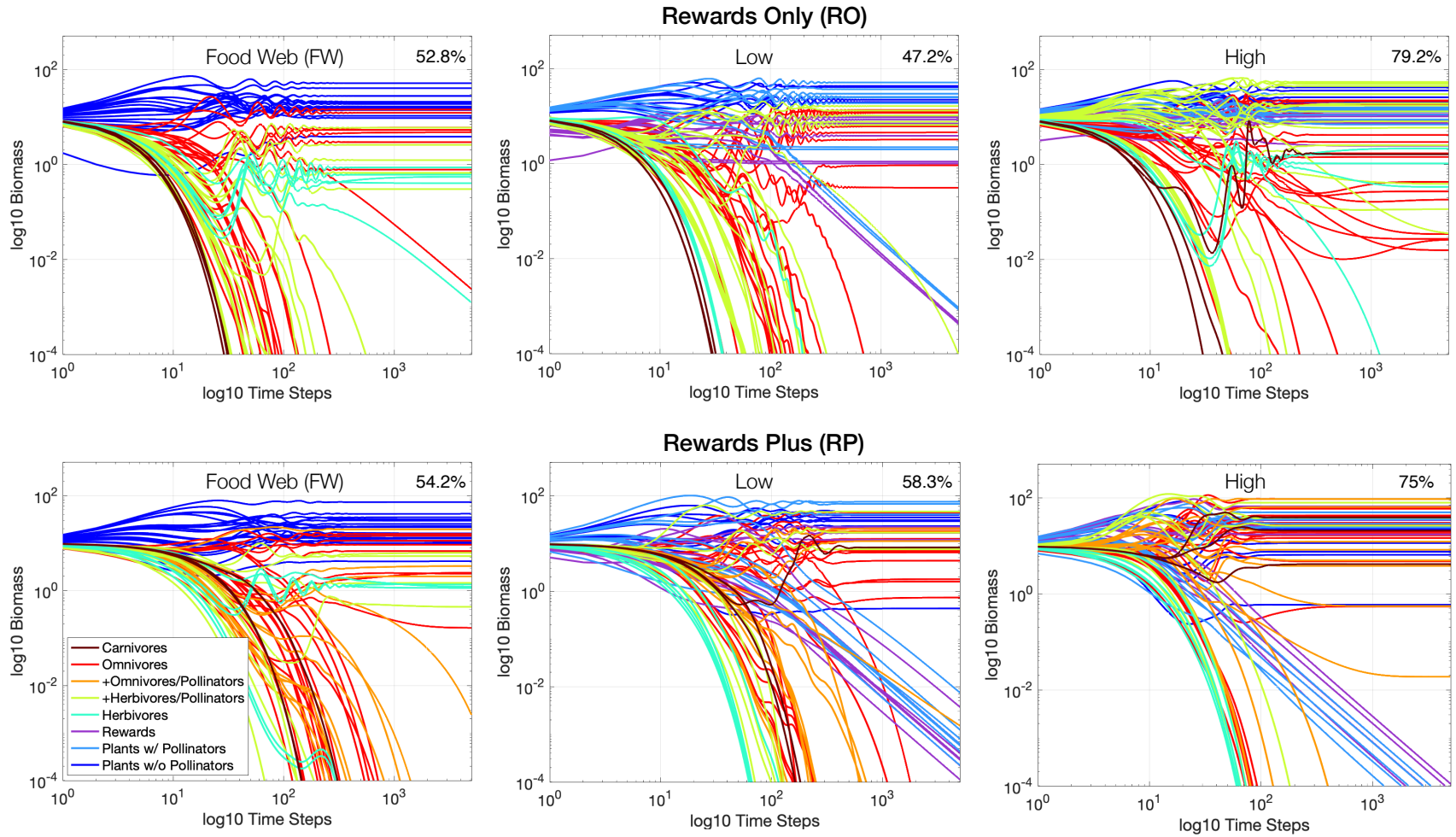

Rewards Only (RO)
Food Web (FW)
52.8%
Low
47.2%
High
79.2%
Rewards Plus (RP)
Food Web (FW)
54.2%
Low
58.3%
High
75%
log10 Biomass
log10 Time Steps
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Rewards
Plants w/ Pollinators
Plants w/o Pollinators

Figure 4.

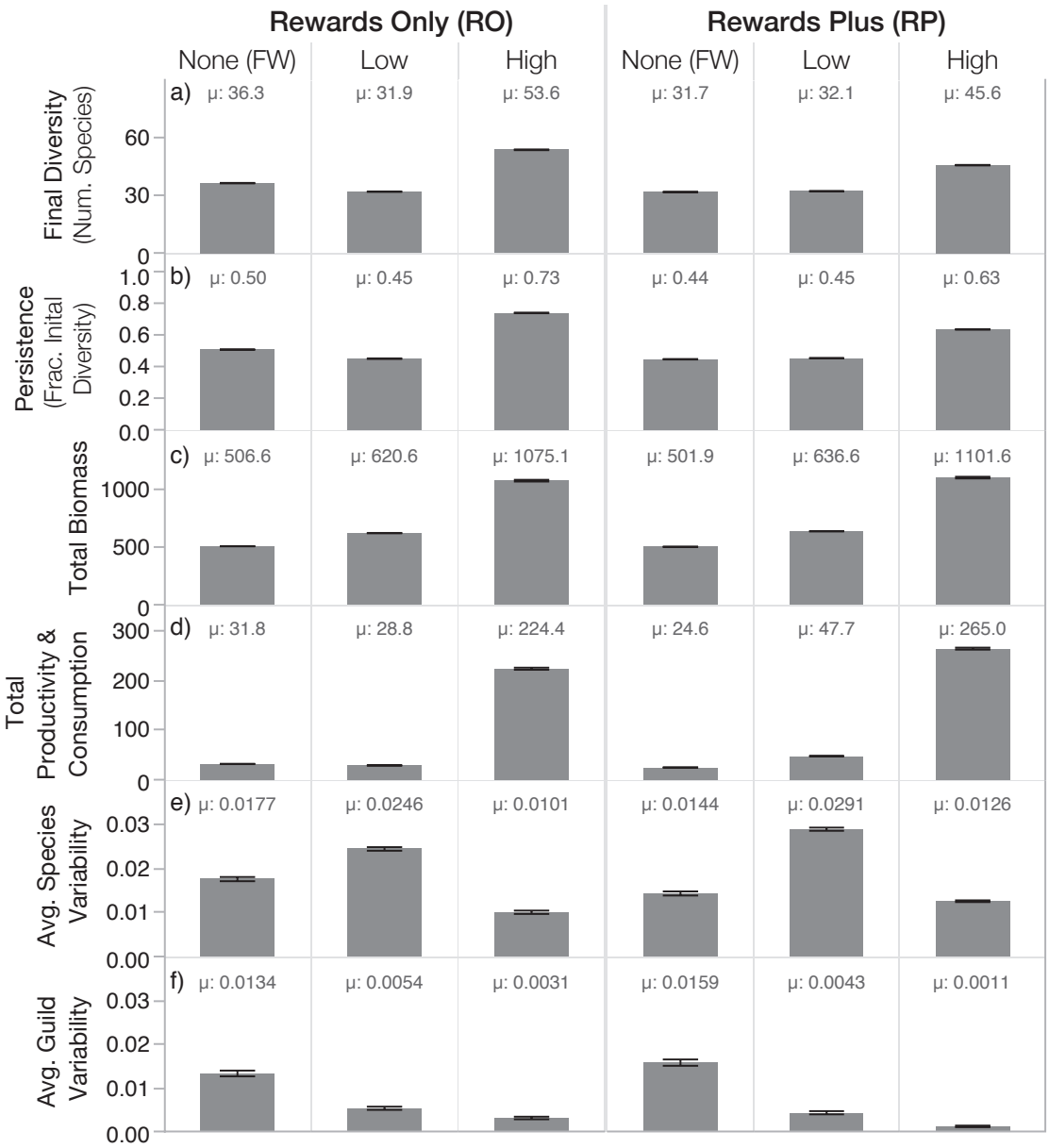

Rewards Only (RO)
Rewards Plus (RP)
None (FW)
Low
High
None (FW)
Low
High
Final Diversity (Num. Species)
a) μ: 36.3
μ: 31.9
μ: 53.6
μ: 31.7
μ: 32.1
μ: 45.6
Persistence (Frac. Inital Diversity)
b) μ: 0.50
μ: 0.45
μ: 0.73
μ: 0.44
μ: 0.45
μ: 0.63
Total Biomass
c) μ: 506.6
μ: 620.6
μ: 1075.1
μ: 501.9
μ: 636.6
μ: 1101.6
Total Productivity & Consumption
d) μ: 31.8
μ: 28.8
μ: 224.4
μ: 24.6
μ: 47.7
μ: 265.0
Avg. Species Variability
e) μ: 0.0177
μ: 0.0246
μ: 0.0101
μ: 0.0144
μ: 0.0291
μ: 0.0126
Avg. Guild Variability
f) μ: 0.0134
μ: 0.0054
μ: 0.0031
μ: 0.0159
μ: 0.0043
μ: 0.0011

Figure 5.

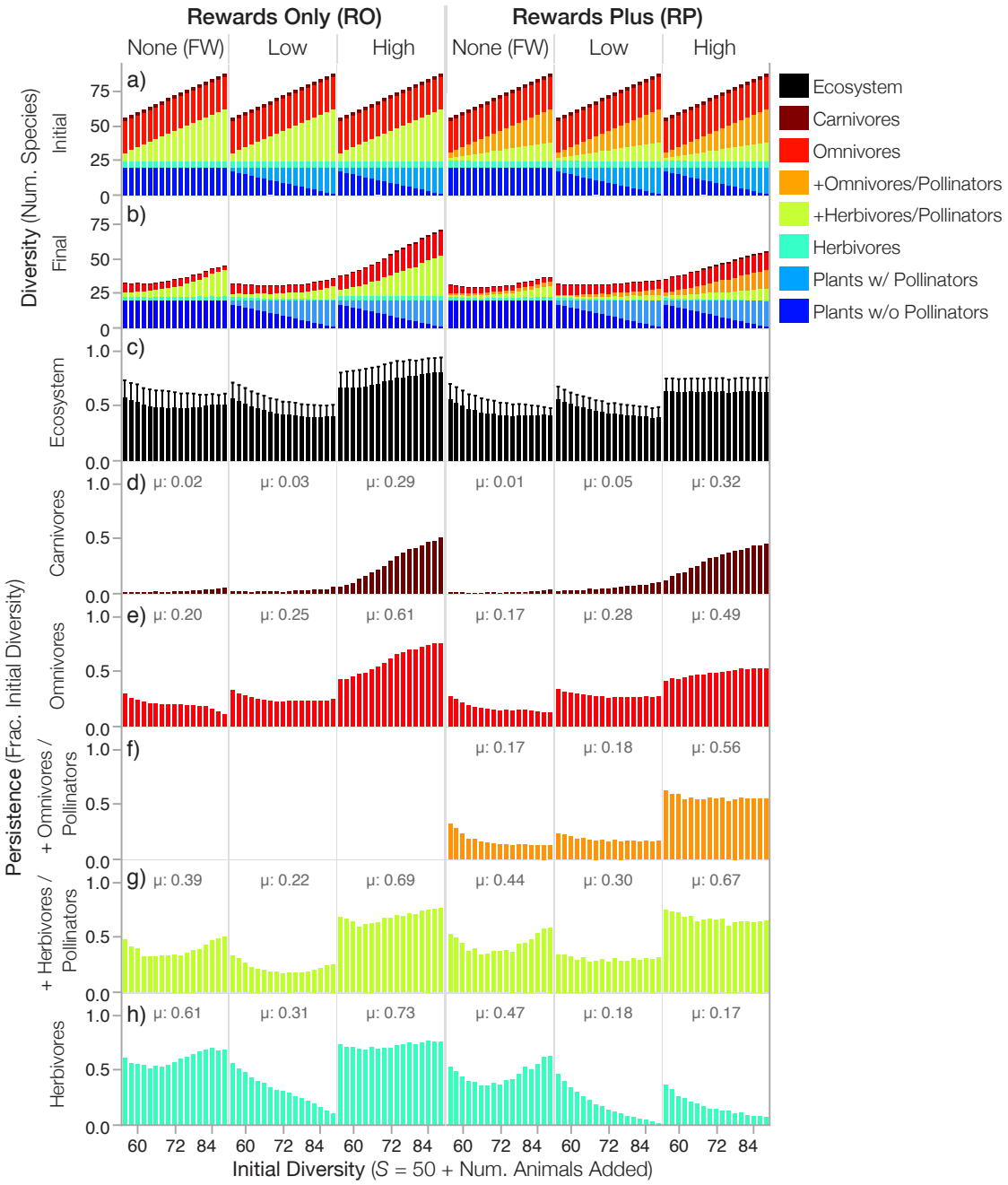
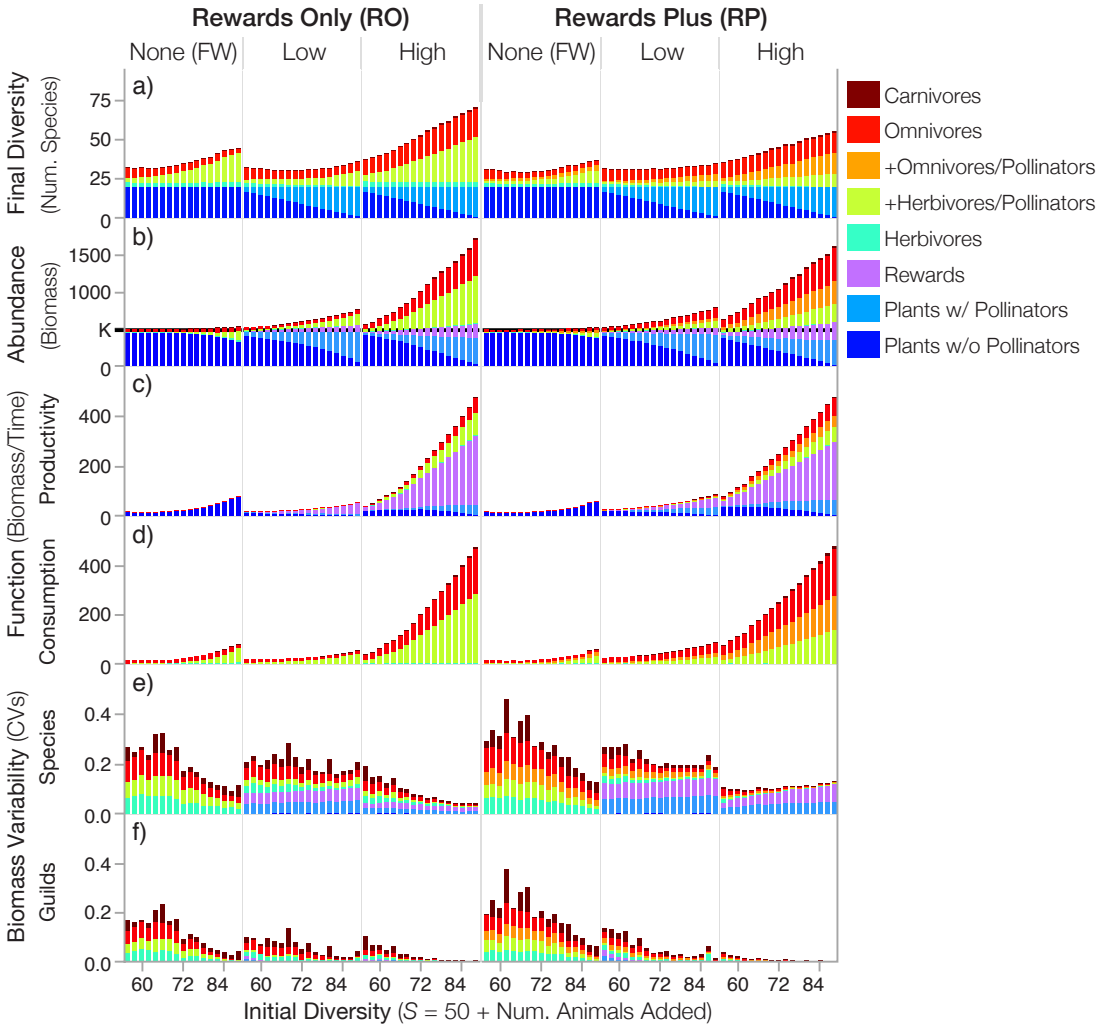

Rewards Only (RO)
Rewards Plus (RP)
None (FW)
Low
High
Diversity (Num. Species)
Initial
Final
Persistence (Frac. Initial Diversity)
Ecosystem
Carnivores
Omnivores
+ Omnivores / Pollinators
+ Herbivores / Pollinators
Herbivores
a)
b)
c)
d) μ: 0.02 μ: 0.03 μ: 0.29 μ: 0.01 μ: 0.05 μ: 0.32
e) μ: 0.20 μ: 0.25 μ: 0.61 μ: 0.17 μ: 0.28 μ: 0.49
f) μ: 0.17 μ: 0.18 μ: 0.56
g) μ: 0.39 μ: 0.22 μ: 0.69 μ: 0.44 μ: 0.30 μ: 0.67
h) μ: 0.61 μ: 0.31 μ: 0.73 μ: 0.47 μ: 0.18 μ: 0.17
Initial Diversity (S = 50 + Num. Animals Added)
Ecosystem
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Plants w/ Pollinators
Plants w/o Pollinators

Figure 6.


Rewards Only (RO)
Rewards Plus (RP)
None (FW)
Low
High
None (FW)
Low
High
Final Diversity (Num. Species)
Abundance (Biomass)
Function (Biomass/Time)
Productivity
Consumption
Biomass Variability (CVs)
Species
Guilds
a)
b)
c)
d)
e)
f)
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Rewards
Plants w/ Pollinators
Plants w/o Pollinators
Initial Diversity (S = 50 + Num. Animals Added)