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

Kayla R. S. Hale[1*], Fernanda S. Valdovinos[1,2] & Neo D. Martinez[3]

[1] Department of Ecology and Evolutionary Biology, University of Michigan, 1105 North University Ave, Biological Sciences Building, Ann Arbor, MI 48109.

[2] Center for the Study of Complex Systems, University of Michigan, Weiser Hall Suite 700, 500 Church St, Ann Arbor, MI 48109

[3] Department of Ecology & Evolutionary Biology, P.O. Box 210088, University of Arizona, Tucson, AZ 85721, USA

*Correspondence to: Kayla R. S. Hale 1105 North University Ave, Biological Sciences Building, Ann Arbor, MI 48109. E-mail: kaylasal@umich.edu

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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 such as those of plants who 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 complex ecosystems. Contrary to classic theory, we find that the dynamics of pollination mutualisms can increase the diversity, stability, and several ecosystem functions of multiplex ecological networks. These effects strongly increase with floral reward productivity and are qualitatively robust to variation in the prevalence of mutualism and pollinators feeding upon vegetation and other species in addition to floral rewards. This work advances the ability of mechanistic network theory to synthesize different types of ecological 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 an integrated consumer-resource theory of feeding and reproductive mechanisms. We use our multiplex network model based on this theory to study how mutualism affects the dynamics, 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, feeding interactions considered "mutualistic" like pollinators foraging on the nectar of flowering plants are often excluded from food web data (e.g., ref [11]), while feeding interactions considered "antagonistic" like herbivory and predation are excluded from mutualistic networks [12]. Additionally, food web research has focused more on aquatic systems [13,14] where feeding interactions are strongly structured by body mass or gape size, 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 [15–17]. Within aquatic ecosystems, the allometric trophic network theory [16,18] of food webs has leveraged body-size considerations to successfully simulate the seasonal dynamics of many interacting species [19,20] and predict the quantitative effects of experimental species manipulations [21–24]. However, the failure of these predictions in the presence of non-trophic facilitation of mussels by barnacles highlights the need for food-web theory to better address positive interactions [21]. Mutualistic network theory has focused on positive interactions in the form of animal-mediated pollination [12,25] motivated in part by large agricultural and evolutionary significance [9,26,27]. The success of mutualistic network theory based on consumer-resource mechanisms in predicting foraging behaviors of pollinators in the field [28] suggests consumer-resource theory can effectively integrate food webs and positive interactions.

Feeding and mutualistic interactions both typically involve food consumption while mutualistic interactions often additionally involve reproductive services provided by consumers such as pollinators, frugivores, and seed dispersers.[25,29,30] Both interaction types also operate within the same ecosystems and often on the same organisms, jointly determining much of the stability and function of these systems.[8,10,31–36] 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 like nectar may profoundly impact the dynamics of pollination, subsequent crop yields,[37] and long-term sustainability of agroecosystems [38].

An outstanding difficulty with understanding the joint effects of feeding and mutualistic interactions is the contradictory conclusions of previous theoretical work on this topic. Classic theory has long held that mutualistic interactions are generally *destabilizing* 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 with randomly assigned mutualistic links when animals have separate effort allocation to feeding and mutualistic interactions [41–43]. Contradictions within these bodies of theory may arise from representing interspecific interactions as randomly parameterized or density-independent *effects* [2,4,35,44] instead of density-dependent *mechanisms* whose effects may dynamically vary quantitatively and even qualitatively. For example, whether a "mutualistic" interaction results in net benefit to both partners often depends upon a threshold past which more reproductive services or food will damage or fail to provide benefits to satiated consumers of these resources [26,29,30,44]. Additionally, the random network architectures [4,41] often misrepresent the empirically observed structure of mutualistic interactions [45]. A broader problem is that narrowly focusing on stability develops inefficient theory [46] that ignores how mutualisms alter the diversity, population dynamics, and overall functioning of complex ecosystems.

To help resolve these contradictions and more broadly understand the ecology of mutualistic interactions, here, we follow repeated calls for synthesizing different types of interactions within networks [8,10,31–35] by developing and applying mechanistic consumer-resource theory to "multiplex" ecological networks [34,36]. Our multiplex networks integrate the structure and dynamics of feeding and reproductive mechanisms from which a interspecific interactions and subsequent effects emerge including predation, mutualism, and resource and apparent competition [29,44,47]. Realistically structured networks were generated by integrating Williams and Martinez' "niche model" of food webs [14] with Thébault and Fontaine's model of mutualistic networks [45] (Fig. 1). The dynamics of these networks were simulated 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 [28,30].

Within this framework, we evaluate the effect of pollinators and their interactions on the diversity and dynamics of ecosystems by comparing persistence, abundance, and dynamics of species, guilds, and whole systems with similar network architectures subjected to three different treatments. Our Food Web (FW) treatment includes only feeding interactions while our Rewards Only (RO) and Rewards Plus (RP) multiplex treatments include both feeding and reproductive interactions. Our RO treatment adds increasing numbers of pollinators that consume only floral rewards to food webs. Our RP treatment adds pollinators that may also consume vegetative biomass and other animals. Thus, pollinators in RO treatments are more purely mutualistic in that they are restricted to exchanging reproductive services for floral rewards while herbivorous and omnivorous pollinators in RP treatments may also engage in the potentially antagonistic interactions of herbivory and carnivory [48,49]. For comparison purposes, our FW treatments add equivalent numbers of herbivores and omnivores but linked only by feeding to the same species that the pollinators in the RO and RP treatments are linked to (Fig. 1). We apply these three treatments to 102 niche-model food webs with 50 species, exactly 20 of which are plants, by adding 6 to 38 herbivorous or omnivorous consumer (in FW treatment) or pollinator (in RO and RP treatments) species according to the structure of 238 plant-pollinator networks such that the initial species diversity of the 24,276 (102 x 238) networks ranges from 56 to 88. As initial diversity increases, plants with pollinators in the multiplex networks increase from 3 to 19 of the 20 plant species and mutualistic interactions increase from directly involving 16% to 65% of species in the networks. Initial herbivory in FW treatments correspondingly increases from directly involving approximately a half to three quarters

of the species in the networks. We thus assess stability and function in networks of increasing initial diversity, which corresponds to increasing mutualism in multiplex networks or increasing herbivory in FW treatments. Within each multiplex network treatment, we varied the reward productivity of plants with pollinators by a factor of five between "Low" and "High" productivity. Species within our networks initialized in this manner persist or go extinct during our simulations lasting 5000 timesteps (Fig. 2). Following transitory dynamics, our analyses of the final 1000 timesteps find that mutualistic interactions increase diversity, stability, and ecosystem function of multiplex networks and that these increases are greatly enhanced by High reward productivity (Fig. 3-4).

RESULTS

Diversity.

Multiplex treatments with High reward productivity (High RO and High RP) had remarkably higher diversity (Fig. 3b, 4a), persistence (Fig. 3c), biomass (Fig. 4b), productivity (Fig. 4c), consumption (Fig. 4d), and stability (Fig. 4e, 4f) than their counterparts in the FW and Low rewards (Low RO and Low RP) treatments. With only one exception (RP treatments in Fig. 4e), these differences increased as larger fractions of the multiplex networks were directly engaged in mutualistic interactions. While all 20 plant species nearly always persisted in all our treatments (Figure S1), final animal diversity in High RO and High RP treatments was at least twice as high as that in FW, Low RO, and Low RP treatments (Fig. 3b). This difference is primarily due to the consistently high persistence of pollinators (~60%) compared to the persistence of added species in the FW treatments (Fig. 3f, 3g) and the increasing persistence of omnivores (Fig. 3e) with increasing mutualism in High rewards treatments. Carnivores made smaller contributions to the elevated diversity of High rewards treatments via

163 increases in persistence from ~5% to 50% with increasing mutualism (Fig. 3d). In
164 contrast, FW and Low rewards treatments had much lower persistence of carnivores (2-
165 3%, Fig. 3d), omnivores (~15-30% Fig. 3e), and pollinators (~15-45%, Fig. 3f, 3g) that,
166 except for carnivores, decreased with increasing mutualism. In the High RO treatment,
167 herbivores achieved higher persistence (73%) than in RO FWs (61%), but in the other
168 multiplex treatments, herbivore persistence was lower (<32%) and declined
169 dramatically with increasing mutualism (Fig. 3h). Nonetheless, the low initial diversity
170 of carnivores (~3 species) and herbivores not added by the treatments (~5 species)
171 resulted in only minor changes to total diversity despite substantial differences in
172 persistence. Additionally, in all treatments, any decreases in persistence were not strong
173 enough to prevent overall increased final diversity (Fig. 3b) with increased initial
174 diversity and mutualism (Fig. 3a).

175 **Function.**

176 Similar to the pattern in final diversity (Fig. 4a), the total biomass (Fig. 4b),
177 productivity (Fig. 4c), and consumption (Fig. 4d) in all multiplex treatments (High and
178 Low) were comparatively higher than in FW treatments with a minor exception in the
179 Low RO treatment. The Low RO treatment had increased biomass (Fig. 4b) but lower
180 diversity (Fig. 4a), productivity (Fig. 4c), and consumption (Fig. 4d) than the
181 corresponding (RO) FW treatment. Total biomass (Fig. 4b) and productivity (Fig. 4c)
182 consistently increased with diversity and mutualism in all treatments, but these
183 increases were strongest in High rewards treatments. Plant abundance (Fig. 4b)
184 decreased below carrying capacity in all but Low RO treatments while increases in the
185 abundance of animals and floral rewards strongly increased and overcompensated for
186 any decreases in plant abundance. As might be expected, abundance and productivity of
187 pollinators, plants with pollinators, and rewards increased with increasing mutualism in

188 multiplex treatments. At the same time, plant productivity increased with increasing
189 diversity and mutualism in all treatments except in Low RO treatments. Overall,
190 biomass was up to twice as high while productivity and consumption were up to an
191 order of magnitude higher in multiplex than in FW treatments. In all treatments, total
192 consumption (Fig. 4d) very closely matched total production and was distributed
193 according to the biomass of animals (Fig. 4d).

194 The higher biomass of multiplex compared to FW treatments (Fig. 4b) was
195 primarily due to increases in animal abundance while productivity differences (Fig. 4c)
196 were primarily due to strong increases in rewards combined with smaller increases in
197 animals. These differences emerge primarily due to the interactive dynamics of rewards
198 whose growth potential, contrary to all other stocks of biomass, depends not on its own
199 abundance but on the abundance of another component i.e., the vegetative biomass of
200 plants with pollinators. This allows rewards to be highly productive even when very
201 rare whereas other network components may simply go extinct. Excluding rewards and
202 moderate decreases of plant abundance in the most diverse FW networks, plant
203 abundance was relatively similar among treatments while vegetative productivity
204 strongly increased in FW treatments but only weakly increased in multiplex treatments
205 as diversity and mutualism increased (Fig. 4b). In FW treatments, the weak increases in
206 biomass (Fig. 4b) and strong increases in productivity (Fig. 4c) emerge from increases
207 in herbivore biomass that reduce plant abundance below their carrying capacity, freeing
208 plants from competition (Fig. 4b). This increases plant productivity (Fig. 4c) and animal
209 abundance enough to lead to a net increase in total biomass (Fig. 4b). Multiplex
210 treatments experience similar decreases of plant abundance and corresponding increases
211 of plant productivity but productivity of rewards dramatically increased as did animal
212 abundance. These increases in reward productivity and animal abundance are mostly

due to increases in pollinator abundance that stimulate reward productivity by depleting rewards below their self-limitation threshold. Animal biomass and productivity is further enhanced by increases in the omnivores and carnivores that feed on the increasingly abundant pollinators. These patterns in production, consumption, and increased animal abundance are greatly enhanced in High rewards treatments.

Stability.

We evaluated the stability of our networks by analyzing coefficients of variation (CV = mean / standard deviation) of abundance during the final 1000 timesteps of our simulations at the species (Fig. 4e), guild (Fig. 4f), and whole community levels. At the community level, all treatments were exceedingly stable ($CV < 0.001$). In contrast, species on average were much more variable ($0.01 \leq CV \leq 0.03$), especially in Low rewards treatments where plants with pollinators and their rewards contributed large amounts of variability (Fig. 4e). Large variability in plant and reward abundance in both multiplex treatments was caused by very low abundance of a few species of plants with pollinators whose abundance decreased throughout the end of the simulations (e.g. Fig. 2). This low and decreasing abundance yields large CVs at the species level but contributes very little to guild-level variation (Fig. 4f) due to the tiny fraction of their guild's biomass comprised by these very rare species. In FW treatments, where extinctions occur relatively early, species-level and guild-level variation are comparable. In contrast, average guild-level variation is only a fraction of the species-level variation in multiplex treatments. In all treatments, variation at both the species and guild levels decrease with increasing diversity and mutualism except for species-level variation in High RP networks (Fig. 4e-f). Overall, mutualism stabilizes population dynamics in multiplex treatments compared to FWs especially as diversity and mutualism increase, with the minor exception of the High RP treatment. The High

238 RP networks are by far the most stable at the guild level. However, at the species level,
239 rare plants with pollinators dominate variability leading to an increase in species
240 variability with increasing mutualism.

241 **Mutualistic feedbacks.**

242 To disentangle the influences of rewards and mutualism on our results, we
243 controlled for key influences of mutualism by severing the dynamic dependence of plant
244 productivity on reproductive services while maintaining the overall productivity rates of
245 plant biomass. We did this by forcing the total biomass produced as vegetation and
246 rewards during the last 1000 timesteps of the original simulations to be produced only
247 as vegetation and transforming pollination links into herbivorous links. We initialized
248 these control simulations with the biomass distributions from timestep 4000 of the
249 original simulations and ran them for 1000 timesteps so that we could compare control
250 to original simulations at 5000 timesteps. The control represents the hypothesis that the
251 effects of pollinators on our systems are solely due to the total productivity of resources
252 at the base of the food web that emerged due to pollination services during the original
253 simulations. Our results contradict this hypothesis in important ways. On average,
254 community species persistence decreased by ~5-6% in RO and ~6-7% in RP treatments
255 (two-tailed $P < 0.0001$), while total community biomass decreased by ~10% in High
256 rewards treatments and ~6% in Low RP treatments (two-tailed $P < 0.0001$), but was
257 unchanged in Low reward RO treatments ($P = 0.49$, Table 1). The magnitude of these
258 reductions became larger as mutualism and diversity increased, with the minor
259 exception of total biomass in Low RO treatments. Compared to the original simulations,
260 total biomass in Low RO controls increased with initial increases of mutualism and
261 diversity but then decreased precipitously with further increases, leading to no
262 substantial change overall. More dramatically, large mean squared deviations in

abundances of species between the control and original simulations indicate large differences between which species were abundant (Table 1). Former pollinators decreased in abundance despite access to up to twice the biomass previously available as rewards. In contrast, original herbivores increased in abundance in response to the increased vegetative biomass in the controls. These changes combined with changes in consumers of species feeding on plants greatly change which species were more and less abundant in the controls while changing total community biomass relatively little. Thus, the dynamic feedbacks of mutualistic interactions, rather than solely increasing productivity at the base of the food web, increase persistence and biomass and substantially alter species abundance distributions in multiplex simulations. Additionally, these differences are exacerbated at higher levels of mutualism and diversity. See Methods S1 for sensitivity analyses that further corroborate the roles of mutualism and rewards as outlined above.

DISCUSSION

In this study, we investigated whether and how mutualisms between plants and their pollinators affect ecosystem structure and function. Our results indicate that high productivity of mutualistic rewards within multiplex networks of reproductive and feeding interactions increase diversity (Fig 2b), persistence (Fig. 2c), biomass (Fig. 3b), productivity (Fig 3c), consumption (Fig 3d), and stability (Fig. 3f) over that of corresponding networks containing only feeding interactions (FW) or mutualistic plants with low rewards productivity. With a few minor exceptions, these differences increased as larger fractions of the multiplex networks were directly engaged in mutualistic interactions. We observed the only broadly positive diversity-persistence relationship (Fig. 2c) in the High Rewards Only (RO) treatment. Within this treatment, networks that contain the highest fraction of mutualistic interactions also exhibited the

highest diversity, persistence, abundance, and stability. Interestingly, all treatments exhibit positive diversity-stability relationships at the species (Fig. 3e) and guild levels (Fig. 3f) excepting the slightly negative relationship at the species-level in the High Rewards Plus (RP) treatment (Fig 3d). High RO and RP networks with the most mutualistic interactions exhibit the highest productivity (Fig. 3c). Multiplex networks (RO and RP) with the most mutualistic interactions have higher abundance (Fig. 3b), productivity (Fig. 3c), and guild-level stability (Fig. 3d) than their corresponding FW networks except for productivity in Low RO networks.

These increases of stability and function due to increases in diversity and mutualism are broadly consistent with empirical observations of the effects of increased pollinator diversity in blueberry, watermelon, and other agroecosystems. [50–53] Though consistent with empirical observations, our results are largely inconsistent with classic theory showing that mutualism destabilizes ecological networks [3–5]. While lower species-level population stability in Low rewards treatments compared to FWs corroborates classic theory (Fig. 4e), higher species- and guild-level stability in High rewards treatments and higher guild-level stability in Low RO treatments contradicts such theory (Fig. 4e-f). More broadly, negative effects of mutualism consistently extend to none of our six other measures of ecosystem structure and function (diversity, persistence, abundance, productivity, consumption, guild-level stability) while positive effects of mutualism apply to all of our High rewards treatments and most of our Low rewards treatments.

As suggested by Levin's assertion that "The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns" (p.1943) [54], our theory's ability to reconcile classic theory and broadly predict empirically observed effects of mutualism on ecological networks appears to emerge from our focus on the

mechanisms that dynamically generate effects of ecological interactions rather than the more phenomenological approach of focusing on less dynamic, fixed effects [25,44]. Our focus on the production and consumption of trophic resources and reproductive services goes beyond the mechanistic details of the dynamics to include realistic architectures of these interactions at the whole system level. Other research employing more realistic architectures find results similar to ours. For example, García-Callejas *et al*. [40] find 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 [31] and interaction types [41,42] compared to more empirically realistic ecological networks. However, unlike the studies that require allocation efforts to be separated between mutualistic and non-mutualistic interactions [41,42], we find that mutualism is stabilizing as defined by increased diversity and persistence and decreased biomass variability when unpartitioned effort is allocated to both types of interactions.

Examining our results in more detail indicates that strong positive effects of mutualism on ecosystems emerge because mutualistic rewards at low and even more so at high productivity levels stabilize ecological networks by increasing persistence of omnivores (Fig. 2e), omnivorous pollinators (Fig. 2f), and carnivores (Fig. 2d) above that of comparable species in food webs containing only feeding interactions. In contrast, pollinators that only consume rewards exceed the persistence of comparable herbivores in FW treatments only at High rewards productivity. These positive effects of mutualism are not fully reproduced by traditional food web dynamics when supplementing food webs with plant productivities similar to that in multiplex networks. The removal of dynamic feedbacks between pollinators and animal-pollinated plants

reduces ecosystem biomass and persistence and alters species composition and abundance distribution at steady state (Table 1). Thus, the combination of rewards availability and dynamic feedbacks lead to the increased stability and function of our multiplex ecological networks.

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 (Fig. 3d-h, Fig. 4b-c) excepting the decrease in herbivore persistence in RP networks (Fig 3h). 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 pollinators' additional herbivorous and carnivorous feeding links in RP networks 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 pollination mutualisms increase within terrestrial ecosystems, the diversity and biomass of upper trophic-level consumers will increase while our predictions for the effects on herbivores are weaker and less certain.

Key limitations of our work concern the match between the network architecture and the bioenergetic parameters in our models and those in nature. While the multi-trophic and mutualistic components of our multiplex network structures correspond to empirical observations, we lack empirical observations of their interconnection into multiplex networks with which to test against our simulated networks [8,36], though recent

363 multiplex networks for rocky intertidal systems that include facilitation [55,56] suggest
364 progress in this direction. Regarding dynamics, the metabolic rates of animals need to
365 be better related to the intrinsic productivities of plants. Most such estimates come from
366 aquatic ecosystems that likely differ from those in terrestrial systems [15]. Also, the
367 cryptic yet critically important rates determining reward availability are only rarely
368 estimated. For example, Baude *et al.* [57] suggest that nectar productivity of meadows in
369 the UK can be up to ~5-10% of net primary productivity and Adgabe *et al.* [58] estimate
370 nearly 1000 kg/ha of floral sugar is produced in a 5-month flowering season by a single
371 tree species. Pollen production may significantly increase such estimates and accounting
372 for seasonality of reward production and pollinator activity could greatly decrease
373 estimates of resource demand needed to sustain pollinators. Bioenergetic costs of
374 reward production compared to vegetation production should also be considered.
375 Accounting for such biomass production efficiencies greatly increased the ability of
376 allometric trophic network theory [16,19,21] to predict realistic stocks and flows of carbon
377 and energy in a complex food webs. [19,59] Compared to the relatively complex
378 compounds that comprise vegetative biomass, production efficiencies of synthesizing
379 simple sugars that provide nearly all the usable energy in nectar may be much higher.
380 Such efficiencies are suggested by estimates for animals that indicate, for example, the
381 energetic efficiency of producing milk is almost six times than that of beef [60]. Attending
382 to these limiting aspects of the structure and function of multiplex networks may
383 advance research on networks including plants and pollinators as well as those
384 involving coral, mycorrhizal fungi, frugivores, and other seed eaters that disperse seeds,
385 all of which involve the exchange of food for increased growth of primary producers.

386 We have advanced theory on multiplex networks in order to explore the effects
387 of mutualism on ecological systems. Our focus on reproductive interactions follows

388 previous extensions of allometric trophic network theory involving plant nutrients [16],
389 detritus [19], ontogenetic niche shifts [61], environmental stochasticity [62], fishing [61,63], and
390 economics [63] integrated into food webs comprised of feeding interactions distinguished
391 by their relative body sizes [16] such as diseases [11], parasites [11,64], parasitoids [11], and
392 predators [65]. Such integration of multiple interaction types into multiplex networks is
393 increasingly recognized as an effective means of accommodating different mechanisms
394 responsible for ecosystem structure and function [8,10,36,66]. Our specific application to
395 mutualistic mechanisms finds a striking ability of mutualism to enhance ecosystems
396 including their diversity, stability, and function. Further work incorporating mutualism
397 into multiplex network theory (e.g., mutualisms between zooxanthellae and coral polyps
398 and between plants and mycorrhizal fungi) may determine whether mutualisms more
399 generally enhance other systems. Such research would help compensate for ecologists'
400 emphasis on competition by better elucidating the much less studied roles of mutualistic
401 and other facilitative interactions[26,67] in biodiversity maintenance,[6] ecosystem function,[7]
402 and evolution[27].

403 METHODS

404 **Network architecture.**

405 We created multiplex networks (Fig. 1) by creating realistic food webs using the
406 stochastic "niche model" (Fig. 1a) parameterized with 50 species ($S_f = 50$) and 10%
407 directed connectance ($C_f = L_f / S_f^2 = 0.1$ where L_f is the number of feeding links.[14] The
408 niche model assigns each species i three traits: (1) a niche value (n_i) drawn randomly
409 from a uniform distribution between 0 and 1, (2) a feeding range (r_i) where $r_i = xn_i$ and x
410 is drawn from randomly from a beta distribution with expected value $2C_f$, and (3) a
411 feeding centre (c_i) drawn randomly from a uniform distribution between $r_i/2$ and $min(n_i,$
412 $1 - r_i/2)$. Species i feeds on j if n_j falls within i's feeding interval $[c_i - r_i, c_i + r_i]$. We

selected the first 102 niche model food webs with $0.0976 < C_f < 0.1024$ that were comprised of 50 species ($S_f = 50$), of which exactly 20 were plants and five were herbivores that only feed on plants (i.e. have trophic level [TL] = 2). We also generated 238 realistic plant-pollinator networks using a stochastic model [45] with 3 to 19 plant-with-pollinator species (P) and twice as many animal-pollinator species ($A = 2 * P$), yielding approximately 16 networks within each of 16 size classes ranging from 9 to 57 species ($S_p = P + A = 9, 12, \ldots, 57$; Fig. 1b, see Methods S2 for more details). We constrained the number of pollination links (L_p) to ensure that pollination connectance ($C_p = L_p / PA$) broadly decreased as S_p increased in an empirically realistic manner (Figure S2). We integrated each of the 238 plant-pollinator networks with one of the 102 food webs, yielding $N = 238*102 = 24{,}276$ networks of increasing species diversity ($S = S_f + A = 56, 58, \ldots, 88$). We did this by randomly choosing P of the 20 plant species already in the food web and assigning the A pollinators to those P plant species as determined by the plant-pollinator network (Fig. 1c). This leaves $20 - P$ plant species without pollinators.

We linked pollinators to consumers in the food web in Rewards Only (RO) treatments by setting each pollinator's n_i to +/– 5% of the n_i of a randomly selected strict herbivore (TL = 2) from the food web (Fig. 1d). Pollinators' r_i and c_i were set to zero. This causes pollinators to be preyed upon by predators similar to predators of herbivores and to consume only floral rewards as determined by the plant-pollinator network. Our parameterization causes connectance ($C = L/S^2$, where L is the total number of links) to decrease on average from 0.091 to 0.061 as species diversity (S) increases from 56 to 88 in RO multiplex networks and corresponding FWs (Figure S3). In the Rewards Plus (RP) treatments (Fig. 1e), we set 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 selected herbivore or omnivore that

eats plants ($2 \leq TL \leq 2.3$). This allowed average connectance of the networks to stay constant ($C = 0.102$) with increasing diversity in RP FW treatments (Figure S3). RP pollinators' ability to feed on both vegetation and floral rewards of the same plant species allows two links between plants and pollinators. When this occurs, the corresponding network subjected to the FW treatment has slightly less C than the RP network because the FW treatment eliminates the link to rewards and maintains only the herbivory link (Figure S3). We ignore this issue to simplify comparisons between all treatments.

Network dynamics.

Network dynamics are modeled according to Allometric Trophic Network (ATN) theory, [16,19,21] developed further here to represent feedbacks between pollinators feeding on floral rewards (R) and plants consuming reproductive services produced by plants. Plants benefit from pollinators depending upon on the quantity and quality of pollinators' visits in terms of rate at which pollinators consume plants' rewards and the fidelity of pollinators' visits to conspecific plants [28,30]. Pollinators in RP treatments also feed on species' biomass according to ATN theory.

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

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

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 consuming B_j, the biomass of species j:

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

where y_{ij} is the allometrically-scaled maximum mass-specific consumption rate. $F_{ij}(B_j)$ is the functional response for 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, [68] and B_{0ij} is the "half-saturation" density of resource j at which i's consumption rate is half y_{ij} [19]. 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" (ω_{ij} = 1/(# of species in i's diet) [69]. 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 "modified" Type II response [68].

We use ATN theory's logistic growth model [19] 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. We model the vegetative biomass dynamics of plant species i with pollinators as:

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

and the dynamics of its floral rewards biomass as:

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

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

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

which is a function of the quantity and quality of pollination provided by pollinator j. Quantity is j's consumption rate on i's floral rewards. Quality is j's consumption of i's rewards as compared to j's consumption of all the resources it consumes. Quality is therefore j's relative consumption rate of i's floral rewards, a measure of j's fidelity that ensures more specialist pollinators typically provide higher quality services than generalist pollinators by, for example, depositing higher concentrations of conspecific pollen [70]. The form of the functional response describing benefit accrual due to pollination (f) reflects the assertion that reproductive services saturate [71] at 1 according to: *reproductive services* / (0.05 + *reproductive services*). As $P(R_i)$ approaches 1, the realized growth rate of animal-pollinated plant i's vegetative component approaches r_i, its maximum growth rate.

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

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

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

Parameterization.

Vital rates for consumers follow previously described allometric scaling for invertebrates [63]. Specifically, we set plant species' "body mass" to a reference value ($m_i = 1$) [16] and calculated consumers' body mass as $m_i = Z_i^{swTLi - 1}$, where $swTL_i$ is i's short-weighted trophic level [72] and Z_i is i's average consumer-resource body size ratio sampled from a lognormal distribution with mean = 10 and standard deviation = 100. Then, for i eating j, i's mass-specific metabolic rate (x_i) is $0.314m_i^{-0.25}$, its maximum mass-specific consumption rate (y_{ij}) is 10, and its assimilation efficiency (e_{ij}) is 0.85 if j is an animal or 0.66 if j is plant vegetation. We set the maximum mass-specific growth rate (r_i) of plant i to be 0.8 for plants without pollinators or 1.0 for plants with pollinators, so that in the presence of sufficient reproductive services provisioning by pollinators, the mass-specific growth rate of plants with pollinators is comparable or can even exceed that of the plants without pollinators.

The remaining parameters are not allometrically constrained. We assigned a "half-saturation" density for consumers of species' biomass or rewards of $B_0 = 60$ or 30, respectively. This reflects the decreased "handling time" for rewards compared to typically 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 the rewards dynamics of animal-pollinated plants, we used a rewards production rate of $\beta_i = 0.2$ or 1 (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 ($\beta_i = 0$) and all plants are parameterized so that they behave as plants without pollinators while pollinators are parameterized as "added-herbivores" that consume vegetation with the associated lower

assimilation efficiency (e_{ij} = 0.66) but otherwise have 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 of the two multiplex treatments (RO & RP) at high (β = 1) and low (β = 0.2) rewards productivity and at zero productivity for the FW treatment for a total of 145,656 simulations. We used MATLAB's (The MathWorks 2018b) built-in differential equation solvers (ode15s for the multiplex treatments and ode45 for FWs) to simulate these networks for 5000 timesteps (Figure S4). By 2000 timesteps, the simulations were approximately at dynamical steady state. 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 (SAS Institute 2018). Our results are qualitatively robust to simulation length (Figure S5). Sensitivity of our results to parameter variation are reported in the Supplementary Information (Tables S1-S3).

Outputs.

We quantified ecosystem stability and function using species persistence, biomass, productivity, and variability at or near the end of the simulations. We calculated these metrics for the whole community and for eight guilds. Two guilds are self-evidently described species of plants without pollinators and plants with pollinators. One guild is just the rewards of all plants with pollinators. Herbivores, omnivores, and carnivores refer only species present in the niche-model food web prior to Step 3 of our network construction algorithms. These three guilds exclude species added by our treatments of those food webs. Herbivores eat only vegetative biomass (TL = 2). Omnivores eat vegetation and animals. Carnivores eat only animals. The meaning of the two remaining guilds 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 treatments that consume only rewards, and pollinators added by the RP treatments that consume rewards and vegetation. Added omnivores/pollinators refer to omnivores added by the FW treatments and pollinators added by the RP treatments that consume rewards, other animals, and potentially vegetation. We calculated species persistence as the fraction of the initial species that survived to the end of the simulation (i.e. whose biomass stayed above the extinction threshold).

We calculated all outputs at the end of the simulations except for biomass variability, which we calculated over the last 1000 timesteps. Species persistence is the fraction of the initial species whose biomass stayed above the extinction threshold throughout the simulation. Final biomass is the total biomass for the whole community and/or each guild of species. Plant productivity is the summed rates of species' biomass increases due to growth minus losses due to rewards production. Rewards productivity is the rate at which all rewards were produced by all plants with pollinators. Consumption is the summed rates of biomass lost by resources due to feeding by animals. Animal productivity is assimilation minus losses due to metabolic maintenance. Biomass variability at the species level is the average coefficient of variation (CV = standard deviation/mean) among surviving species and, at the guild level, the CV of the summed biomass of all species in each guild. Mean guild CV (μ, Fig. 4f) was calculated as the average of five guilds (all plants, herbivores, all added species, omnivores, and carnivores) to standardize the grouping of species into guilds across treatments.

Dynamical controls.

To disentangle effects of mutualistic feedbacks from effects of floral reward production, we ran multiplex simulations with mutualism turned off [73]. To do this, we

first recorded average net rewards production ($\overline{\beta_i B_i - s_i R_i}$), vegetative ($\overline{B_i}$) and rewards biomass ($\overline{R_i}$), and realized growth rate ($\widehat{r_i} = \overline{r_i P(R_i)}$) for each animal-pollinated plant *i* during the last 1000 timesteps of our multiplex simulations (Fig. 2). Then at timestep 4000, we set the biomass of each plant *i* with pollinators to $\widehat{B_i} = B_i + R_i$ and their dynamics were modified to:

$$\frac{d\widehat{B_i}}{dt} = \left(1 - \frac{1}{K}\sum_{j \in plants}(\widehat{B_j} - \overline{R_j})\right)\widehat{r_i}\widehat{B_i} - \sum_{j \in consumers} C_{ji}(\widehat{B_i})/e_{ji} + (1 - \kappa_i)(\overline{\beta_i B_i - s_i R_i}) \quad (5\text{-}1)$$

Eqn. 5-1 severs the dynamic feedback of mutualistic benefit due to provisioning of reproductive services to plants ($P(R_i)$ in Eqn. 5) while preserving the total biomass of each plant (vegetation plus rewards), the realized growth rate of the plant, the total rewards production rate, and the exclusion of rewards from interspecific competitive interactions between plants. We then ran the simulation for an additional 1000 timesteps beginning with the biomass distribution at timestep 4000. As in the FWs, we switched pollinators' consumption from rewards to consumption of vegetative biomass so that pollinators' dynamics followed Eqn. 1 instead of 1-1 or 1-2. All other species dynamics followed their original equations. We compared the results of these simulations with those of the original multiplex simulations by measuring differences in persistence, total community biomass, and the mean squared deviation between each species' biomass in the multiplex and control simulations at timestep 5000.

Data availability.

Network structures and simulation outputs are available in the online repository at https://github.com/fsvaldovinos/Multiplex_Dynamics.

Code availability.

Simulation and analysis code is available in the online repository at https://github.com/fsvaldovinos/Multiplex_Dynamics.

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787 **Table 1. Average (SD) effects of severing mutualistic feedbacks on species'**

788 **persistence and abundance.**

Treatment	**Rewards Only (RO)**		**Rewards Plus (RP)**	
Reward Productivity	Low	High	Low	High
Persistence	**–4.8 (6.1)**	**–5.7 (6.3)**	**–8.1 (7.6)**	**–7.1 (6.0)**
Total Biomass	–0.1 (15.9)	**–9.9 (10.0)**	**–5.5 (21.4)**	**–9.8 (14.6)**
Species' Biomass	**13 (12)**	**11 (10)**	**16 (12)**	**17 (18)**

789 Controls sever mutualistic feedbacks while preserving plant productivity in multiplex
790 simulations. Mean (Standard Deviation) differences in Persistence and Total Biomass
791 equal the average percent change in controls compared to the original multiplex
792 simulations (N = 24,276 for all treatments). Negative differences indicate that after
793 starting from the same biomass distributions among species achieved over the first 4000
794 timesteps of the simulations, on average, properties of the controls decrease below those
795 of the original simulations over the following 1000 of the simulations' full 5000
796 timesteps. Bold entries designate mean values significantly different from zero ($P <$
797 0.0001, N = 24,276, two-tailed t-tests). Average differences (SD) in Species Biomass at
798 the end of simulations are quantified by the mean squared deviations (SD) of each
799 species' abundance between the control and original simulations in units of biomass.
800

801 **Figure Legends**

802 **Figure 1. Network construction steps.** Nodes are vertically arranged by trophic level
803 with plant species at the bottom and carnivores at the top. All (grey, red, orange) links
804 represent feeding by the consumer above the resource except the bi-directional
805 pollination links (light blue) representing pollinators consuming plants' floral rewards
806 (e.g., nectar) and plants consuming pollinators' reproductive services. **a) Step 1:** Food
807 web generated using the Niche Model with diversity S_f and connectance C_f [14]. **b) Step 2:**
808 Plant-pollinator network generated using Thébault & Fontaine's [45] algorithm with
809 diversity S_p and connectance C_p. **c) Step 3:** Plant-pollinator network integrated with the
810 food web by adding pollinators (yellow nodes) and their links (light blue links) from b)
811 by randomly assigning plant species in a) to become the animal-pollinated plants in b)
812 (light blue nodes). **d) Step 4 of Rewards Only (RO) treatments:** stochastically link
813 predators of herbivores in c) to pollinators to construct the multiplex treatment and then,
814 for the Food Web (FW) treatment, transform pollinators into herbivores and animal-
815 pollinated plants into plants without pollinators. **e) Step 4 of Rewards Plus (RP)**
816 **treatments:** stochastically link predators of herbivores and diets of herbivores and
817 herbivorous omnivores in c) to pollinators for the multiplex treatment and then, for the
818 Food Web (FW) treatment, transform omnivorous and herbivorous pollinators and
819 animal-pollinated plants into omnivores, herbivores, and plants without pollinators,
820 respectively. Resulting diversity (S) and connectance (C) is shown under each treatment
821 (d–e). See Methods.

822 **Figure 2. Timeseries of a 72-species ecological network subjected to several**
823 **treatments.** This example uses a 50-species niche-model food web integrated with a
824 33-species plant-pollinator network following the same color scheme as in Fig. 1 (see
825 Methods). Note that 11 plant species in the food web are chosen to represent the 11

plant species in the plant-pollinator network (light blue). The top row shows the Rewards Only (RO) Food Web (FW, left) and Multiplex treatments subjected to Low (center) and High rewards productivity (right). The bottom row shows the Rewards Plus (RP) Food Web (FW, left) and Multiplex treatments subjected to Low (center) and High rewards productivity (right). Simulations last 5000 timesteps. Resulting species persistence is labeled in the upper right corner of each panel. Species that fall below a biomass of 10^{-4} continue to extinction (10^{-6}). The vast majority of species' abundances achieve steady state by 2000 timesteps with nearly all animal extinctions occurring before then, while several low-abundance plants with pollinators (light blue) continue slow declines well past 2000 timesteps.

Figure 3. Effects of mutualism on diversity and persistence within complex ecological networks. Column headings label the treatments described in Figures 1-2. Colors represent guilds of species described in Figures 1-2 and Methods. Initial diversity (*S*) on the x-axis and in a) describes the initial number of species in food webs with added herbivores and omnivores in the Food Web (FW) treatment and the corresponding pollinators added in multiplex networks. Increasing *S* corresponds to both an increasing fraction of the 20 plants without pollinators (darkest blue) that are assigned to be plants with pollinators (light blue) and to an increasing number of added (+) herbivorous, omnivorous, and pollinating consumers. μ is the mean across all $N =$ 24,276 simulations in each treatment. Bars show the mean values across networks of a given initial species diversity in increments of 2 species. Stacked diversity bar graphs show the mean number of species in each guild (colors) that contribute to initial a) or final b) community composition. c) Error bars are standard deviations. Persistence, the fraction of the initial diversity that persists to the end of the simulations, is shown for c)

the entire community and d-h) for each guild of consumers. Plants nearly always persist in our treatments, so their guild persistence is not shown (but see Figure S1).

Figure 4. Effects of mutualism on diversity, abundance, function and stability in complex ecological networks. Column headings, stacked bar graphs, and colors follow Fig. 3 with the addition of floral rewards shown in purple. a) The final diversity from Fig. 3 is shown again for reference. μ is the mean across all $N = 24{,}276$ simulations in each treatment for total (summed) b) abundance, c) productivity, and d) consumption or average variability of e) species or f) guilds, with colors representing the average variability of the guild (f) or species within the guild (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.

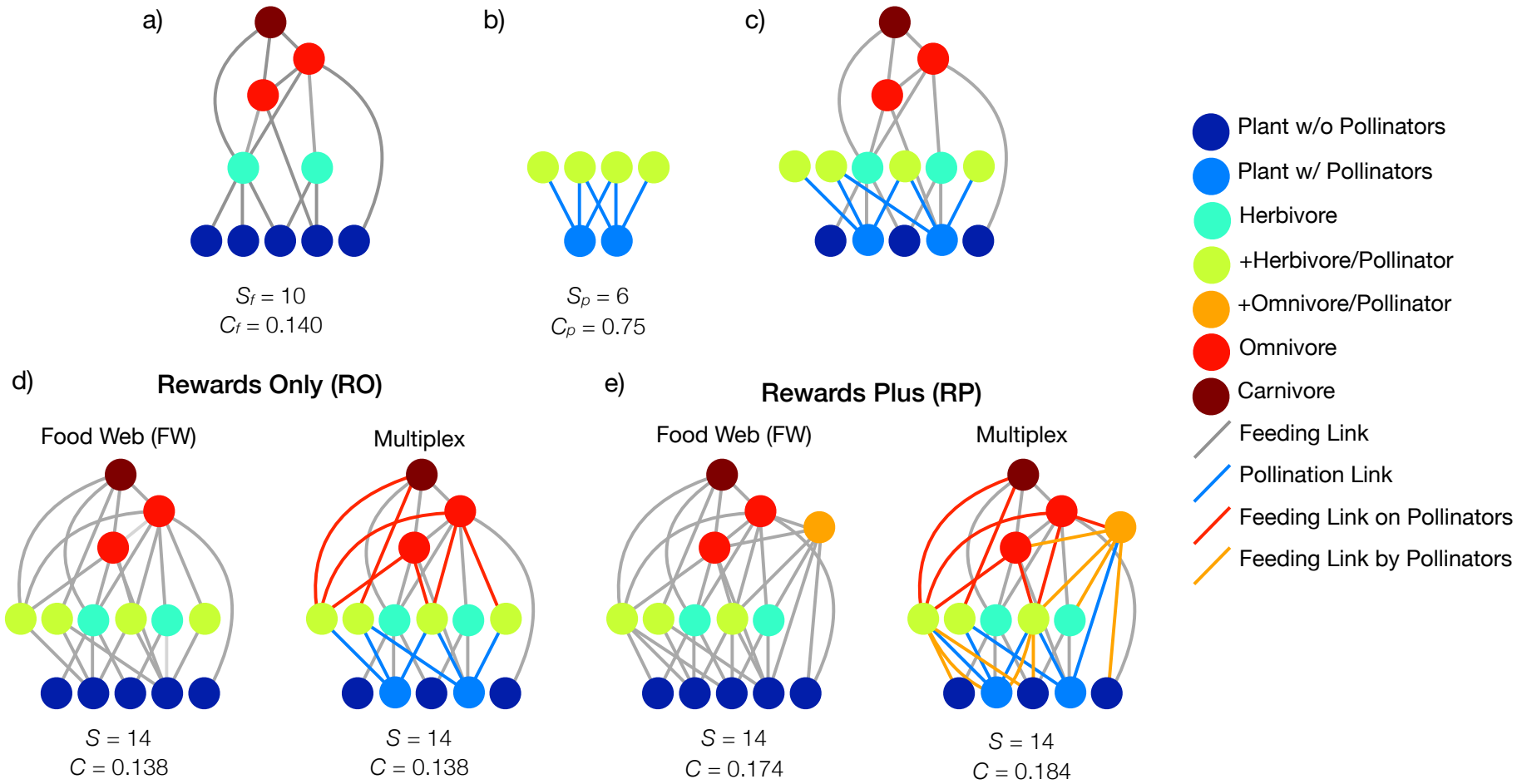

a)
S_f = 10
C_f = 0.140
b)
S_p = 6
C_p = 0.75
c)
Plant w/o Pollinators
Plant w/ Pollinators
Herbivore
+Herbivore/Pollinator
+Omnivore/Pollinator
Omnivore
Carnivore
Feeding Link
Pollination Link
Feeding Link on Pollinators
Feeding Link by Pollinators
d)
Rewards Only (RO)
Food Web (FW)
Multiplex
S = 14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

Figure 2.

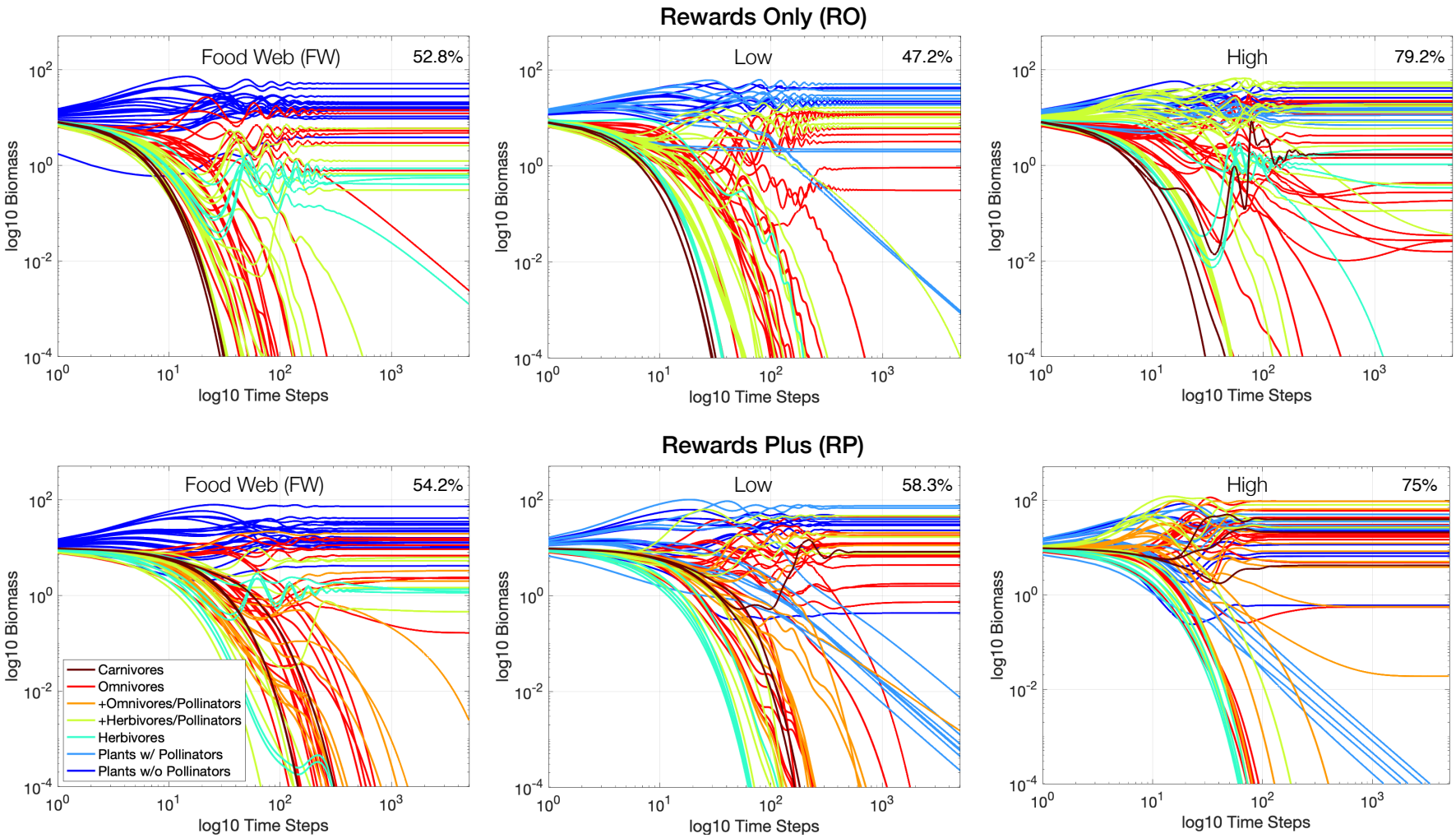

Rewards Only (RO)
Food Web (FW)
52.8%
Low
47.2%
High
79.2%
Rewards Plus (RP)
Food Web (FW)
54.2%
Low
58.3%
High
75%
log10 Biomass
log10 Time Steps
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Plants w/ Pollinators
Plants w/o Pollinators

Figure 3.

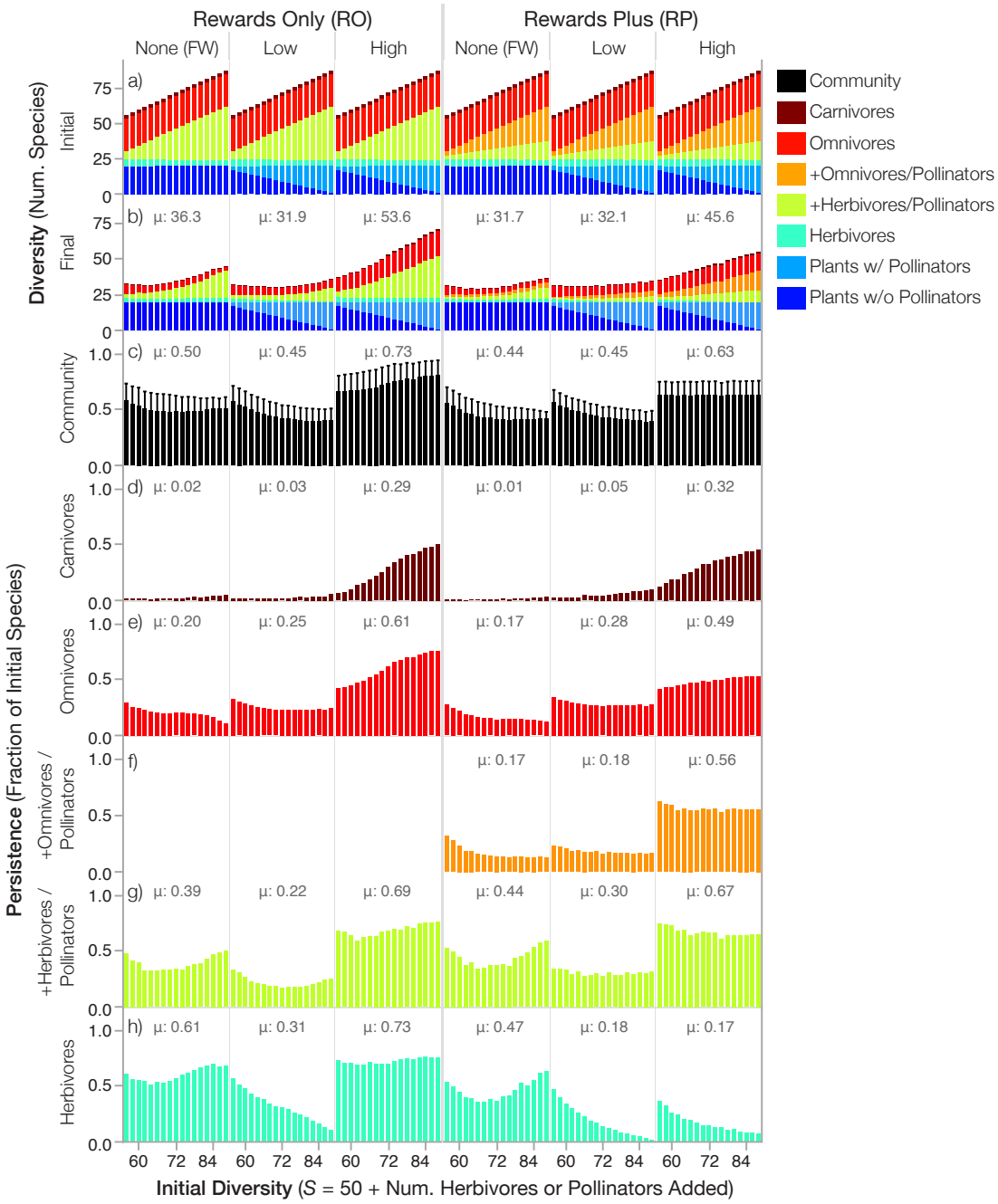
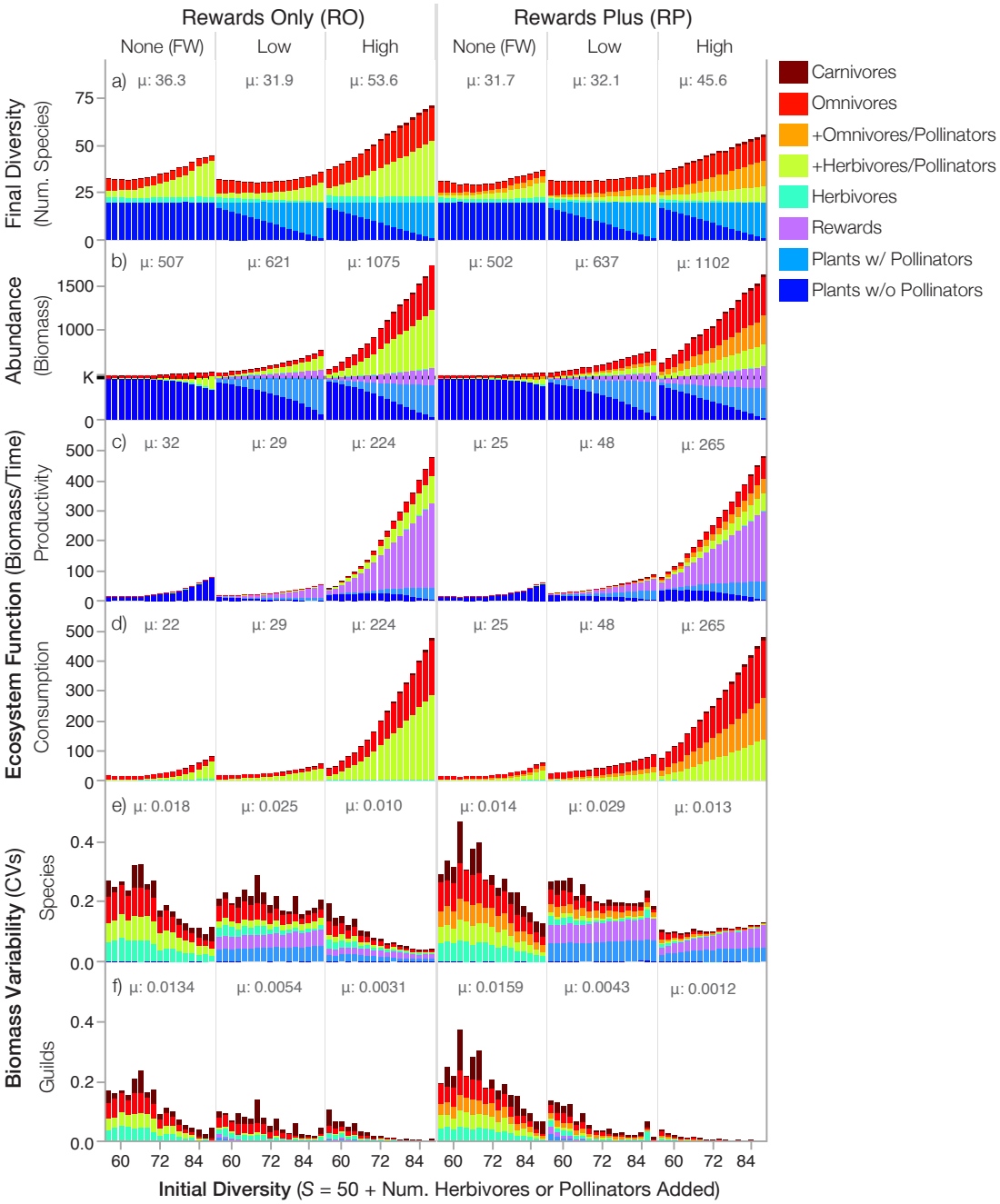

Rewards Only (RO)
Rewards Plus (RP)
None (FW)
Low
High
Diversity (Num. Species)
Initial
Final
Persistence (Fraction of Initial Species)
Community
Carnivores
Omnivores
+Omnivores / Pollinators
+Herbivores / Pollinators
Herbivores
a)
b) μ: 36.3 μ: 31.9 μ: 53.6 μ: 31.7 μ: 32.1 μ: 45.6
c) μ: 0.50 μ: 0.45 μ: 0.73 μ: 0.44 μ: 0.45 μ: 0.63
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. Herbivores or Pollinators Added)
Community
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Plants w/ Pollinators
Plants w/o Pollinators

Figure 4.


Rewards Only (RO)
Rewards Plus (RP)
None (FW)
Low
High
None (FW)
Low
High
Carnivores
Omnivores
+Omnivores/Pollinators
+Herbivores/Pollinators
Herbivores
Rewards
Plants w/ Pollinators
Plants w/o Pollinators
Final Diversity (Num. Species)
a) μ: 36.3
μ: 31.9
μ: 53.6
μ: 31.7
μ: 32.1
μ: 45.6
Abundance (Biomass)
b) μ: 507
μ: 621
μ: 1075
μ: 502
μ: 637
μ: 1102
Ecosystem Function (Biomass/Time)
Productivity
c) μ: 32
μ: 29
μ: 224
μ: 25
μ: 48
μ: 265
Consumption
d) μ: 22
μ: 29
μ: 224
μ: 25
μ: 48
μ: 265
Biomass Variability (CVs)
Species
e) μ: 0.018
μ: 0.025
μ: 0.010
μ: 0.014
μ: 0.029
μ: 0.013
Guilds
f) μ: 0.0134
μ: 0.0054
μ: 0.0031
μ: 0.0159
μ: 0.0043
μ: 0.0012
Initial Diversity (S = 50 + Num. Herbivores or Pollinators Added)