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Niche partitioning due to adaptive foraging reverses effects of 4 nestedness and connectance on pollination network stability

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Abstract

40 Much research debates whether properties of ecological networks such as nestedness and
connectance stabilize biological communities while ignoring key behavioral aspects of
42 organisms within these networks. Here, we computationally assess how adaptive foraging
(AF) behavior interacts with network architecture to determine the stability of plant-
44 pollinator networks. We find that AF reverses negative effects of nestedness and positive
effects of connectance on the stability of the networks by partitioning the niches among
46 species within guilds. This behavior enables generalist pollinators to preferentially forage
on the most specialized of their plant partners which increases the pollination services to
48 specialist plants and cedes the resources of generalist plants to specialist pollinators. We
corroborate these behavioral preferences with intensive field observations of bee foraging.
50 Our results show that incorporating key organismal behaviors with well-known biological
mechanisms such as consumer-resource interactions into the analysis of ecological
52 networks may greatly improve our understanding of complex ecosystems.

Introduction

54 Several major discoveries in biology over the last four decades include the
systematic effects of the architecture of biological networks on their dynamics, especially
56 their stability in the face of complexity and disturbance (Pascual & Dunne 2005, Barabási
2012). Such discoveries within the field of ecological networks show how the density of
58 interactions among species in a community (Dunne et al. 2002, Okuyama & Holland 2008,
James et al. 2012) and specific patterns in the architecture of those interactions (Bascompte
60 et al. 2003, Martinez et al. 2006, Bastolla et al. 2009) affect the dynamics of complex
ecological systems. Recent research illuminates how the dynamics of species' interactions
62 resulting from adaptive foraging (AF) affects the stability of ecological networks (Kondoh
et al. 2003, Valdovinos et al. 2010, Kaiser-Bunbury 2010, Ramos-Jiliberto et al. 2012,
64 Suweis et al. 2013), where AF is the commonly observed behavior whereby organisms shift
consumption effort from less- to more-available resources (Stephens & Krebs 1986).
66 Factors concerning network architecture and AF are typically found to have monotonic
effects on the stability of network dynamics. However, interactions between these factors
68 can alter both the strength and direction of purportedly monotonic effects. Here, we find
this to be the case whereby adaptive foraging reverses two of the most prominently asserted
70 monotonic effects of network architecture on the dynamics of pollination networks.

Finding such interactions between factors within plant-pollinator networks is
72 especially important because these systems help generate and maintain large amounts of
terrestrial biodiversity (Thompson 1994). Unfortunately, these highly diversified
74 mutualistic associations and the ecosystem functions they provide are threatened by a range
of anthropogenic environmental changes (Potts et al. 2010), which underscores the

76 importance of understanding the mechanisms that stabilize mutualistic networks. We focus
here on how the stability of pollination systems is affected by two well-known and well-
78 studied properties of network architecture, nestedness and connectance. Nestedness is a
nearly ubiquitous property in empirical mutualistic networks (Bascompte et al. 2003) in
80 which specialists (species with few partners) tend to interact with subsets of the mutualistic
partners of generalists (species with many partners). Different studies assert that nestedness
82 either stabilizes (Bascompte et al. 2003, Okuyama & Holland 2008, Bastolla et al. 2009,
Thèbault & Fontaine 2010, Rohr et al. 2014) or destabilizes (Allesina & Tang 2012, James
84 et al. 2012) mutualistic networks. Connectance is the fraction of all possible links that are
topologically realized among mutualistic partners, i.e. the density of interactions in the
86 network. While increasing connectance is widely thought to increase the stability of
mutualistic networks (Okuyama & Holland 2008, James et al. 2012), this property is
88 relatively low (e.g., < 0.3) in nearly all documented mutualistic networks. This raises the
question of why mutualistic networks do not have higher connectance in nature.

90 Previous studies of the effects of nestedness and connectance on the stability of
mutualistic networks (Bascompte et al. 2006, Bastolla et al. 2009, Allesina & Tang 2012,
92 James et al. 2012, Rohr et al. 2014) model individual plant-pollinator interactions as
positive and qualitatively invariant (Vázquez et al. 2015). These studies have neither
94 integrated AF nor used a more recent and much-discussed approach that models population
dynamics among mutualists using consumer-resource interactions whose interspecific
96 effects are qualitatively variable (Holland & DeAngelis 2010, Valdovinos et al. 2013).
Using this consumer-resource approach, Valdovinos et al. (2013) found that AF stabilizes
98 pollination networks by increasing both the amount of floral resources consumed by
specialist pollinators and the pollination services received by specialist plants. In that work,

100 we proposed that AF enhances those processes through niche partitioning among species of
the same guild. Here, we use Valdovinos et al.'s (2013) approach to evaluate how AF
102 interacts with the network architecture to stabilize pollination systems. We hypothesize: i)
in absence of AF (Fig. 1A), increased niche overlap caused by increasing both nestedness
104 and connectance destabilizes pollination systems by increasing the number of shared
resources among species of the same guild (Kondoh et al. 2010); and ii) decreased niche
106 overlap caused by AF (Fig. 1B) stabilizes pollination systems by allowing generalist
pollinators to prefer less shared resources which cedes floral rewards of generalist plants to
108 specialist pollinators and increases pollination services to specialist plants (Valdovinos et
al. 2013). Testing these hypotheses helps illuminate why pollination networks exhibit
110 nested and moderately connected architectures, and helps elucidate the relevance of
organismal behavior to the architecture and dynamics of biological networks and
112 communities.

114 **Material and methods**

Simulating the architecture and dynamics of pollination networks

116 Following previous studies of ecological networks (e.g. Brose et al. 2006, Ramos-
Jiliberto et al. 2009, Valdovinos et al. 2009), we distinguish two fundamental components
118 of these networks: the architecture of the networks and the dynamics occurring on those
networks. Here, the architecture of a network broadly describes which links are present or
120 absent between all plant and pollinator species in a system irrespective of the strength of
the link. This architecture is typically thought to be constrained by the match among
122 species' phenological (e.g., temporal co-occurrence) and morphological traits (e.g.,

proboscis length and corolla depth), and restrictions on mobility (e.g., spatial co-
 124 occurrence) though variable observation effort (Martinez et al. 1999) and species'
 abundances (Blüthgen et al. 2008) may confound documentation of such links and observed
 126 network properties. The dynamics occurring within pollination networks consist of changes
 in the abundance of the interacting species and/or the strength of the interactions, that is,
 128 changes in the values of the nodes and/or links, respectively. We generated the architecture
 of networks using the simple and much-used stochastic algorithm proposed by Thèbault &
 130 Fontaine (2010), which allows us to vary species richness (S), connectance (C) and
 nestedness of the generated networks.

132 In order to test our hypotheses (Fig. 1), we simulated the dynamics within those
 networks using Valdovinos et al.'s (2013) consumer-resource model of population and
 134 adaptive dynamics both with and without adaptive foraging (AF). This model describes the
 population dynamics of each plant and animal species, the dynamics of the total floral
 136 rewards of each plant species, and the adaptive dynamics of the per-capita foraging
 preferences of each pollinator species for each plant species. Pollinator j 's foraging
 138 preference on plant i (α_{ij}) increases whenever its rewards intake from plant i , $f_{ij}(R_i)$, is
 higher than its average rewards intake from all the plants (subset P_j) constituting its diet,

140 $\sum_{k \in P_j} \alpha_{kj} f_{kj}(R_k)$, as:

$$\frac{d\alpha_{ij}}{dt} = G_j \alpha_{ij} \left(f_{ij}(R_i) - \sum_{k \in P_j} \alpha_{kj} f_{kj}(R_k) \right) \quad (1)$$

142 where G_j is the basal adaptation rate of foraging preference and $\sum_{i \in P_j} \alpha_{ij} = 1$ for all plants that
 each pollinator j visits. See Appendix S1 for further details of the model. While α_{ij} is called

144 “foraging effort” in our model’s original description (Valdovinos et al. 2013), we call α_{ij}
 “preference” here because foraging effort is better understood as an amount of an
 146 individual’s activity as determined by its preference and abundance of plants that it
 pollinates. Also, foraging effort, as used here, is what is directly measured in the field,
 148 which facilitates comparing our model and field data (see below). A pollinator in networks
without AF forages equally on all individuals among all of its plant-species partners, i.e.
 150 $\alpha_{ij}=1/d_j$ where d_j is the number of plant species that pollinator j visits (Fig. 1A). Pollinators
 in networks *with* AF dynamically allocate foraging effort to different plant species based on
 152 reward levels (Fig. 1B). Since all plant individuals within a species have identical reward
 levels in our model, specialists that visit only one plant species do not adaptively forage.

154 We generated 1200 networks using Thèbault & Fontaine’s algorithm with species
 richness (S) and connectance (C) similar to those found in empirical systems (Fig. S1,
 156 Table S1), consisting of 400 networks each distributed around the following parameter
 combinations: $S=40$ and $C=0.25$, $S=90$ and $C=0.15$, $S=200$ and $C=0.06$ (hereafter *1200*
 158 *realistically connected networks*). In each of these three basic S/C combinations, we
 generated two sets of 200 networks one of which was significantly more nested than
 160 expected due to chance and the other of which was not (see Table 1). We used a standard
 measure of nestedness, *NODF_{st}* (Almeida-Neto et al. 2008, see Appendix S1 for more
 162 details), which vary from -0.33 to 2.3 in our generated networks. This range is similar to
 that in the empirical networks of Table S1, which vary from -0.37 to 1.3. Our simulations
 164 explore a range of nestedness values beyond those observed in empirical networks in order
 to understand what might happen outside the empirically observed range. We present our
 166 simulated values of connectance and nestedness both as categories (see Table 1) and as

continuous variables (see Fig. 2). We use categories to illustrate effects of connectance, nestedness and AF on total, plant and animal species persistence (i.e. fraction of initial species that persisted through to the end of the simulations, Table 1, Fig. 3). We use continuous variables to depict how niche overlap changes with connectance, nestedness and AF (Fig. 2). Similar to our approach to nestedness values, we simulated an additional set of 200 unrealistically over-connected networks of $S=200/C=0.3$ (100 nested and 100 non-nested, see Table 1) to explore the behaviour of plant-pollinator networks outside empirically observed values of connectance. Lower values of connectance often result in nodes disconnected from the network and are therefore beyond our focus on connected networks. Our over-connected networks together with a subset of 200 of the previously mentioned $S=200/C=0.06$ networks (100 nested and 100 non-nested, see Table 1) constitute a factorial design of 400 networks (hereafter *400 networks with $S=200$*) with two levels of nestedness (non-significantly and significantly nested) and two levels of connectance (realistically and over-connected networks). This factorial design allows us to powerfully analyze interactions between factors and their effect on persistence.

We ran our model both without and with AF on all the stochastically generated networks briefly described above and more thoroughly explained in Appendix S1. To more clearly describe the results of our simulations, we used high mortality rates for animals and low mortality rates for plants to highlight the stability of animal species; and low mortality rates of animals and high mortality rates of plants to highlight the stability of plant species (see Table S2). We defined specialist and generalist species as the 30% least and 30% most connected species, respectively, to reduce ambiguity between specialist and generalist categories. The degree heterogeneity in these networks causes the 30% most generalized species to always have more than one partner and the 30% most specialized species to

always have only one partner except in unrealistically over-connected networks. This
 192 corresponds to the fact that over half of the 4823 pollinator species in the 49 empirical webs
 visualized in Fig. S1 pollinate only one plant species, though this level of extreme
 194 specialization may be overestimated due to sampling limitations (Blüthgen et al. 2008).

196 **Analysis of the model's results**

We evaluated how niche overlap between pollinator species varies with nestedness
 198 and connectance in both networks without and with AF using Horn's similarity index
 (1966) of foraging preferences α_{ij} (Eq. 1) between pollinator species j and k :

$$200 \quad H'(j, k) = \frac{2 \sum_{i \in P} (\alpha_{ij} \alpha_{ik})}{\sum_{i \in P} (\alpha_{ij}^2) + \sum_{i \in P} (\alpha_{ik}^2)} \quad (2)$$

where the set P refers to all the plant species of the network. $H'(j,k)=1$ when j and k exhibit
 202 exact same preferences for the same plant species. $H'(j,k)=0$ when the pollinators do not
 share any plant species. We analyzed nonparametric Kendall's rank correlations between
 204 mean H' without and with AF with the nestedness and connectance of each network.

We studied the effects of AF, connectance, nestedness, and their interactions on
 206 network stability measured as the fraction of initial species that persisted 3000 time steps
 during the simulations hereafter called species persistence. We statistically analyzed these
 208 effects in terms of fixed-effects regression coefficients emerging from two types of
 Generalized Linear Mixed-Effects Models (GLMMs) on the *400 networks with $S=200$* (see
 210 above). The first type estimates the effect of AF on species persistence alone by modeling
 AF presence/absence as the only fixed effect. The second type estimates the effects of
 212 nestedness and connectance on species persistence as well as the influence of AF on those
 effects by modeling AF and either connectance or nestedness as fixed effects and the

214 statistical interaction between the two fixed effects. A statistically significant interaction
term indicates that the impact of network architecture (connectance or nestedness) on
216 persistence differs depending on whether or not AF was considered. We assessed these
models for seven different datasets: all species combined (i.e., plants and animals), for
218 plants and animals separately, and for specialist and generalist plants and animals
separately (four datasets). See Appendix S1 for further details of our GLMM analyses.

220

Empirical data and the analysis of foraging efforts

222 Since the behavior and removal of generalist pollinators strongly affect the species
diversity and robustness of pollinator networks (Valdovinos et al. 2013), we tested
224 predictions of our dynamic model against empirically observed foraging behaviors of
generalist pollinators. These empirical data describe flower visits by bumble bees (*Bombus*
226 spp) from the unmanipulated or “control” data of a pollinator removal experiment
conducted over three summer field seasons (Brosi & Briggs 2013). Plant abundance and
228 foraging sequences of individual bees including ≥ 5 flower visits were observed during a
single day at 27 different sites surrounding the Rocky Mountain Biological Laboratory,
230 Gunnison County, Colorado, USA. Overall, the data describe a total of 30,050 individual
visits involving 1012 individual bumble bees among 8 species foraging on 35 plant species.
232 Although this plant-bumble bee assemblage is a small subset of the whole plant-pollinator
community, it constitutes an appropriate dataset to test our predictions for the foraging
234 behavior of the generalist pollinator species in our simulations.

We analyzed foraging effort of bumble bees within the particular network (site \times year)
236 that they were located in. We used site, plant and bee species as random effects to account
for the fact that there are likely differences across those groups, and different data points

238 within one of those groups do not represent statistically independent samples. We measured
 foraging effort in terms of an abundance-normalized visitation rate calculated as the relative
 240 foraging effort of pollinator species j on plant species i normalized by i 's abundance
 relative to the abundance all plants visited by j :

242

Fraction of visits from individual pollinator j to flowers of plant i

244

$$\left(\frac{\text{Floral abundance of plant } i}{\sum \text{Floral abundance of plant species that pollinator species } j \text{ visits}} \right) \quad (3)$$

246

for all individual bees visiting each plant species during the day and within the plot where
 248 the foraging sequence was observed. In other words, Eq. 3 calculates the fraction of a
 pollinator's visits to a plant relative to that plant's abundance among partners of that
 250 pollinator. We compared field data on the 8 species of bumble bees with the simulated
 foraging of the 30% most general species in nested networks with AF, mean $S=90$, and
 252 mean $C=0.15$. These networks include the subset of simulated webs that appear closest to
 our field data given that the simulated webs contain an average of 30 plant species and an
 254 average of 7 highly general pollinator species.

We statistically assessed the relationship between normalized log foraging effort and
 256 plant connectivity using GLMMs in both our model and field data. This enabled us to
 account for the non-independence of multiple observations of the same animal and plant
 258 species (in both model and empirical data) within networks (model data) and within sites on
 the day of observation (empirical data). We thus used plant species, animal species, and
 260 network ID as random effects in the analysis of the modelling data, and plant species,
 animal species, and site ID as random effects in the empirical analysis. We used plant

262 degree (the number of pollinator species a plant species is connected to in a network) as the
fixed effect in analyses of both empirical and modelling data. We log-transformed foraging
264 effort (the response variable) to better conform to model assumptions. This analysis was
run using the “lme4” (Bates et al. 2014) and “lmerTest” (Kuznetsova et al. 2013) packages
266 for the R Statistical Programming Language (R Core Team 2013).

268 **Results**

Our hypotheses involving niche overlap as the primary mechanism responsible for
270 differences in species persistence among networks are both corroborated and refined by the
variation in species persistence among our simulated networks. More specifically, our
272 hypothesis that asserts AF decreases niche overlap is strongly corroborated by the decrease
in niche overlap from a mean of 0.206 (95% CI +/- 0.007, Figs.2A,B) in networks without
274 AF to a mean of 0.109 (95% CI +/- 0.004, Figs.2C,D) in networks with AF. Our
hypothesized effect of this decrease is also corroborated by the increase in species
276 persistence due to AF ($P=3\times 10^{-11}$, Table S3: ‘AF Only’, ‘all plants and animals’). More
surprisingly, AF reverses the effects of nestedness on niche overlap and network stability.
278 Without AF, nestedness increases niche overlap (Fig.2B). With AF, nestedness decreases
niche overlap (Fig.2D). As we hypothesize from such changes in overlap, AF also reverses
280 the destabilizing effect of nestedness on species persistence ($P=4\times 10^{-13}$, Fig.3, Table S3
‘AFxN’, ‘all species’). Regarding connectance, it is positively correlated with niche
282 overlap ($P<2\times 10^{-16}$; Fig.2A) in networks without AF and even more so in networks with
AF ($P<2\times 10^{-16}$; Figs.2C). This increase in niche overlap is consistent with the change from
284 the stabilizing effect of connectance on species persistence to a destabilizing effect (Fig.3,

Table S3: ‘AFxC’, ‘all species’, $P=2\times 10^{-11}$). We explain these results in more detail below
286 and then describe our test of a central result regarding foraging behavior against our
empirical data.

288 AF eliminates the strong negative effect of nestedness on animal persistence (Fig.3,
Table S3: ‘AF x N’, ‘all animals’, $P<0.05$), and reverses the negative effect of nestedness
290 on plant persistence (Fig.3, Table S3: ‘AF x N’, ‘all plants’, $P=2\times 10^{-15}$). AF increases
overall persistence in realistically connected networks by increasing the persistence and
292 abundance of *specialist* species of both animals and plants (Table 1: ‘Specialists’ in
‘Realistically connected’, Figs.4A-C). This increase in the persistence of specialist
294 pollinators occurs because generalists exhibiting AF reduce foraging effort on generalist
plants (Figs.1B,5A) due to the reduced reward levels in these plants that result from sharing
296 their rewards with many other pollinator species (Figs.1B, 4D). Generalist pollinators
balance this reduction by increasing foraging effort on specialist plants (Figs1A, 5A) whose
298 resources are shared by fewer pollinators and therefore are more abundant (Figs.4D). This
shift by generalists from generalized to more specialized plants increases the population
300 growth rates of generalist pollinators in the near term (Fig. S2C), but has two subsequent
outcomes that are intensified by nestedness (Fig. S3). First, the shift away from generalist
302 plants allows their floral resource levels to increase (Figs. 1B, 4D). This increase in
resources increases the persistence and abundance of pollinators specialized on generalist
304 plants (Table 1: ‘Specialists’ ‘Animals’ in ‘Realistically connected’, Figs. 4A, 4B, S3A).
The increased abundance of non-generalist pollinators (Fig. 4B), in turn, decreases the total
306 amount of floral rewards in the community (Fig. 4D), which ultimately reduces the long-
term abundance of generalist pollinators (Figs. 4B, S3B). Second, this shift increases

308 pollination services to specialist plants, which increases their persistence relative to
networks without AF (Table 1: ‘Specialists’ ‘Plants’ in ‘Realistically connected’, Figs. 4C,
310 S3C).

AF eliminates the positive effect of connectance on animals while converting the
312 negative effect on plants to a stronger negative effect (Fig. 3, Table S3: ‘AF x C’, ‘all
plants’, $P=2\times 10^{-12}$). Without AF, increasing connectance enhances the diversity and
314 therefore abundance of food available to the pollinators which greatly increases the
persistence of these animals (Fig. 3) and ensures that animal species almost always persist
316 in over-connected networks. With AF, animals always persist irrespective of connectance
levels. This explains the very small effects of AF on animal persistence (Table 1:
318 ‘Animals’ in ‘Over-connected’). Plants respond to connectance differently. Without AF,
increased connectance destabilizes generalist plants due to increased pollinator generality
320 degrading pollination services by decreasing deposition of conspecific pollen. With AF,
such degradation is exacerbated to the point that increased connectance enables specialized
322 pollinators, which can visit multiple plant species only in over-connected networks, to
decrease the persistence generalist plants by 19-41% (Table 1: ‘Generalists’ ‘Plants’ in
324 ‘Unrealistically over-connected’).

We tested our hypothesis (Fig.1B) and model results (Fig.5A) asserting generalist
326 pollinators prefer specialist plants against our empirical data on foraging behavior of
bumble bees, which are generalist pollinators within their plant-pollinator community (see
328 Methods). Our analysis reveals a striking match between the model results of generalist
pollinators allocating more foraging effort on specialist plants (Fig.5A) and the distribution
330 of foraging effort obtained from the field data (Fig.5B). Both data sets suggest that
generalists’ normalized foraging effort (Eq.3) decreases approximately an order of

332 magnitude among plants whose number of partners increases by six as illustrated by
statistically significant negative trends in foraging effort with increased plant generality
334 (model: $P < 2 \times 10^{-16}$; field data: $P = 0.0189$). A more precise comparison is prevented
because, in contrast to the simulated data, the complete set of pollinators and therefore the
336 actual degree of each plant species is unknown in the field data. However, the relative
generality of plants, and therefore their placement on the x-axis of Fig. 5B, appears to be
338 well estimated by the empirically observed number of generalist partners of the plants.

340 **Discussion**

Our study shows how niche partitioning due to adaptive foraging (AF) stabilizes
342 realistically structured plant-pollinator networks but not over-connected networks. This
partitioning consists of generalist pollinators preferring specialist plants (Fig. 5A), while
344 ceding floral rewards of generalist plants to specialist pollinators (Fig. 1B, Fig. 4D). This
partitioning also explains how AF reverses the broadly destabilizing effect of nestedness
346 and the broadly stabilizing effect of connectance (Fig. 3) and may help explain why
pollination networks exhibit nested and moderately connected architectures.

348 The negative impact of nestedness on animal persistence in networks without AF is
caused by the increase in resource sharing between specialist and generalist pollinators that
350 results from increasing nestedness (Kondoh et al. 2010). This lack of niche partitioning
causes specialist pollinators to be outcompeted by generalist pollinators and degrades
352 pollination services to specialist plants by increasing specialist plants' number of generalist
pollinators with heterospecific pollen loads (Fig. 1A, Ashman & Arceo-Gómez 2013,
354 Briggs et al. 2015). AF counteracts these negative effects of nestedness. AF within nested

networks causes generalist pollinators to prefer specialist plants, which increases the
356 quantity and quality of visits to specialist plants while increasing their persistence (Figs.
4C, S3C). This shift in preference also decreases negative effects of competition on
358 specialist pollinators by ceding to them floral rewards that ultimately reduces the
abundance of generalist pollinators (Fig. 4B). Such counterintuitive reductions in
360 organismal abundance resulting from their adaptive behavior have been identified
elsewhere as ‘evolutionary deterioration’ (Dieckmann & Ferrière 2004).

362 Niche partitioning also explains how AF reverses the stabilizing effect of
connectance. Without AF, increasing connectance enhances the diversity and therefore
364 abundance of food sources available to the pollinators which has the effect of greatly
increasing the persistence of pollinators but has a slight negative effect on plant persistence
366 (Fig. 3). With AF and its attendant partitioning of niches, pollinators escape the negative
consequences of competition which allows all pollinators to persist and eliminates the
368 possibility of increased persistence due to increased connectance (Fig.3). Additionally, AF
amplifies negative effects of increased connectance on plants (Fig.3) because, in over-
370 connected networks, all pollinators pollinate more than one species of plant which allows
all pollinators to decrease their visits to their most generalized plants and subsequently
372 decrease these plants’ persistence (Table 1) due to degradation of pollination services.

These findings on the negative impact of increasing connectance on plant
374 persistence suggest that AF may explain why such highly connected pollination networks
are not found in nature and contradict previous work that asserts positive relationships
376 between the stability of species abundances and the connectance of the mutualistic
networks (Okuyama & Holland 2008, James et al. 2012). This contradiction appears due to
378 the dynamics of floral rewards (Eq. 1) that can create negative effects between pollinators

and plants in contrast to the qualitatively invariant positive effects in previous models
380 which cause species persistence to always increase with the number of interactions, i.e.,
connectance.

382 Our results regarding the effects of nestedness in the absence of adaptive foraging
also contrast with other model results including those (e.g., Bastolla et al. 2009) that found
384 that nestedness stabilizes mutualistic networks by reducing effective interspecific
competition. This stabilizing effect of nestedness occurred because all species of the same
386 guild (i.e. plants or pollinators) in their models directly compete through competition
coefficients independent of the degree of resource sharing. However, in their models
388 positive effects on population growth rates among species of the same guild depend on
resource sharing and increase with increasing the abundance of common mutualist partners.
390 This causes positive effects among plants (or pollinators) in their model to increasingly
outweigh negative effects as the number of shared pollinators (or plants) increases.
392 Nestedness stabilizes these networks because it increases resource sharing which increased
these positive effects. In contrast, we found that nestedness decreases species persistence
394 in the absence of AF by increasing competition for both floral resources shared among
pollinators and also for pollination vectors shared among plants. AF adapts to and
396 counteracts these negative effects of nestedness in realistically connected networks by
allowing foraging effort to shift such that adaptive foragers increase niche partitioning,
398 which increases visits to specialist plants and resources available for specialist pollinators
(Fig. 1).

400 Beyond determining how network structure and dynamics influence stability,
another key role of the theory motivating our model is illuminating previously
402 unrecognized behaviors in nature. Our theory fulfills this role by predicting that foraging

effort is distributed such that generalist pollinators expend more effort on less-connected
404 plants, a result that is strikingly consistent with a large, detailed field dataset on plant
visitation by bumble bees. To our knowledge, this is the first time that predictions of
406 variable foraging effort among topologically available resources have been tested against
field observations of mutualistic networks. Although other factors besides competition
408 between bees for the floral rewards of generalist plants may drive this result, our data
(Brosi and Briggs 2013) suggest that when competition is relaxed via pollinator removals,
410 the statistically significant negative relationship between foraging effort and plant degree
disappears (unpublished results). These relationships are consistent with previous
412 theoretical work (Valdovinos et al. 2013, Staniczenko et al. 2013) but contradict a previous
meta-analysis of field data (Bascompte et al. 2006). This discrepancy is straightforward to
414 explain: while the meta-analysis found that more-connected plants are visited more
frequently than less-connected plants, it did not account for the effects of plant abundance
416 on visitation (Blüthgen 2008), which is critical given that more-connected plants tend to be
much more abundant than less-connected ones (Vázquez et al. 2007). In contrast, our
418 analysis of foraging effort normalized to plant abundance allows the predicted signal to be
expressed in the field data. Further tests of our predictions against additional empirical
420 data, especially those that document larger fractions of plant-pollinator communities, are
needed to determine the applicability of our findings to other species and communities.

422 Given our study's overall results and their relation to other findings, we suggest that
the pollination behaviors and network structures found in nature effectively balance a
424 conflict between strategies that benefit pollinators and plants. Pollinator species benefit
from consuming more rewards available from more plant species (MacArthur 1965). Plant
426 species benefit from less diluted conspecific pollen carried by their pollinators that visit

fewer plant species (Brosi 2016). Intermediately connected networks that are highly nested
428 and contain adaptive foragers appear to resolve this conflict. Such networks allow many
pollinator species to persist with more than one plant partner while avoiding excessive
430 degradation of pollination services critical to plant persistence. It would be interesting to
explore whether such systems-level solutions to this conflict are optimal or naturally
432 emerge during the evolution of species within networks (Allhoff et al. 2015).

Several of our model's simplifying assumptions would be particularly interesting to
434 explore in future work. One is the lack of evolutionary dynamics in our model (e.g.
Bronstein 1994, Guimarães et al. 2011, Melián et al. 2011). Though beyond our scope,
436 such dynamics are especially interesting (Dieckmann & Ferrière 2004) given selective
pressures that may prevent generalists from evolving behaviors such as adaptive foraging
438 that lower generalists' population size over the longer term while increasing it over the
shorter term. Future work should also explore our model's spatial mean-field assumption
440 asserting that pollinators can forage on any plant individual with no travel time or cost,
which can be relaxed by including spatial heterogeneity and temporal heterogeneity in
442 phenology. We also assume perfect knowledge by pollinators of the floral resources of all
plants in the landscape, which could be addressed by including limitations in pollinator
444 learning and memory (Leonard et al. 2011). Empirical estimates of model parameters
could relate model time to real time and greatly inform many of these explorations.

446 Future work also needs to better control the degree distribution when generating
nested networks (Saavedra & Stouffer 2013). For example, specialists were more general in
448 our non-nested than in our nested networks (results not shown). The strong correlations
between fundamental properties such as nestedness, connectance and degree distributions
450 (James et al. 2012b) highlights the difficulty in determining which of several highly

correlated properties are driving the stability effects. Finally, our theory assumes that a
452 significant fraction of pollinator species that co-occur in time and space are single-species
specialists. The heterogeneities discussed above suggest that this assumption at the local
454 scale of our model may be none-the-less consistent with suggestions that ‘true’ specialists
on single species are very rare based on observations at larger geographic, spatial, and
456 evolutionary scales.

Here, we illuminate the interplay between network architecture and organismal
458 behavior by integrating several approaches to mutualistic networks that were previously
kept separate. First, we incorporated adaptive foraging, which is common in consumers
460 utilizing spatially or temporally varying resources (Stephens & Krebs 1986). Second, we
dynamically modeled interaction strengths using empirically tractable mechanisms
462 (Vázquez et al. 2015) including visitation, feeding, pollination and reproduction. Third, we
more explicitly modeled direct positive interactions between trophic levels (Holland &
464 DeAngelis 2010) and also direct negative interactions between and within trophic levels
involved in plant-animal mutualisms. Our findings on the interplay between network
466 architecture and adaptive foraging via niche partitioning may be found in other networks
with adaptive behavior such as food webs, which are also often nested (Kondoh et al. 2010)
468 and have limited connectance (Beckerman et al. 2006).

470

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646

Figure Legends

648

Fig. 1. Hypothesized effects of adaptive foraging (AF) on pollination networks.

650 Without AF (A), each pollinator equally prefers all of its plant partners as indicated by lines
to plants of equal width. This leads to lower visitation levels to specialist relative to
652 generalist plants, and to lower reward levels in generalist plants relative to specialists as
indicated by the fill levels in the bars below the flowers. These visitation and rewards
654 levels typically result in the competitive exclusion of plants and pollinators specializing on
generalist species. With AF (B), generalist pollinators prefer specialist plants, which
656 partitions animal and plant niches between generalist and specialist species. This niche
partitioning stabilizes network dynamics by ceding resources of generalist plants to
658 specialist pollinators and increasing pollination services to specialist plants. Bees and
flowers represent an average individual within each species' population arranged from top
660 to bottom by decreasing numbers of interactions.

Fig. 2. Niche overlap as a function of connectance and nestedness in networks without and with adaptive foraging (AF).

662 Without AF (A, B), Kendall's rank correlations of 0.26
664 ($P=0$) and 0.49 ($P=0$), respectively indicate that increasing both connectance and
nestedness increases pollinators' niche overlap, which corroborates our hypothesis (i).
666 Including AF (C, D) decreases this overlap in half from a mean of 0.206 (95%CI +/- 0.007)
without AF to a mean of 0.109 (95%CI +/- 0.004), which supports our hypothesis (ii). AF
668 reverses the correlation of niche overlap with nestedness to -0.29 ($P<10^{-16}$, compare B and
D) and increases the correlation with connectance to 0.64 ($P=0$, compare A and C). Niche
670 overlap corresponds to Horn's similarity index on foraging preferences for pollinator

species within the *1200 realistically connected networks* (see Methods). Unfilled, grey, and
 672 black data points correspond to networks with connectance $C < 0.1$, $0.1 \leq C \leq 0.2$, and $C > 0.2$,
 respectively.

674

Fig. 3. Effects of nestedness and connectance on species persistence in networks

676 **without and with adaptive foraging (AF).** Results correspond to the *400 networks with*
S=200 (see Methods) consisting of four groups of 100 networks factorially divided among
 678 two categories of two different variables: realistically connected ($C=0.06$), over-connected
 ($C=0.3$), non-nested, and nested (more than expected at random). For each network, we ran
 680 the model without (grey bar) and with (black bar) AF. Effects of nestedness and
 connectance were estimated as the fixed-effects regression coefficients emerging from
 682 generalized linear mixed-effects models (GLMMs) including AF and either nestedness or
 connectance as fixed effects. Different mortality rates are useful for highlighting different
 684 results. Results for animal persistence were obtained from simulations with high animal-
 and low plant-mortality rates, whereas those for plant persistence used high plant- and low
 686 animal-mortality rates (Table S2). Error bars show 95% binomial confidence intervals
 estimated by our GLMMs.

688

Fig. 4. Effects of adaptive foraging (AF) on animal and plant species with different

690 **levels of specialization within the *1200 realistically connected networks*.** All networks
 have realistic levels of species richness *S* and connectance *C* (i.e. $S/C = 40/0.3$, $90/0.25$,
 692 $200/0.06$). Different mortality rates are useful for highlighting different results (see legend
 of Fig. 3). Results for animal persistence (A) and abundance (B), and per-plant species
 694 resource density (D) are shown for simulations with high animal mortality rates and low

plant mortality rates (Table S2). Panel C shows plant persistence for high plant mortality
696 and low animal mortality rates. Orange-solid, blue-dashed and back-dotted lines represent
all, generalist and specialist animal (or plant) species. Symbols and error bars represent
698 mean and 95% confidence intervals. Note that high persistence of generalists in networks
without AF (A, C) provides little opportunity for AF to increase their persistence.

700

Fig. 5. Effects of plant connectivity on relative foraging effort in model (A) and field

702 **(B) data.** Points depict the normalized mean log-foraging effort of individuals in a
population of one animal species on individuals in a population of one plant species (y-
704 axis), as a function of plant degree (the number of animal species that visit that plant
species, x-axis). Lines depict best-fit estimates from linear mixed-effects models, with the
706 95% confidence intervals (CIs) shaded. Model data consist of 200 nested networks with
average species richness $S=90$ and average connectance $C=0.15$. This subset of simulated
708 webs appear the closest to our field data given that they contain on average 30 plant species
and on average 7 animal species are the most general pollinators within the networks,
710 whereas the empirical data consist of 8 generalized pollinator species foraging on 35 plant
species.

712 **Table 1. Effects of adaptive foraging (AF) on species persistence for each architecture type in our simulation design.** Effects
 were calculated as the difference in the fraction of persistent species between networks with and without AF, for all, generalist and
 714 specialist animal and plant species. ‘Realistically connected’ refers to 1200 networks with species richness (S) and connectance (C)
 around the S/C combinations: S=40/C=0.25, S=90/C=0.15, S=200/C=0.3 (400 networks each, 200 non-significantly and 200
 716 significantly nested). ‘Unrealistically over-connected’ refers to 200 networks (100 non-significantly and 100 significantly nested)
 averaging S=200/C=0.3. First and second numbers in each non-nested/nested column correspond to the mean and the 95% confidence
 718 intervals of the mean. We only discuss effects higher than 0.15 in the text. Bold numbers indicate effects higher than 0.15.

	S=40, C=0.25				Realistically connected S=90, C=0.15				S=200, C=0.06				Over-connected S=200, C=0.3			
	non-nested		nested		non-nested		nested		non-nested		nested		non-nested		nested	
Animals																
All	0.01	0.00	0.15	0.03	0.01	0.00	0.26	0.03	0.02	0.01	0.36	0.03	0	0	0.00	0.00
Generalists	0	0	0.03	0.01	0	0	0.07	0.02	0.00	0.00	0.16	0.02	0	0	0	0
Specialists	0.02	0.01	0.28	0.04	0.03	0.01	0.43	0.04	0.05	0.01	0.50	0.03	0	0	0.02	0.00
Plants																
All	0.00	0.00	0.07	0.01	0.00	0.00	0.10	0.01	0.01	0.00	0.13	0.01	-0.25	0.01	0.04	0.01
Generalists	0	0	0	0	0	0	0	0	0	0	0.00	0.00	-0.41	0.04	-0.19	0.02
Specialists	0.01	0.01	0.21	0.04	0.02	0.01	0.26	0.03	0.03	0.01	0.31	0.03	-0.02	0.04	0.43	0.03

