LETTER

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

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Abstract

Much research debates whether properties of ecological networks such as nestedness and connectance stabilise biological communities while ignoring key behavioural aspects of organisms within these networks. Here, we computationally assess how adaptive foraging (AF) behaviour interacts with network architecture to determine the stability of plant–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 species within guilds. This behaviour enables generalist pollinators to preferentially forage on the most specialised of their plant partners which increases the pollination services to specialist plants and cedes the resources of generalist plants to specialist pollinators. We corroborate these behavioural preferences with intensive field observations of bee foraging. Our results show that incorporating key organismal behaviours with well-known biological mechanisms such as consumer-resource interactions into the analysis of ecological networks may greatly improve our understanding of complex ecosystems.

Keywords

Adaptive behaviour, community stability, consumer-resource interactions, mechanistic models, mutualistic networks, population dynamics.

Ecology Letters (2016) **19**: 1277–1286

INTRODUCTION

Several major discoveries in biology over the last four decades include the systematic effects of the architecture of biological networks on their dynamics, especially their stability in the face of disturbance (Pascual & Dunne 2006; Barabási 2012). Such discoveries within the field of ecological networks show how the density of interactions among species in a community (Dunne *et al.* 2002; Okuyama & Holland 2008; James *et al.* 2012a,b) and specific patterns in the architecture of those interactions (Bascompte *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 resulting from adaptive foraging (AF) affects the stability of ecological networks (Kondoh 2003; Valdovinos *et al.* 2010; Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012; Suweis *et al.* 2013), where AF is the commonly observed behaviour whereby organisms shift consumption effort from less- to more-available resources (Stephens & Krebs 1986). Factors concerning network architecture and AF are typically found to have monotonic effects on the stability of network dynamics. However, interactions between these factors 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 monotonic effects of network architecture on the dynamics of pollination networks.

Finding such interactions between factors within plant–pollinator networks is especially important because these systems help generate and maintain large amounts of terrestrial biodiversity (Thompson 1994). Unfortunately, these highly diversified mutualistic associations and the ecosystem functions they provide are threatened by a range of anthropogenic environmental changes (Potts *et al.* 2010), which underscores the importance of understanding the mechanisms that stabilise mutualistic networks. We focus here on how the stability of pollination systems is affected by two well-known and well-studied properties of network architecture, nestedness and connectance. Nestedness is a nearly ubiquitous property in empirical mutualistic networks (Bascompte *et al.* 2003) in 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 either stabilises (Bascompte *et al.* 2003; Okuyama & Holland 2008; Bastolla *et al.* 2009; Thébault & Fontaine 2010; Rohr *et al.* 2014) or destabilises (Allesina & Tang 2012; James *et al.* 2012a) mutualistic networks. Connectance is the fraction of all possible links that are topologically realised among mutualistic partners, that is, the density of interactions in the network. While increasing connectance is widely thought to

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increase the stability of mutualistic networks (Okuyama & Holland 2008; James *et al.* 2012a,b), connectance is 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.

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; James *et al.* 2012a,b; Rohr *et al.* 2014) model individual plant–pollinator interactions as positive and qualitatively invariant (Vázquez *et al.* 2015). These studies have neither integrated AF nor used a more recent and much discussed approach that models population dynamics among mutualists using consumer-resource interactions whose interspecific effects are qualitatively variable (Holland & DeAngelis 2010; Valdovinos *et al.* 2013). Using this consumer-resource approach, Valdovinos *et al.* (2013) found that AF stabilises 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, 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 interacts with the network architecture to stabilise pollination systems. We hypothesise: i) in the absence of AF (Fig. 1a), increased niche overlap caused by increasing both nestedness and connectance destabilises pollination systems by increasing the number of shared resources among species of the same guild (Kondoh *et al.* 2010); and ii) decreased niche overlap caused by AF (Fig. 1b) stabilises pollination systems by allowing generalist pollinators to prefer less shared resources which cedes floral rewards of generalist plants to specialist pollinators and increases pollination services to specialist plants (Valdovinos *et al.* 2013). Testing these hypotheses helps illuminate why pollination networks exhibit nested and moderately connected architectures, and helps elucidate the relevance of organismal behaviour to the architecture and dynamics of biological networks and communities.

MATERIAL AND METHODS

Simulating the architecture and dynamics of pollination networks

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 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 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 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-occurrence) though variable observation effort (Martinez *et al.* 1999) and species' abundances (Blüthgen *et al.* 2008) may confound documentation of such links and observed network properties. The dynamics occurring within pollination networks consist of changes in
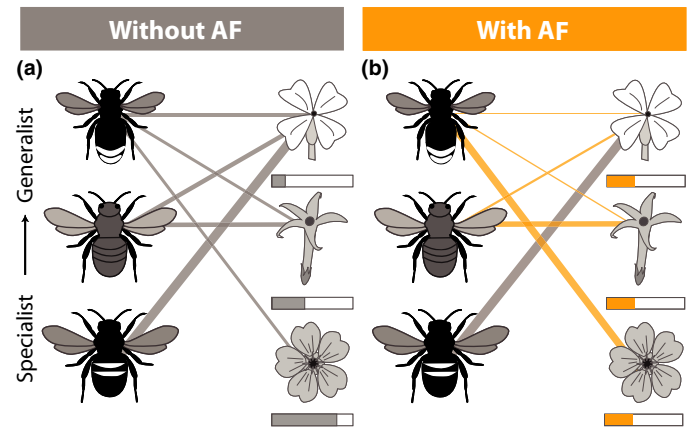

Figure 1 Hypothesised effects of adaptive foraging (AF) on pollination networks. Without AF (a), each pollinator equally prefers all of its plant partners as indicated by lines to plants of equal width. This leads to lower visitation levels to specialist relative to generalist plants, and to lower reward levels in generalist plants relative to specialists as indicated by the fill levels in the bars below the flowers. These visitation and reward levels typically result in the competitive exclusion of plants and pollinators specialising on generalist species. With AF (b), generalist pollinators prefer specialist plants, which partitions animal and plant niches between generalist and specialist species. This niche partitioning stabilises network dynamics by ceding resources of generalist plants to specialist pollinators and increasing pollination services to specialist plants. Bees and flowers represent an average individual within each species' population arranged from top to bottom by decreasing numbers of interactions.

the abundance of the interacting species and/or the strength of the interactions, that is, 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 & Fontaine (2010), which allows us to vary species richness (S), connectance (C) and nestedness of the generated networks.

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 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 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 preference on plant i (α_{ij}) increases whenever its reward intake from plant i, $f_{ij}(R_i)$, is higher than its average reward intake from all the plants (subset P_j) constituting its diet, $\sum_{k \in P_j} \alpha_{kj} f_{kj}(R_k)$, as:

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

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 '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

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, 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, that is, $\alpha_{ij} = 1/d_j$ 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 reward levels (eqn 1, 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.

We generated 1200 networks using Thèbault and Fontaine's algorithm with species richness (S) and connectance (C) similar to those found in empirical systems (Fig. S1, 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 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 expected due to chance and the other of which was not (see Table 1). We used a standard measure of nestedness, *NODFst* (Almeida-Neto *et al.* 2008; see Appendix S1 for more 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 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 simulated values of connectance and nestedness both as categories (see Table 1) and as continuous variables (see Fig. 2). We use categories to illustrate the 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 analyse the interactions between factors and their effect on persistence.

We ran our model 3000 time steps 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 generalised species to always have more than one partner and the 30% most specialised species to always have only one partner except in unrealistically over-connected networks. This corresponds to the fact that over half of the 4823 pollinator species in the 49 empirical webs visualised in Fig. S1 pollinate only one plant species, though this level of extreme specialisation may be overestimated due to sampling limitations (Blüthgen *et al.* 2008).

Table 1 Effects of adaptive foraging (AF) on species persistence for each architecture type in our simulation design

| | Realistically connected | | | | | | | | | | | | Over-connected | | | |
| | $S = 40$, $C = 0.25$ | | | | $S = 90$, $C = 0.15$ | | | | $S = 200$, $C = 0.06$ | | | | $S = 200$, $C = 0.3$ | | | |
	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

Effects were calculated as the difference in the fraction of persistent species between networks with and without AF, for all generalist and 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 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 intervals of the mean. We only discuss effects higher than 0.15 in the text. Bold numbers indicate effects higher than 0.15.
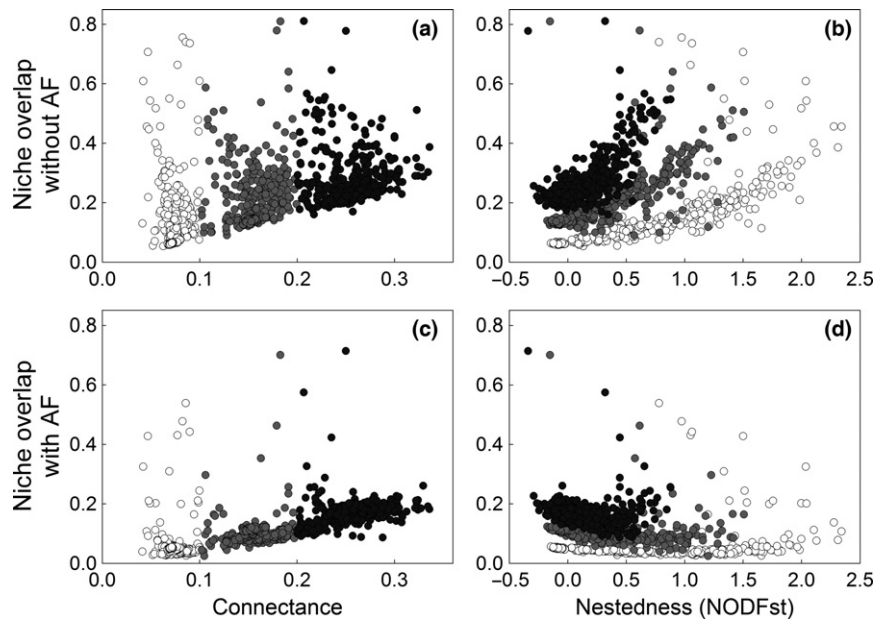
Figure 2 Niche overlap as a function of connectance and nestedness in networks without and with adaptive foraging (AF). Without AF (a, b), Kendall's rank correlations of 0.26 ($P = 0$) and 0.49 ($P = 0$), respectively, indicate that increasing both connectance and nestedness increases pollinators' niche overlap, which corroborates our hypothesis (i). Including AF (c, d) decreases this overlap in half from a mean of 0.206 (95% CI $\pm$ 0.007) without AF to a mean of 0.109 (95% CI $\pm$ 0.004), which supports our hypothesis (ii). AF 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 overlap corresponds to Horn's similarity index on foraging preferences for pollinator species within the *1200 realistically connected networks* (see Methods). Unfilled, grey and black data points correspond to networks with connectance $C < 0.1$, $0.1 \le C \le 0.2$ and $C > 0.2$ respectively.

Analysis of the model's results

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

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

where the set P refers to all the plant species of the network. $H'(j,k) = 1$ when j and k exhibit exact same preferences for the same plant species. $H'(j,k) = 0$ when the pollinators do not share any plant species. We analysed nonparametric Kendall's rank correlations between 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 species persistence. We statistically analysed these effects in terms of fixed effects regression coefficients emerging from two types of generalised linear mixed-effects models (GLMMs) on the *400 networks with S = 200* (see above). The first type estimates the effect of AF on species persistence alone by modelling AF presence/absence as the only fixed effect. The second type estimates the effects of nestedness and connectance on species persistence as well as the influence of AF on those effects by modelling AF and either connectance or nestedness as fixed effects and the statistical interaction between the two fixed effects. A statistically significant interaction term indicates that the impact of

network architecture (connectance or nestedness) on 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 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.

Empirical data and the analysis of foraging efforts

Since the behaviour and removal of generalist pollinators strongly affect the species diversity and robustness of pollination networks (Valdovinos *et al.* 2013), we tested predictions of our dynamic model against empirically observed foraging behaviours of generalist pollinators. These empirical data describe flower visits by bumble bees (*Bombus* spp.) from the unmanipulated or 'control' data of a pollinator removal experiment conducted over three summer field seasons (Brosi & Briggs 2013). Plant abundance and 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, Gunnison County, Colorado, USA. Overall, the data describe a total of 30 050 individual visits involving 1012 individual bumble bees among eight species foraging on 35 plant species. 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 behaviour of the generalist pollinator species in our simulations.
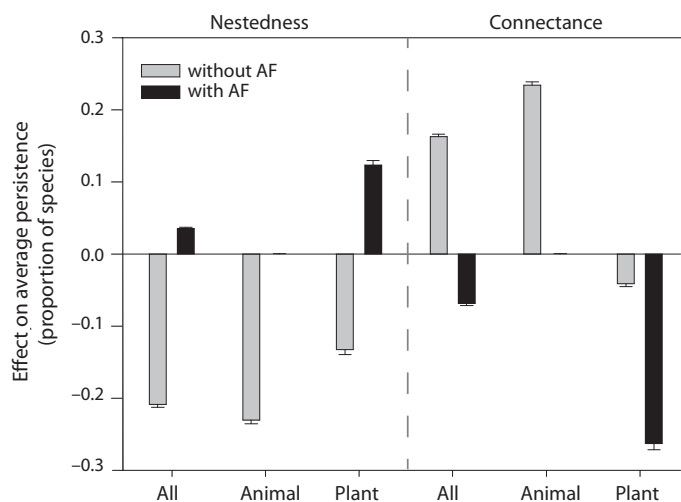
Figure 3 Effects of nestedness and connectance on species persistence in networks without and with adaptive foraging (AF). Results correspond to the *400 networks with S = 200* (see Methods) consisting of four groups of 100 networks factorially divided among two categories of two different variables: realistically connected ($C = 0.06$), over-connected ($C = 0.3$), non-nested and nested (more than expected at random). For each network, we ran 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 generalised linear mixed-effects models (GLMMs) including AF and either nestedness or connectance as fixed effects. Different mortality rates are useful for highlighting different 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 mortality rates and low animal mortality rates (Table S2). Error bars show 95% binomial confidence intervals estimated by our GLMMs.

We analysed foraging effort of bumble bees within the particular network (site × year) 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 within one of those groups do not represent statistically independent samples. We measured foraging effort in terms of an abundance-normalised visitation rate calculated as the relative foraging effort of pollinator species j on plant species i normalised by i's abundance relative to the abundance all plants visited by j:

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

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

for all individual bees visiting each plant species during the day and within the plot where the foraging sequence was observed. In other words, eqn 3 calculates the fraction of a pollinator's visits to a plant relative to that plant's abundance among partners of that pollinator. We compared field data on the eight species of bumble bees with the simulated foraging of the 30% most general species in nested networks with AF, mean $S = 90$ and 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 average of seven highly general pollinator species.

We statistically assessed the relationship between normalised log foraging effort and 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 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 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 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 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 for the R Statistical Programming Language (R Core Team 2013).

RESULTS

Our hypotheses involving niche overlap as the primary mechanism responsible for differences in species persistence among networks are both corroborated and refined by the variation in species persistence among our simulated networks. More specifically, our 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, Fig. 2a,b) in networks without AF to a mean of 0.109 (95% CI ± 0.004, Fig. 2c,d) in networks with AF. Our hypothesised effect of this decrease is also corroborated by the increase in species 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. Without AF, nestedness increases niche overlap (Fig. 2b). With AF, nestedness decreases niche overlap (Fig. 2d). As we hypothesise from such changes in overlap, AF also reverses the destabilising 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 overlap ($P < 2 \times 10^{-16}$; Fig. 2a) in networks without AF and even more so in networks with AF ($P < 2 \times 10^{-16}$; Fig. 2c). This increase in niche overlap is consistent with the change from the stabilising effect of connectance on species persistence to a destabilising effect (Fig. 3, Table S3: 'AFxC', 'all species', $P = 2 \times 10^{-11}$). We explain these results in more detail below and then describe our test of a central result regarding foraging behaviour against our empirical data.

AF eliminates the strong negative effect of nestedness on animal persistence (Fig. 3, Table S3: 'AF × N', 'all animals', $P < 0.05$), and reverses the negative effect of nestedness on plant persistence (Fig. 3, Table S3: 'AF × N', 'all plants', $P = 2 \times 10^{-15}$). AF increases overall persistence in realistically connected networks by increasing the persistence and abundance of *specialist* species of both animals and plants (Table 1: 'Specialists' in 'Realistically connected', Fig. 4a,c). This increase in the persistence of specialist pollinators occurs because generalists exhibiting AF reduce foraging effort on generalist plants (Figs 1b and 5a) due to the reduced reward

levels in these plants that result from sharing their rewards with many other pollinator species (Figs 1b and 4d). Generalist pollinators balance this reduction by increasing foraging effort on specialist plants (Figs 1a and 5a) whose rewards are shared by fewer pollinators and therefore are more abundant (Fig. 4d). This shift by generalists from generalised to more specialised plants increases the population 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 plants allows their floral rewards levels to increase (Figs 1b and 4d). This increase in rewards increases the persistence and abundance of pollinators specialised on generalist plants (Table 1: 'Specialists' 'Animals' in 'Realistically connected', Figs 4a,b and S3a). The increased abundance of non-generalist pollinators (Fig. 4b), in turn, decreases the total amount of floral rewards in the community (Fig. 4d), which ultimately reduces the long-term abundance of generalist pollinators (Figs 4b and S3b). Second, this shift increases pollination services to specialist plants, which increases their persistence relative to networks without AF (Table 1: 'Specialists' 'Plants' in 'Realistically connected', Figs 4c and S3c).

AF eliminates the positive effect of connectance on animals while converting the 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 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 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: 'Animals' in 'Over-connected'). Plants respond to connectance differently. Without AF, increased connectance destabilises generalist plants due to increased pollinator generality degrading pollination services by decreasing deposition of conspecific pollen. With AF, such degradation is exacerbated to the point that increased connectance enables specialised pollinators to visit multiple plant species, which decreases the persistence of generalist plants by 19–41% (Table 1: 'Generalists' 'Plants' in 'Unrealistically over-connected').

We tested our hypothesis (Fig. 1b) and model results (Fig. 5a) asserting generalist pollinators prefer specialist plants against our empirical data on foraging behaviour of bumble bees, which are generalist pollinators within their plant–pollinator community (see 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 of foraging effort obtained from the field data (Fig. 5b). Both datasets suggest that generalists' normalised foraging effort (eqn 3) decreases approximately an order of magnitude among plants whose number of partners increases by six as illustrated by statistically significant
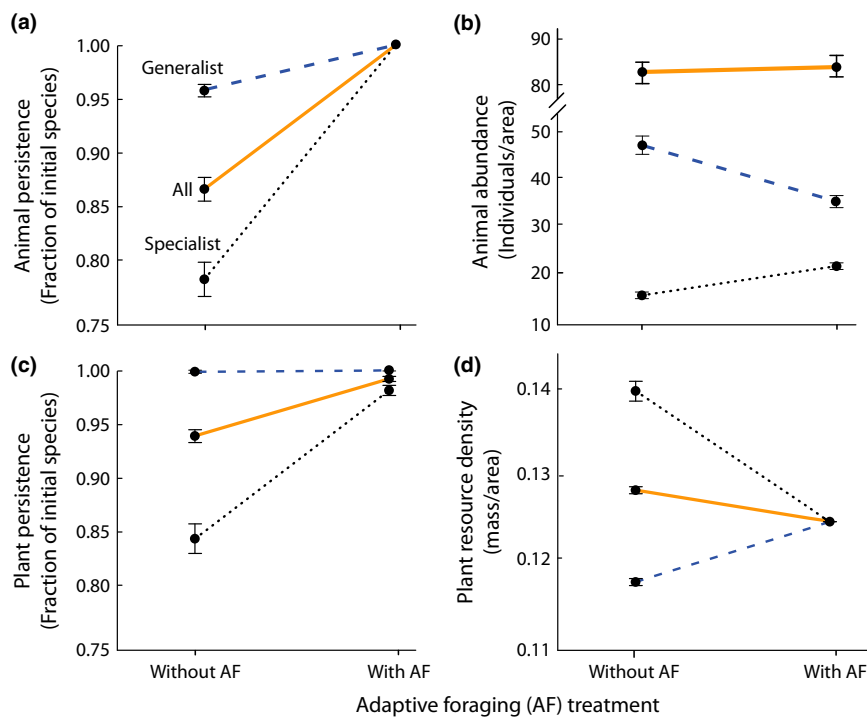

Figure 4 Effects of adaptive foraging (AF) on animal and plant species with different levels of specialisation within the *1200 realistically connected networks*. All networks have realistic levels of species richness S and connectance C (i.e. S/C = 40/0.3, 90/0.25, 200/0.06). Different mortality rates are useful for highlighting different results (see legend of Fig. 3). Results for animal persistence (a) and abundance (b), and per-plant species resource density (d) are shown for simulations with high animal mortality rates and low plant mortality rates (Table S2). (c) Shows plant persistence for high plant mortality 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 mean and 95% CIs. Note that high persistence of generalists in networks without AF (a, c) provides little opportunity for AF to increase their persistence.
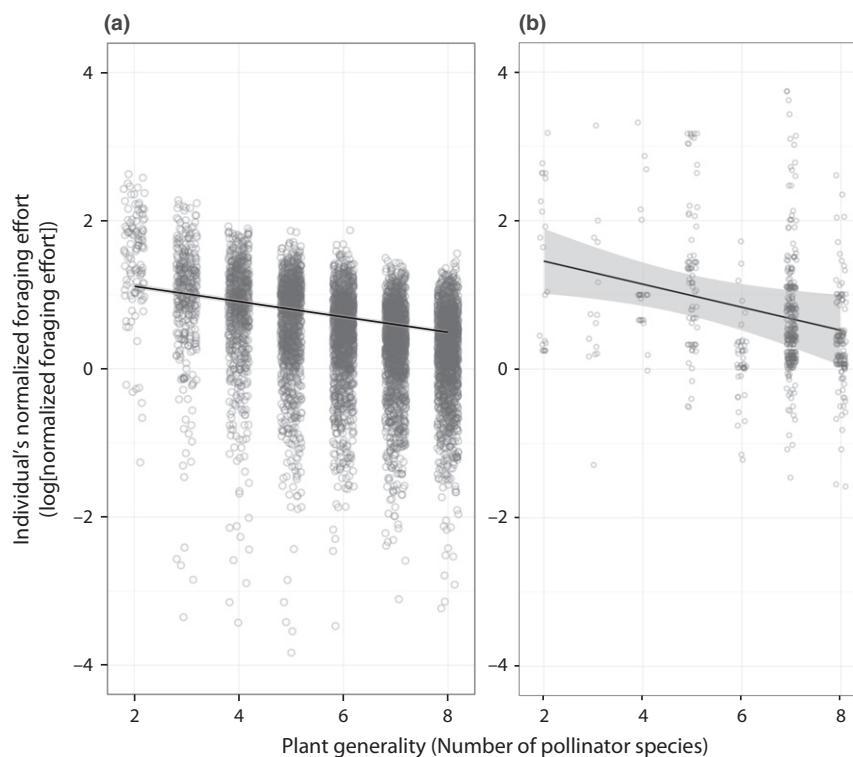
Figure 5 Effects of plant connectivity on relative foraging effort in model (a) and field (b) data. Points depict the normalised mean log foraging effort of individuals in a population of one animal species on individuals in a population of one plant species (y-axis), as a function of plant degree (the number of animal species that visit that plant species, x-axis). Lines depict best-fit estimates from linear mixed-effects models, with the 95% 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 webs appear the closest to our field data given that they contain on average 30 plant species and on average seven animal species are the most general pollinators within the networks, whereas the empirical data consist of eight generalised pollinator species foraging on 35 plant species.

negative trends in foraging effort with increased plant generality (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 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 well estimated by the empirically observed number of generalist partners of the plants.

DISCUSSION

Our study shows how niche partitioning due to adaptive foraging (AF) stabilises realistically structured plant–pollinator networks but not over-connected networks. This partitioning consists of generalist pollinators preferring specialist plants (Fig. 5a), while ceding floral rewards of generalist plants to specialist pollinators (Figs 1b and 4d). This partitioning also explains how AF reverses the broadly destabilising effect of nestedness and the broadly stabilising effect of connectance (Fig. 3) and may help explain why pollination networks exhibit nested and moderately connected architectures.

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 results from increasing nestedness (Kondoh et al. 2010). This lack of niche partitioning causes specialist pollinators to be

outcompeted by generalist pollinators and degrades pollination services to specialist plants by increasing the number of visits from generalist pollinators with heterospecific pollen loads (Fig. 1a, Ashman & Arceo-Gómez 2013; 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 quantity and quality of visits to specialist plants while increasing their persistence (Figs 4c and S3c). This shift in preference also decreases negative effects of competition on specialist pollinators by ceding to them floral rewards that ultimately reduces the abundance of generalist pollinators (Fig. 4b). Such counterintuitive reductions in organismal abundance resulting from their adaptive behaviour have been identified elsewhere as 'evolutionary deterioration' (Dieckmann & Ferrière 2004).

Niche partitioning also explains how AF reverses the stabilising effect of connectance. Without AF, increasing connectance enhances the diversity and therefore abundance of food sources available to the pollinators which greatly increases the persistence of pollinators but also slightly decreases plant persistence (Fig. 3). With AF and subsequent niche partitioning, pollinators escape the negative consequences of competition which allows all pollinators to persist and eliminates the 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-connected networks, all pollinators pollinate

more than one species of plant which allows all pollinators to decrease their visits to their most generalised plants and subsequently decrease these plants' persistence (Table 1) due to degradation of pollination services.

These findings on the negative impact of increasing connectance on plant 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 between the stability of species abundances and the connectance of the mutualistic networks (Okuyama & Holland 2008; James *et al.* 2012a,b). This contradiction appears due to the dynamics of foraging preferences (eqn 1) that can create negative effects between pollinators and plants in contrast to the qualitatively invariant positive effects in previous models which cause species persistence to always increase with the number of interactions, that is, connectance.

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 that nestedness stabilises mutualistic networks by reducing effective interspecific competition. This stabilising effect of nestedness occurred because all species of the same 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, 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. 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. Nestedness stabilises these networks because it increases resource sharing which increased these positive effects. In contrast, we found that nestedness decreases species persistence 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 counteracts these negative effects of nestedness in realistically connected networks by allowing foraging effort to shift such that adaptive foragers increase niche partitioning, which increases visits to specialist plants and resources available for specialist pollinators (Fig. 1).

Beyond determining how network structure and dynamics influence stability, another key role of the theory motivating our model is illuminating previously unrecognised behaviours in nature. Our theory fulfils this role by predicting that foraging effort is distributed such that generalist pollinators expend more effort on less-connected plants, a result that is strikingly consistent with a large, detailed field dataset on plant visitation by bumble bees. To the best of our knowledge, this is the first time that predictions of variable foraging effort among topologically available resources have been tested against field observations of mutualistic networks. Although other factors besides competition between bees for the floral rewards of generalist plants may drive this result, our data (Brosi & Briggs 2013) suggest that when competition is relaxed via pollinator removals, the statistically significant negative relationship between foraging effort and plant degree disappears (unpublished results). These relationships are consistent with previous theoretical work (Staniczenko *et al.* 2013; Valdovinos

et al. 2013) but contradict a previous meta-analysis of field data (Bascompte *et al.* 2006). This discrepancy is straightforward to 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 on visitation (Blüthgen *et al.* 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 analysis of foraging effort normalised to plant abundance allows the predicted signal to be expressed in the field data. Further tests of our predictions against additional empirical 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.

Given our study's overall results and their relation to other findings, we suggest that the pollination behaviours and network structures found in nature effectively balance a conflict between strategies that benefit pollinators and plants. Pollinator species benefit from consuming more rewards available from more plant species (MacArthur 1965). Plant 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 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 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 emerge during the evolution of species within networks (Allhoff *et al.* 2014).

Several of our model's simplifying assumptions would be particularly interesting to 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, such dynamics are especially interesting (Dieckmann & Ferrière 2004) given selective pressures that may prevent generalists from evolving behaviours such as adaptive foraging 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 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 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 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.

Future work also needs to better control the degree distribution when generating nested networks (Saavedra & Stouffer 2013). For example, specialists were more general in our non-nested than in our nested networks (results not shown). The strong correlations between fundamental proprieties such as nestedness, connectance and degree distributions (James *et al.* 2012b) highlight the difficulty in determining which of several highly correlated properties are driving the stability effects. Finally, our theory assumes that a 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 scale of our model may be nonetheless consistent with suggestions that 'true' specialists on single species are very rare based on the observations at larger geographic, spatial and evolutionary scales.

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

AUTHORSHIP

F.S.V. and N.D.M. designed the study; F.S.V. and P.M.de E. performed the simulations; B.J.B. and H.M.B. collected and analysed the empirical data; F.S.V., N.D.M. and B.J.B. analysed the model data. F.S.V., N.D.M., B.J.B. and H.M.B. wrote the manuscript; R.R.J. gave technical support and conceptual advice.

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