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

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22   ABSTRACT

23   Ecosystems are composed of complex networks of many species interacting in different

24   ways. While ecologists have long studied food webs of feeding interactions, recent studies

25   increasingly focus on mutualistic networks including plants that exchange food for

26   reproductive services provided by animals such as pollinators. Here, we synthesize both

27   types of consumer-resource interactions to better understand the controversial effects of

28   mutualism on ecosystems at the species, guild, and whole-community levels. We find that

29   consumer-resource mechanisms underlying plant-pollinator mutualisms can increase the

30   persistence, productivity, abundance, and temporal stability of both mutualists and non-

31   mutualists in food webs. These effects strongly increase with floral reward productivity

32   and are qualitatively robust to variation in the prevalence of mutualism and pollinators

33   feeding upon resources in addition to rewards. This work advances the ability of

34   mechanistic network theory to synthesize different types of interactions and illustrates how

35   mutualism can enhance the diversity, stability, and function of complex ecosystems.

36

37   INTRODUCTION

38   As elegantly illustrated by Darwin's "tangled bank," [1] ecosystems are complex,

39   composed of many different types of interactions among many different species. However,

40   theory has classically predicted that complexity in terms of the number and strength of

41   interspecific interactions destabilizes ecological systems [2]. Mutualistic interactions like

42   those between plants and their pollinators are thought to be particularly destabilizing [3,4].

43   Robert May famously emphasized this point by calling mutualism an "orgy of mutual

44   benefaction" (pg. 95) [5] whose instability due to positive feedback loops helps explain why

45   mutualism is infrequent and unimportant in natural systems [3]. Yet, mutualisms appear to

46   be not only frequent but key to maintaining much of the biodiversity that drives ecosystems

47   [6,7], especially agricultural ecosystems essential to human wellbeing [8,9]. Here, we address

48   such disparities between theory and observation by developing and applying consumer-

49   resource theory of feeding and reproductive mechanisms that integrates food webs and

50   mutualistic networks into "multiplex" networks containing different types of interactions.

51   We use our multiplex model to study how mutualism affects the diversity, stability, and

52   function of complex ecosystems.

53   The integration pursued here benefits from long but largely separate traditions of

54   research on feeding and mutualistic interactions [8,10]. For example, "mutualistic" feeding

55   interactions between species with positive effects on each other (+,+), e.g. pollinators

56   foraging on the nectar of flowering plants, are often excluded from food web data (e.g., ref

57   [11]), while "antagonistic" feeding interactions (+, −), e.g. herbivory and predation, are

58   typically excluded from mutualistic networks [12]. Additionally, food web research has

59   focused more on aquatic systems [13] where feeding interactions are strongly structured by

60   body mass or gape size [13,14], while mutualism research has focused more on terrestrial

61   systems where feeding interactions may be more strongly structured by other organismal

62   traits like chemical defense and shape of mouth parts [13–15]. Within aquatic ecosystems, the

63   allometric trophic network theory [16,17] of food webs has leveraged body-size considerations

64   to successfully simulate the seasonal dynamics of many interacting species [18,19] and predict

65   the quantitative effects of experimental species manipulations [20–22]. However, the failure of

66   these predictions in the presence of facilitation (+, 0), e.g. habitat provisioning for mussels

67   by barnacles, highlights the need for food-web theory to better address interactions with

68   positive effects beyond nutrition [20]. Mutualistic network theory has focused on animal-

69   mediated pollination, an interaction involving trophic and reproductive effects [12,23],

70   motivated in part by large agricultural and evolutionary significance [9,24,25]. Merging these

71   distinct traditions requires a more unified approach that addresses several problems.

72   One significant problem is that classifying interactions based on positive and/or

73   negative effects ignores logical inconsistencies such as when "antagonistic" herbivory or

74   predation respectively increase plant fitness [26] or prey abundance [27] and when "mutualistic"

75   pollinators parasitize plants by robbing their floral rewards without transferring pollen [24].

76   We resolve such conflicts by modelling mechanisms by which organisms interact and

77   allowing effects to emerge from the interactions rather than asserting such effects *a priori*.

78   We do this by developing consumer-resource theory that has long been applied to food web

79   theory [16,28] and more recently applied to mutualistic interactions [29,30] with success

80   predicting pollinators' foraging preferences in the field [31]. Both feeding and mutualistic

81   interactions typically involve food consumption while mutualistic interactions also often

82   involve reproductive services provided by animals such as pollinators and seed dispersers

83   [27,29,30]. Positive, negative, and neutral interspecific effects dynamically emerge from the

84   benefits and costs of participating in these interactions, which often both involve the same

85   organisms and jointly determine much of the stability and function of ecosystems [8,10,32–36].

86   For example, feeding interactions such as parasitism and predation on pollinators,

87   herbivory on animal-pollinated plants, and feeding by pollinators on animals and plant

88   vegetation in addition to floral rewards such as nectar and pollen profoundly affect

89   pollination dynamics, crop yields [37], and long-term sustainability of agroecosystems [38].

90   Another outstanding problem with understanding the joint effects of feeding and

91   mutualistic interactions concerns contradictory conclusions of previous theoretical work.

92   Classic "effects-based" theory has long held that mutualistic interactions are generally

93   *destabilizing* (Table 1) especially at high complexity [3,4]. However, more recent theory

94   finds that mutualisms *stabilize* ecological systems under conditions such as high levels of

95   complexity of mutualism relative to antagonism in "merged" plant-pollinator and plant-

96   herbivore networks [35,39], low levels of complexity in hierarchical networks of all types of

97   interactions [40], or intermediate levels of mutualism when mutualistic links are randomly

98   assigned and animals allocate effort to feeding and mutualistic interactions separately [41–43].

99   Contradictions among these findings may arise from different definitions of stability (i.e.

100   local stability or persistence, Table 1) and network architectures [4,41] that often misrepresent

101   empirically-observed structure [40]. A broader problem is that narrowly focusing on stability

102   develops inefficient theory [44] that ignores how mutualisms alter the diversity, population

103   dynamics, and overall functioning of complex ecosystems.

104   To more broadly understand the ecology of mutualistic interactions, here, we follow

105   repeated calls to synthesize different types of interactions within networks [8,10,32–36,45] by

106   developing and applying mechanistic consumer-resource theory to "multiplex" ecological

107   networks (Table 1) [34,36]. Our model based on this theory integrates the structure and

108   dynamics of feeding and reproductive mechanisms from which effects of interspecific

109   interactions emerge including predation (+, –), mutualism (+, +), and resource and apparent

110   competition (–, –) [46,47]. We simulate network *dynamics* by extending Brose *et al.*'s

111   allometric trophic network theory [16] to incorporate Valdovinos *et al.*'s theory of the

112   exchange of food for reproductive services between plants and their pollinators (Fig. 1)

113   [30,31]. We simulate network *structures* by integrating Williams and Martinez' "niche model"

114   of food webs [48] with Thébault and Fontaine's model of mutualistic networks [49] (Fig. 2).

115   Using this multiplex model, we investigate how the presence, prevalence, and intensity of

116   mutualism affect multiple dimensions of ecological stability [50] by assessing diversity,

117   persistence, dynamics, and function at the species, guild, and ecosystem levels.

118   RESULTS

119   **The multiplex model.**

120   We synthesize the *structure* and *dynamics* of feeding and reproductive interactions

121   by integrating food webs and mutualistic networks and extending Allometric Trophic

122   Network (ATN) theory [16-18,20,51] to include the consumption of floral rewards produced by

123   plants and reproductive services produced by pollinators (Fig. 1, Methods). In addition to

124   ATN theory's logistically growing "plants without pollinators," "plants with pollinators" in

125   our multiplex model must consume reproductive services produced by their pollinators to

126   vegetatively grow. This involves partitioning the biomass of plants with pollinators into

127   coupled pools of vegetation and floral rewards [30] that plants produce at an energetic cost

128   [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

221   multiplex treatments. Concurrently, plant productivity increased with initial diversity and

222   mutualism in all but Low RO treatments. Total consumption (Fig. 6d) in all treatments

223   very closely matched total production (Fig. 6c) and was distributed similarly to that of

224   animal species' biomass (Fig. 6b).

225   The higher biomass of multiplex compared to FW treatments was primarily due to

226   increases in animal biomass (Fig. 6b), while differences in productivity were due to

227   decreases in vegetative productivity coupled with strong increases in productivity of

228   rewards and smaller increases in animals (Fig. 6c). These differences emerge primarily due

229   to the interactive dynamics of rewards in which growth potential, unlike all other stocks of

230   biomass, depends not on its own abundance but on the abundance of another component,

231   i.e., the vegetative biomass of plants with pollinators (Methods, Eqn. 6). This allows

232   rewards to be highly productive even when very rare whereas other network components

233   would be unproductive or could even go extinct. In FW treatments, the overall weak

234   increases in ecosystem biomass and strong increases in total productivity with increasing

235   initial diversity emerge from increasing herbivore biomass that reduces plant vegetation

236   below carrying capacity (Fig. 6b), freeing plants from competition. This increases plant

237   productivity (Fig. 6c) and animal biomass enough to lead to small net increases in total

238   biomass with initial diversity (Fig. 6b). Multiplex treatments experience similar decreases

239   of plant biomass and corresponding increases in vegetative plant productivity (Fig. 6b-c),

240   but rewards productivity dramatically increases as does animal biomass. These increases

241   are mostly due to increases in pollinator abundance that stimulate rewards productivity by

242   depleting rewards below their self-limitation threshold. Then, animal biomass and

243   productivity are further elevated by increases in the biomass of omnivores and carnivores

244 that feed on the increasingly abundant pollinators. These patterns in production,

245 consumption, and increased animal biomass are greatly enhanced in High rewards

246 treatments.

Stability.

247

248 We evaluated the temporal stability of our networks by analyzing coefficients of

249 variation (CV = standard deviation / mean) of biomass during our simulations' final 1000

250 timesteps for each species, for the sum of each species within each guild (Fig. 6f), and for

251 the sum of each species within the ecosystem. We calculated a species-level CV for each

252 guild by summing each species' CV within the guild and dividing by the number of species

253 in the guild (Fig. 6e) and a species-level CV for each ecosystem by doing the same thing

254 for all species within the network (Fig. 4e). We calculated a guild-level CV for each guild

255 as the CV for the total biomass in each guild (Fig. 6f), and a guild-level CV for each

256 ecosystem by summing all guilds' CVs and dividing by the number of guilds (standardized

257 across treatments, Fig. 4f). Finally, we calculated an ecosystem-level CV as the CV of the

258 total biomass of the ecosystem.

259 At the ecosystem level, all treatments were exceedingly stable (CV < 0.001). In

260 contrast, species on average were much more variable (Fig. 4e), especially in Low rewards

261 treatments where plants with pollinators and their rewards contributed large amounts of

262 variability (Fig. 6e). Large variability in plant and reward biomass in multiplex treatments

263 was caused by the very low biomass of a few plant with pollinators species whose biomass

264 decreased throughout the end of the simulations (e.g. Fig. 3). This low and decreasing

265 biomass yields large CVs at the species level but contributes very little to guild-level

266 variation (Fig. 6e-f) due to the tiny fraction of their guild's biomass comprised by these

267   very rare species. In FW treatments, where extinctions occur relatively early (Fig. S2),

268   species-level and guild-level variation are comparable (Fig. 4e-f). In contrast, average

269   guild-level variation (Fig. 4f) is only a fraction of the species-level variation (Fig. 4e) in

270   multiplex treatments. Variation at both the species and guild levels decrease with initial

271   diversity and mutualism in all treatments except for species-level variation in High RP

272   networks where large decreases in animal variability only partly compensate for larger

273   increases in rewards variability (Fig. 6e-f). High RP networks are by far the most stable at

274   the guild level however, both on average (Fig. 4f) and with increasing mutualism (Fig. 6f).

275   Overall, mutualism broadly stabilizes the dynamics of multiplex networks by reducing

276   variability of animal populations compared to those in FWs.

277   **Overall effects of mutualism.**

278   Excepting Low RO networks, multiplex treatments had higher average diversity,

279   persistence, biomass, productivity, and consumption than their FW counterparts (Fig. 4).

280   Multiplex treatments were also more temporally stable than FW treatments at the guild

281   level and, for animal populations, at the species and guild levels. Interestingly, though Low

282   RO networks displayed lower average diversity, persistence, productivity, and overall

283   species-level stability than FW treatments, these effects were ameliorated in Low RP

284   networks, in which pollinators had additional food available to them in the form of plant

285   and animal resources. This suggests that the positive effects of mutualism are reasonably

286   restricted to systems that provide sufficient food for mutualistic animals to survive (also see

287   S2) and that the low persistence of the many added pollinators in Low RO networks (Fig.

288   5g) throttles the positive effects of mutualisms from more generally increasing ecosystem

289   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

359   traditional food web dynamics when supplementing food webs with rewards productivity

360   similar to that in multiplex networks. The removal of dynamic feedbacks between

361   pollinators and animal-pollinated plants alters species composition and abundance by

362   reducing persistence and abundance of omnivores but increasing abundance of plants

363   formerly dynamically partnered with pollinators (Fig. S7-8). Thus, the combination of

364   dynamic feedbacks and mutualistic interaction strength, in terms of rewards productivity,

365   lead to the increased stability and function we observed in our multiplex ecological

366   networks.

367   Our theory embraces Levin's assertion that "The key to prediction and

368   understanding lies in the elucidation of mechanisms underlying observed patterns" (p.1943)

369   [58] by using trophic and reproductive mechanisms underlying the observed structure and

370   dynamics of multiplex networks to understand and predict how mutualism affects complex

371   ecosystems. Previous theory obscures key dynamics of such mechanisms by assuming

372   their effects [23,47,59]. For example, the few studies of ecological networks involving both

373   feeding and mutualistic interactions assert species have constant per-capita direct effects on

374   each other's fitness or abundance [36,45]. Such effects can rarely be reproducibly measured

375   due to, e.g., context-dependence and temporal variability [59,60]. We instead focused on

376   mechanisms such as more reproducibly observed rates of production and consumption of

377   food in terms of biomass [18,61] and reproductive services in terms of pollinator visits [36]. We

378   also focused on more realistic (i.e., empirically-corroborated) network architectures – as

379   have others with results similar to ours. For example, García-Callejas *et al.* [40] found that

380   mutualism increases or leaves unaffected persistence of ecological networks containing

381   different types of interactions structured according to realistic species abundance

382   distributions among different trophic levels. Several studies of near-equilibrium stability

383   similarly find that destabilizing effects of mutualism may be overstated in models of fewer

384   species [32] and interaction types [41] compared to more realistic ecological networks.

385   However, unlike studies that require the "peculiar" constraint that animals' interaction

386   efforts are allocated separately between mutualistic and non-mutualistic interactions [41–43],

387   we find that mutualism is stabilizing according to empirically-relevant metrics (Table 1)

388   when unpartitioned effort is allocated to both types of interactions.

389   Our multiplex treatments may bound the diet breadth of pollinators in the field by

390   providing pollinators unrealistically few resources in RO networks and unrealistically many

391   resources in RP networks. This suggests results intermediate between RO and RP networks

392   may best predict empirical observations. For example, in both RO and RP treatments, High

393   rewards productivity increases the persistence, biomass, and productivity on average of all

394   consumer guilds over that in Low rewards networks (Figs. 5d-h, 6b-c) excepting the

395   decrease in herbivore persistence in RP networks (Fig. 5h). This suggests that, in natural

396   systems, we may expect the weakest increases in persistence, biomass, and productivity due

397   to increased mutualism to occur among herbivores. The different effects of our treatments

398   on herbivores may be due to RP pollinators' additional herbivorous and carnivorous

399   feeding links compared to RO pollinators. These additional links increase competition and

400   predation pressure on herbivores by pollinators, omnivores, and carnivores. More broadly,

401   our results suggest that, as the prevalence of pollination mutualisms increase, the diversity

402   and biomass of upper trophic-level consumers will increase while our predictions for the

403   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 ($S_p = P + A = 9, 12, …, 57$)

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 ($S = S_f + A = 56, 58, …, 88$). 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 ($2 \leq$ TL ≤ 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   $$\frac{dB_i}{dt} = \sum_{j \in resources} C_{ij}(B_j) - x_i B_i - \sum_{j \in consumers} C_{ji}(B_i)/e_{ji} \qquad (1)$$

517   where x_i is the allometrically-scaled mass-specific metabolic rate of species i and e_{ji} is the

518   assimilation efficiency of species j eating i. C_{ij} is the rate of species i assimilating B_j, the

519   biomass of species j:

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

521   where y_{ij} is the maximum consumption rate per metabolic rate. $F_{ij}(B_j)$ is the functional

522   response of i eating j:

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

524   where ω_{ij} is i's relative preference for j, h is the Hill coefficient [71], and B_{0ij} is the "half-

525   saturation" density of resource j at which i's consumption rate is half y_{ij} [18]. The form of the

526   preference term, ω_{ij}, determines if a trophic generalist (i) is treated either as a "strong

527   generalist" ($\omega_{ij} = 1$) or "weak generalist" ($\omega_{ij} = 1/($# of species in i's diet) [72]. Here, we

528   present results only for weak generalists that search for each of their resources equally even

529   if one or more of their resources are extinct. Eqn. 3 is a Type II functional response when h

530     $= 1$ and a Type III response when $h = 2$. We use $h = 1.5$ for a weak Type III response [71].

531   We use ATN theory's logistic growth model [18] to simulate biomass dynamics of

532   plants without pollinators as:

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

534   where r_i is the maximum mass-specific growth rate of plant i, and K is the carrying capacity

535   of the plant community. For plant with pollinators i (Fig. 1), we model its vegetative

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

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

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

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 $m_i = Z_i^{swTL_i - 1}$, 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 $0.314 m_i^{-0.25}$, 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-

577   wide carrying capacity for plant vegetative biomass of $K = 480$, and an assimilation

578   efficiency of $e_{ij} = 1.0$ for pollinator species i consuming the floral rewards of j. For plants

579   with pollinators, we used a rewards production rate of $\beta_i = 0.2$ or 1.0 (Low or High rewards

580   productivity treatments, respectively), a self-limitation rate of $s_i = 0.4$, and a vegetative cost

581   of rewards production of $\kappa_i = 0.1$. In FW treatments, rewards are zeroed out ($R_i = \beta_i = 0$)

582   and all plants are parameterized so that they behave as plants without pollinators while

583   pollinators are parameterized as "added animals" (herbivores or omnivores) that consume

584   vegetation with the associated lower assimilation efficiency ($e_{ij} = 0.66$) but have otherwise

585   unchanged vital rates. See Table S4 for a summary of model parameters and values.

586   **Simulations.**

587   We simulated each of our $N = 24,276$ networks subjected to each six treatments

588   (High RO, Low RO, RO FW, High RP, Low RP, and RP FW) for a total of 145,656

589   simulations. We used MATLAB's [74] differential equation solvers (ode15s for the multiplex

590   treatments and ode45 for FWs) to simulate these networks for 5000 timesteps (Fig. 3). By

591   2000 timesteps, the simulations were approximately at dynamical steady-state, which we

592   assessed through small changes in persistence with increased simulation length. More

593   specifically, persistence decreased by 5% on average between 2,000 and 500,000 timesteps

594   in a sample of 90 networks from each treatment (Fig. S2). We initialized all biomasses (B_i

595   and R_i) to 10 and used an extinction threshold of $B_i < 10^{-6}$. Statistical analyses were

596   performed in JMP 14 [75]. Our results are qualitatively robust to simulation length (Fig. S2).

597   Sensitivity of our results to parameter variation are reported in the Supplementary

598   Information (Tables S1-S3) and qualitative effects of each parameter are summarized in

599   Table S2.

600 **Outputs.**

601   We quantified ecosystem stability and function using species persistence, biomass,

602 productivity, consumption, and variability at or near the end of the simulations, when the

603 dynamics were approximately at steady state (Table 1). We calculated these metrics for the

604 whole ecosystem (Fig. 4) and for seven guilds of species (Figs. 5-6). Two guilds are self-

605 evidently described as species of plants without pollinators and plants with pollinators.

606 Herbivores, omnivores, and carnivores refer only to species present in the niche-model food

607 webs prior to integrating animals from plant-pollinator networks in Fig. 2c. Herbivores eat

608 only vegetative biomass. Omnivores eat vegetation and animals. Carnivores eat only

609 animals. The meanings of the two remaining guilds (collectively referred to as the "added

610 animals") depend on the treatment that adds them to the food web. Added

611 herbivores/pollinators refer to herbivores added by the FW treatments, pollinators added by

612 the RO or RP multiplex treatments that consume only rewards, and pollinators added by the

613 RP multiplex treatment that consume rewards and vegetation. Added

614 omnivores/pollinators refer to omnivores added by the RP FW treatment and analogous

615 pollinators added by the RP multiplex treatment that consume rewards, other animals, and

616 potentially vegetation. When relevant (e.g. in Fig. 6), we considered the rewards biomass

617 of all plants with pollinators as an eighth guild.

618   We calculated all outputs at the end of the simulations (timestep 5000) except for

619 biomass variability, which we calculated over the last 1000 timesteps. Final diversity and

620 persistence are the *number* and the *fraction*, respectively, of the initial species whose

621 biomass stayed above the extinction threshold throughout the simulation. Biomass

622 abundance, productivity, and consumption are calculated as summed totals for the whole

623   ecosystem and/or each guild of species. Plant productivity is the rate of biomass increase

624   due to growth minus loss due to rewards production. Rewards productivity is the rate

625   rewards production minus self-limitation. Animal productivity is the rate of biomass

626   increase due to assimilation minus losses due to metabolic maintenance. Consumption is

627   the rate of biomass assimilated by consumers divided by assimilation efficiency. Species-

628   level variability for the whole ecosystem (Fig. 4e) is the averaged coefficients of variation

629   of biomasses (CV = standard deviation / mean) of all surviving species in the ecosystem.

630   Species-level variability for each guild (Fig. 6e) is the averaged CVs of all surviving

631   species within that guild. Guild-level variability for each guild (Fig. 6f) is the CV of the

632   summed biomass of all species in that guild. Guild-level variability of the whole ecosystem

633   (Fig. 4f) is the averaged CVs for five guilds (all plants, herbivores, all added animals,

634   omnivores, and carnivores), which standardizes the grouping of species into guilds across

635   treatments. Ecosystem-level variability (not shown) is the CV of the summed biomass of all

636   species in the ecosystem.

637   **Feedback control.**

638   To disentangle effects of mutualistic feedbacks from effects of floral rewards, we

639   ran multiplex simulations with mutualism "turned off" ("feedback control"), in which all

640   feedbacks (blue arrows in Fig. 1) between vegetation, rewards, and pollinators are severed.

641   This control transforms plants with pollinators into two *independent* biomass pools: a plant-

642   without-pollinators (vegetation) pool and a rewards pool, both with constant production

643   rates. In this way, rewards production is forced to match that of the multiplex model in the

644   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 $(\overline{\beta_i B_i - s_i R_i})$ 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 $R_i = \overline{R_i}$, 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
$$\frac{multipex\ final\ guild\ diversity}{multiplex\ final\ diversity} - \frac{control\ final\ guild\ diversity}{control\ final\ diversity} \qquad (8)$$

666   and the fraction of ecosystem biomass composed by each guild:

667
$$\frac{multipex\ guild\ biomass}{multiplex\ total\ biomass} - \frac{control\ guild\ biomass}{control\ total\ biomass}. \qquad (9)$$

668   If these *effects of feedbacks* evaluate to positive numbers, feedbacks in multiplex

669   simulations have a positive effect, i.e. they increase persistence or biomass of the

670   ecosystem or guild. If *effects of feedbacks* are negative, feedbacks decrease persistence or

671   biomass. If, instead, *effects of feedbacks* are approximately zero, stability and function in

672   our multiplex treatments can be attributed to the overall rates of plant (vegetative and

673   rewards) productivity that emerge during those simulations.

674   **Data availability.**

675   Network structures and simulation outputs are available in the online repository at

676   https://github.com/kayla-hale/Multiplex-Dynamics/.

677   **Code availability.**

678   Simulation and analysis code are available in the online repository at

679   https://github.com/kayla-hale/Multiplex-Dynamics/.

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867

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
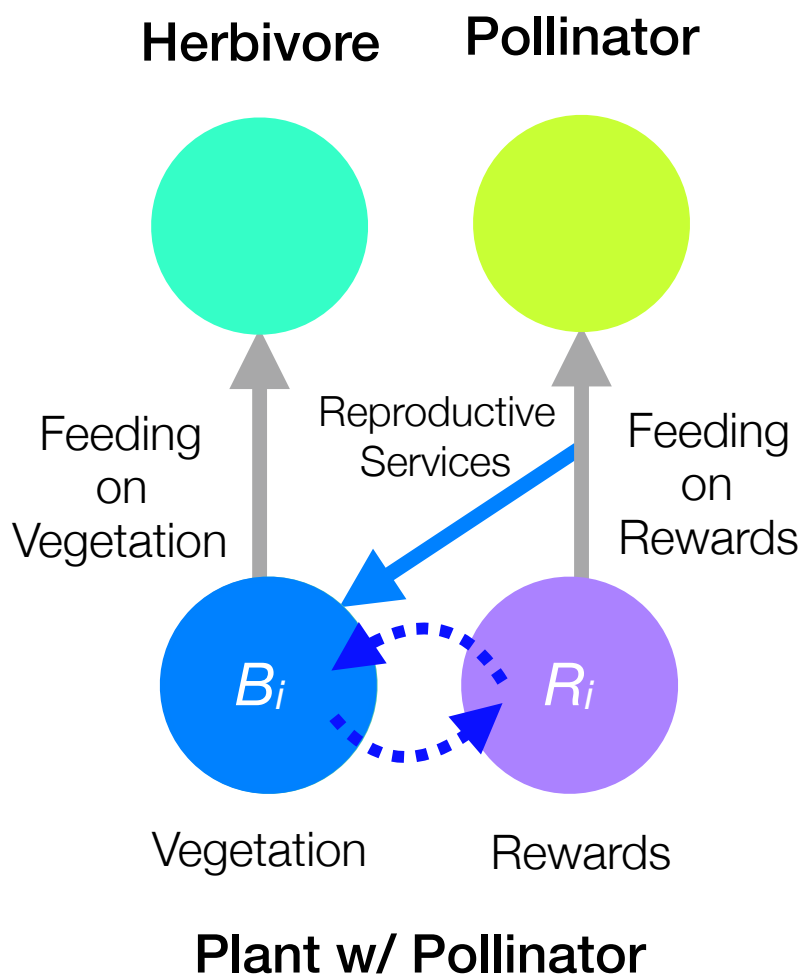
933   shown in one row (d).

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

939   added (+) animals and to an increasing *fraction* of the 20 plants without pollinators that are

940   assigned to be plants with pollinators, and thus to *increasing prevalence of mutualism* in

941   multiplex treatments. Bars show mean values for networks of a given initial S in

942   increments of 2 species. Stacked bar graphs show the mean number of species in each

943   guild (colors) that contribute to a) initial or b) final ecosystem diversity. Persistence, the

944   fraction of the initial diversity that persists to the end of the simulations, is shown for c) the

945   entire ecosystem (i.e. network of species) and d-h) for each guild of animals. c) Error bars

946   show standard deviations. d-h) μ is the mean guild persistence over all $N = 24,276$

947   simulations in each treatment. Plants nearly always persist in our treatments (Fig. S1), so

948   their persistence is not shown.

949   **Figure 6. Effects of increasing mutualism on diversity, abundance, function, and**

950   **temporal stability in complex ecosystems.** Formatting follows Fig. 5 with the addition of

951   floral rewards shown in purple. a) Final diversity from Fig. 5 is shown again for reference.

952   Stacked bar graphs show the contribution of each guild (colors) to total ecosystem b)

953   abundance, c) productivity, d) consumption, and average variability over time of e) species

954   and f) guilds, with colors representing the average variability of the guild in f) or species

955   within the guild in e). b) The community-wide carrying capacity for plant vegetative

956   biomass (K) is marked on the y-axis; total plant vegetative biomass (summed vegetation of

957   plants with and without pollinators) does not exceed this value.
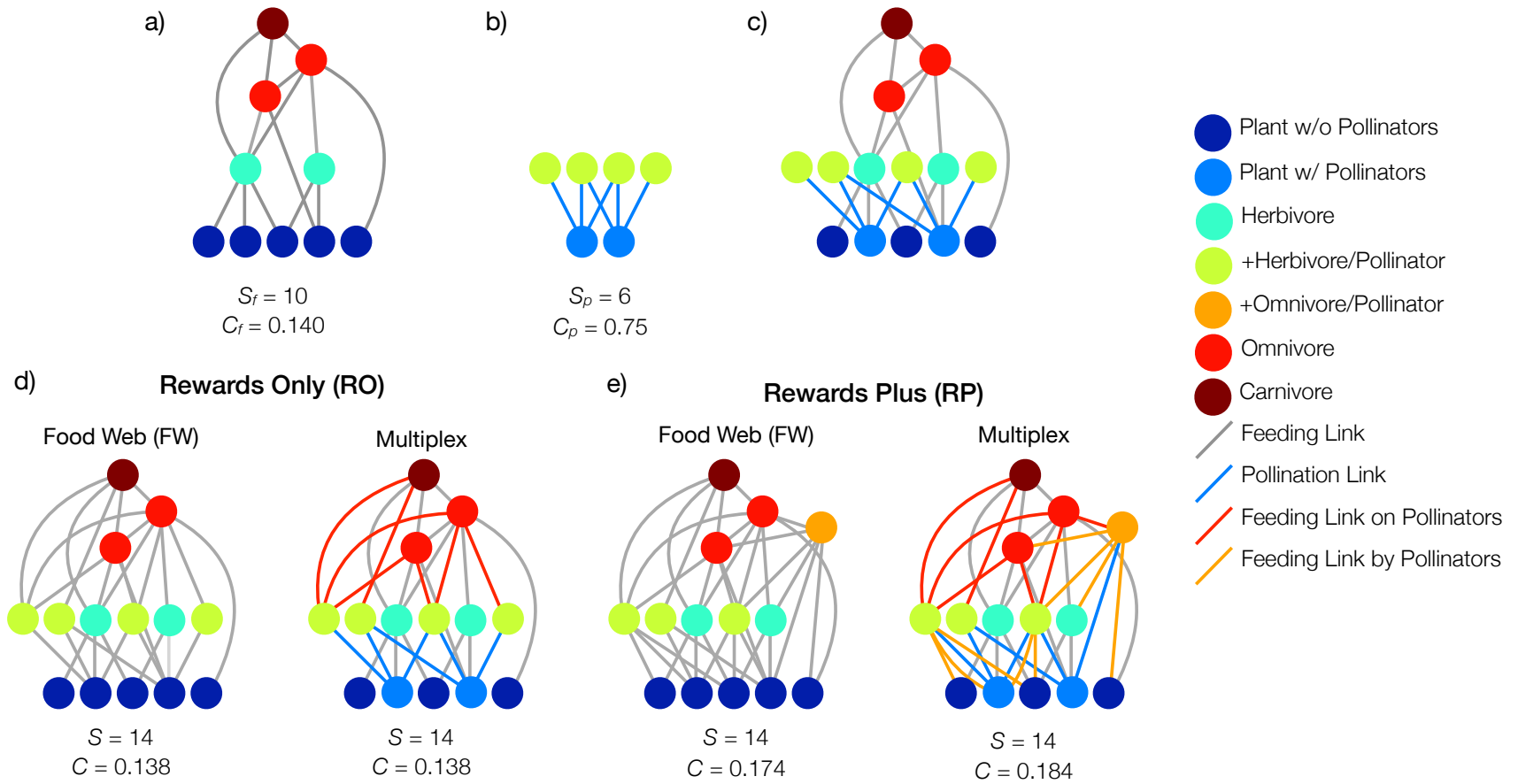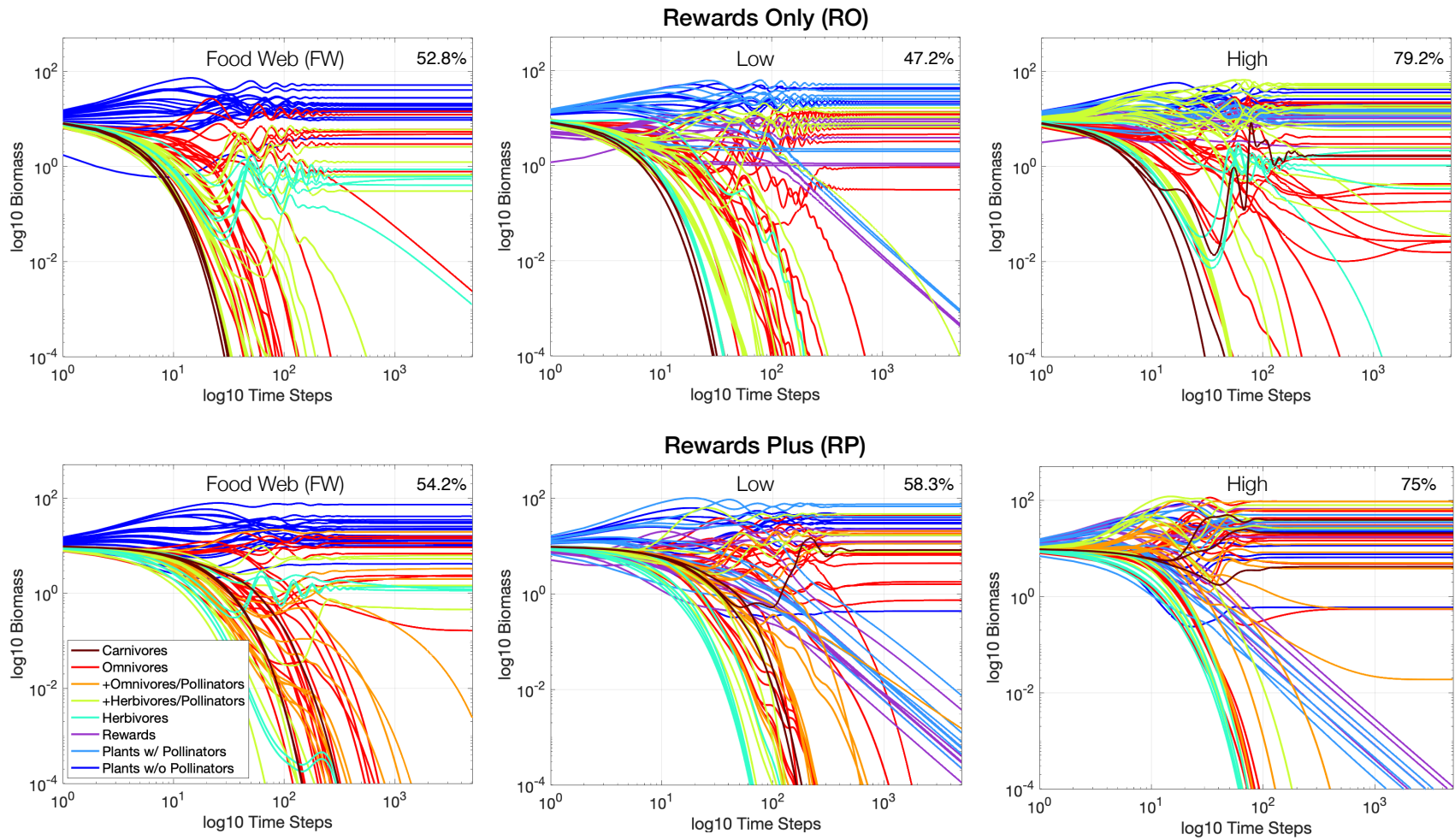
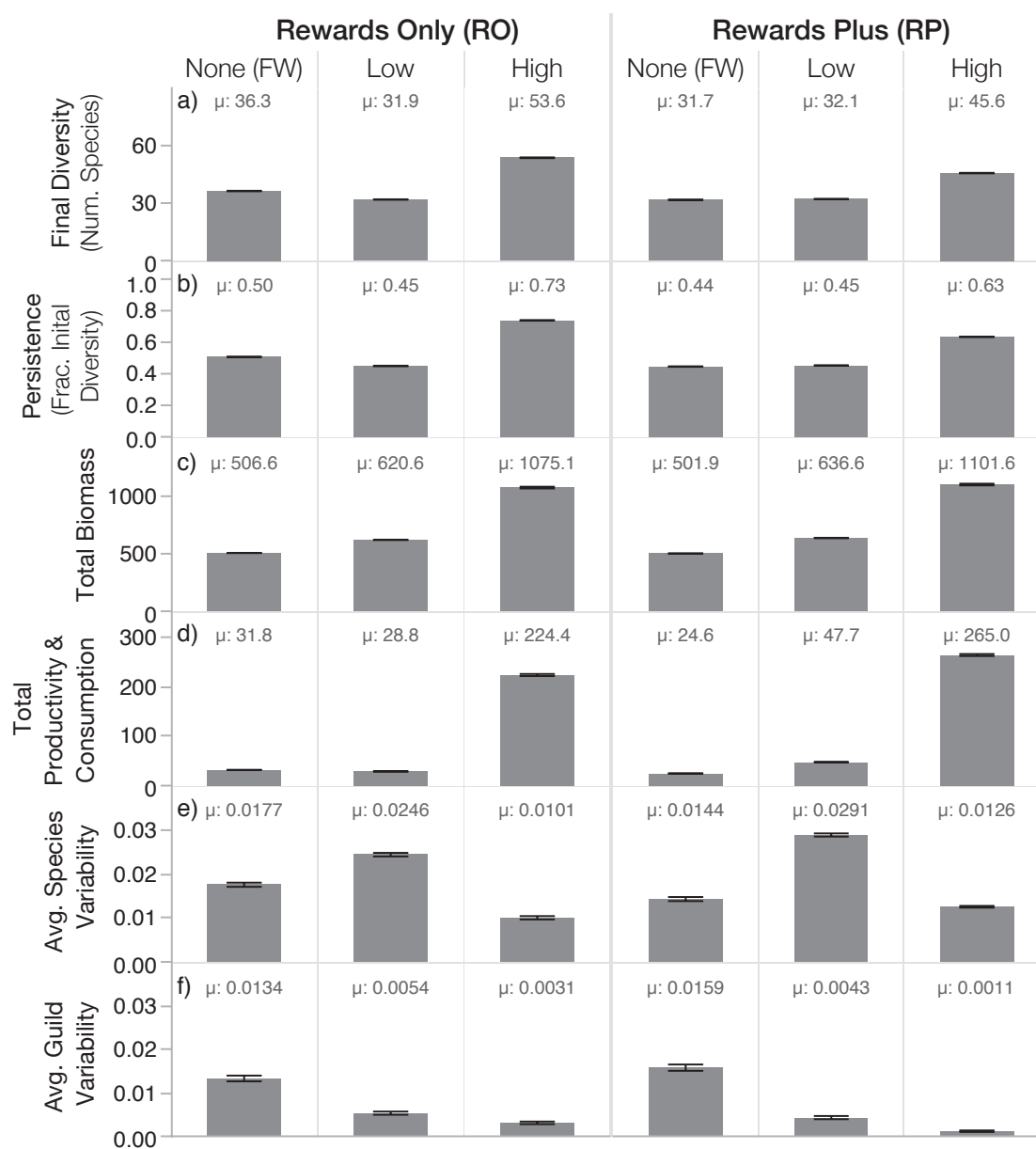958

959   **Figure 1.**

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961

962 **Figure 2.**

a)
$S_f = 10$
$C_f = 0.140$

b)
$S_p = 6$
$C_p = 0.75$

c)

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
$S = 14$
$C = 0.184$

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

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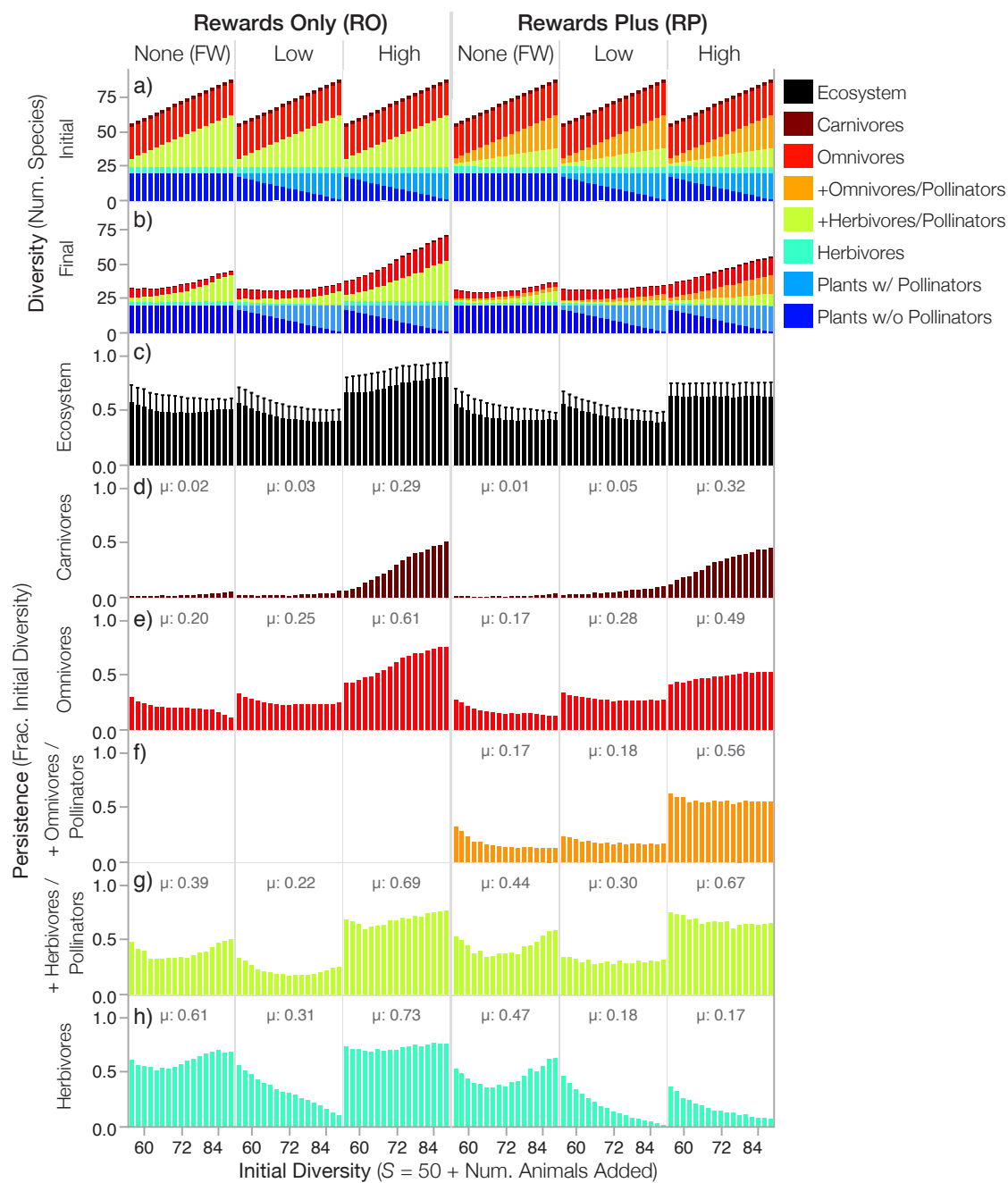
964 **Figure 3.**

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966   **Figure 4.**

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970   **Figure 5.**

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974 **Figure 6.**

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