A new model for ecological networks using species-level traits

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Summary

1. Recent studies on plant–pollinator networks have focused on explaining network structure through linkage rules, including spatio-temporal overlap, and phenotypic trait or phylogenetic signal complementarity. Few studies, however, have quantified the extent to which functional traits affect the probability of plants and pollinators interacting with each other.

2. Dirichlet-multinomial (DM) regression is a consumer-resource model for the interaction probabilities in a mutualistic network. This flexible model accommodates network heterogeneity through random effects and overdispersion and can estimate the contribution of species-level traits to plant–pollinator interactions.

3. Using artificial networks based on linkage rules and neutrality, we evaluate the performance of DM regression and explore the model's parameter space. We also analyse an empirical network in which the interaction probabilities are modelled by species characteristics.

4. Study results show that such random effects models can provide good fits to observed data. The characteristics pollinators seek in plant species may be better anticipated if species interactions are modelled by the functional traits that drive them.

Key-words: complementary traits, Dirichlet-multinomial regression, forbidden links, interaction probabilities, linkage rules, network structure, pollen transfer network, pollination webs

Introduction

Species and their interactions assemble into large, complex networks that shape and maintain ecological systems. Hence, effects upon one species may (in-)directly impact other species and processes such as pollination, seed dispersal and host–parasitoid relationships (Montoya & Solé 2002; Montoya, Pimm & Solé 2006). Using adjacency matrices that represent these interactions, interest often lies in describing which species interact with each other, quantifying the frequency of interaction and understanding the driving mechanisms of *why* species interact. However, several knowledge gaps need to be overcome to better predict which species are connected to each other. Although we focus on plant and pollinator systems, these methods can be easily adapted to other ecological systems.

Studies suggest that ecological networks are nested organizations of pairwise interactions (Jordano, Bascompte & Olesen 2006; Montoya, Pimm & Solé 2006; Bascompte & Jordano 2007; Vázquez *et al.* 2009a) that may be driven by both evolutionary and ecological processes. Functional traits, such as the varied morphological and behavioural characteristics of pollinator taxa, have been identified as strong candidates to quantify ecosystem service delivery (Kremen 2005; Díaz *et al.* 2011;

Lavorel & Grigulis 2012) because of their effects on quantity and quality of pollination services. For example, body size measures correlate with pollination efficiency (Larsen, Williams & Kremen 2005), foraging duration (Stone & Willmer 1989; Stone 1994), foraging distance in some bees (Greenleaf *et al.* 2007) and susceptibility to land-use change (Winfree *et al.*, 2009; Williams *et al.* 2010). Pollinator preferences in plant characteristics, detectability of plant–pollinator links and the development of plant–pollinator linkage rules may thus be better anticipated if interactions are modelled as a function of these important functional attributes.

In fact, using functional traits or linkage rules as a proxy to infer biotic interactions has progressed our understanding about the dynamics and organization of communities (Santamaría & Rodríguez-Gironés 2007; Allesina, Alonso & Pascual 2008; Stang *et al.* 2009; Blüthgen 2010; Rohr *et al.* 2010; Olesen *et al.* 2011; Gravel *et al.* 2013; Bartomeus 2013; Eklöf *et al.* 2013; Junker *et al.* 2013). Santamaría & Rodríguez-Gironés (2007) demonstrated that two to four linkage rules were sufficient in reproducing much of the structure in empirical networks. Eklöf *et al.* (2013) found that only a few traits were required to represent the structure of 200 bipartite networks and that three trait models were often similar to all trait models. For food webs, body size tends to dominate species interactions (Gravel *et al.* 2013), though latent traits could increase the number of predicted links from 20% to 73% (Rohr *et al.* 2010).

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Complementarily, empirical and theoretical works have supported neutral models, in which the probability of species interacting is proportional to their relative abundances. As such, network properties are the direct result of frequency distributions of different guilds. Several aspects of network structure could be explained by neutrality (Blüthgen, Menzel & Blüthgen 2006; Vázquez *et al.* 2009a); however, the determinants of abundances themselves are not accounted for and are likely nonrandom. Olito & Fox (2015) used the multinomial model of Vázquez, Chacoff & Cagnolo (2009b) to evaluate the contribution of neutrality to network structure and found that the best predictive models are network-metric dependent, but all failed to predict interaction frequencies. Poisot, Stouffer & Gravel (2015) discussed the dynamic nature of interaction networks and noted that by neutrality, local variations in abundance can affect the overall network structure. However, even if two species meet, local trait distributions affect which interactions will be realized. Which theory dominates in the real world is unclear – it is likely that both theories contribute, but few models incorporate them simultaneously. The model we propose here can accommodate both theories.

The motivation of our research is to model interaction probabilities as a function of multiple factors much the way econometricians model consumers choosing among a set of brand products (Mosimann 1962; McFadden 1974; Hausman, Hall & Griliches 1984; Shonkwiler & Hanley 2003; Guimarães & Lindrooth 2007). In particular, we adapt Dirichlet-multinomial (DM) regression (Guimarães & Lindrooth 2007) to analysing ecological networks such as pollination webs. We assume that pollinators assign a level of utility to every plant species it is faced with, based on the plant species' attributes and random effects, and choose the ones that provide maximum utility. These utilities are then translated into interaction probabilities (see Fig. 1). Individual pollinators of the same species choose plant species according to the same probabilities as each other, but they may ultimately select different plant species.
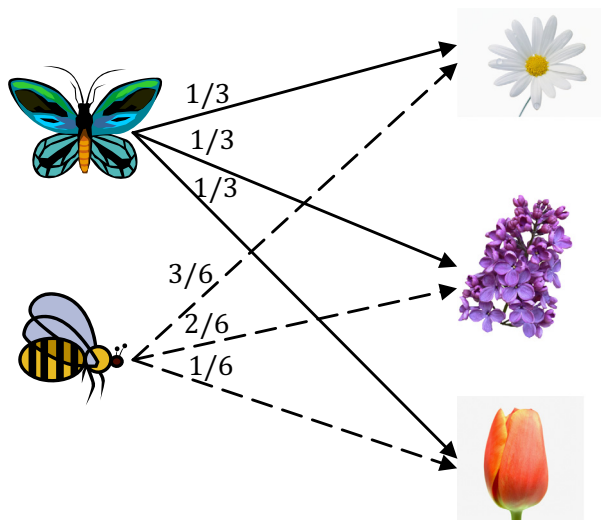

Fig. 1. Pollination network with two pollinator and three plant species. Interaction probabilities appear above arrows.

The model is called 'Dirichlet-multinomial regression' because it is based on assuming that pollinator species choose plants species according to a multinomial distribution with multinomial (interaction) probabilities that are themselves random. These probabilities follow what is known as a Dirichlet distribution and are related to the species traits and/or linkage rules through the utilities mentioned above (Guimarães & Lindrooth 2007). The unconditional distribution for the number of interactions is known as the Dirichlet-multinomial distribution (Mosimann 1962). However, by Bayes' Theorem, the posterior distribution for the interaction probabilities is itself a Dirichlet distribution. If there were only one pollinator species and two plant species in the system, then the multinomial distribution reduces to a binomial distribution, the Dirichlet distribution is equivalent to a beta distribution, and the (unconditional) distribution for the number of interactions is the beta-binomial distribution.

A benefit of DM regression is that it can account for pollinator species heterogeneity through an overdispersion parameter. Since plant–pollinator networks are known to be heterogeneous (Bascompte & Jordano 2007), the interactions of a given pollinator species may be observed more frequently than predicted by the multinomial distribution. Accordingly, the overdispersion parameter is pollinator specific (possibly a function of pollinator traits) and accounts for this extra-multinomial variation. Ultimately, DM regression can be used to estimate the relative contribution of the factors that affect the interaction probabilities, which in turn provides insights into the mechanisms driving the observed network structure.

Unlike previous models, DM regression accommodates *all* of the following features and advantages: (i) extra-multinomial variation in observed counts can be modelled using an overdispersion parameter; (ii) interaction probabilities can be modelled as a function of plant and pollinator characteristics and/or linkage rules; (iii) only detailed information at the species level is needed to supplement the quantitative observed network; and (iv) it is easy to fit the model, calculate standard errors and confidence intervals, and interpret the results. It should also be noted that if the model is fit using only relative abundances, then the model is equivalent to assuming neutrality.

Our specific questions of interest are as follows: (i) Is the DM model capable of simulating networks with diverse network structures? (ii) Can the interaction probabilities be well estimated, given count data and detailed trait information? (iii) Is the model robust to misspecifications of overdispersion? (iv) Even when linkage rule information is not available, can DM regression provide useful insights into which species characteristics contribute to network structure?

We address (1) to (3) by generating artificial plant–pollinator networks, driven by three linkage rules and relative species abundances, with varying dispersion structures (none, constant, function of traits and intra-class correlation) and fitting all networks using DM regression assuming each of these dispersion structures. We address (4) by analysing a real-world network in which the factors that affect the interaction probabilities are unknown. Note that here, we focus on the simplest scenario, in which there is only a single network of interest, so

that the reader can better understand DM regression. Understanding the factors driving interactions in a particular ecosystem can facilitate development of improved species management strategies.

Materials and methods

DIRICHLET-MULTINOMIAL REGRESSION

Consider a plant–pollinator network represented by a count matrix Y with G pollinator species (rows) and J plant species (columns). Interaction probabilities are modelled as a function of K plant species attributes or linkage rules similar to Vázquez, Chacoff & Cagnolo (2009b). In particular, we use X to represent the $G{\times}J{\times}K$ array of covariates (species attributes and/or linkage rules), with entries x_{gjk}, and use x_{gj} to represent the K-length vector of covariates associated with each pollinator species g and plant species j. We assume that the counts for pollinator species g follow a multinomial distribution with interaction probabilities π_{gj}, summarized as follows:

$$y_{g1}, \dots, y_{gJ} \sim \text{multinomial}(n_{g1}, \dots, n_{gJ}; \pi_{g1}, \dots \pi_{gJ}), \text{ for } g = 1, \dots, G$$

where n_{gj} is the number of interactions made between pollinator species g and plant species j, and the sum of the probabilities for pollinator g sums to one: $\sum_j \pi_{gj} = 1$. Further, we assume that each individual pollinator i of species g assigns a utility U_{igj} to plant species j as follows:

$$U_{igj} = \beta' x_{gj} + \eta_{gj} + \varepsilon_{igj}$$

for $g = 1, \dots, G; j = 1, \dots, J;$ and $i = 1, \dots, N$, where $\beta' = (\beta_1, \beta_2, \beta_3, \dots, \beta_K)$ is a K-length vector of unknown regression coefficients associated with the covariates in x_{gj}, η_{gj} is a scalar random group effect, and ε_{igj} is a random error term for the ith pollinator of species g that visits plant species j. Since pollinators seek plant species that maximize their utility, the errors follow independent (type I) extreme value distributions; see Appendix S1. It is these utilities that relate the interaction probabilities to the covariates using random utility theory.

To simplify the discussion, let us consider the special case in which there is only one pollinator species and two plant species. The above scenario simplifies considerably because we can omit the subscripts g and j, the number of visits across the two plant species reduces to a binomial distribution, and there is only one interaction probability to estimate (by letting $\pi_1 = \pi$ and noting that $\pi_2 = 1 - \pi$). Further, the log odds of visiting plant species 1 can be modelled by the average (expected) utility assigned to plant species 1 as follows:

$$\log\left(\frac{\pi}{1-\pi}\right) = \beta' x + \eta \qquad \text{eqn 1}$$

With a little rearranging of terms, (1) can be shown to give interaction probabilities by the following:

$$\pi = \frac{\exp(\beta' x + \eta)}{1 + \exp(\beta' x + \eta)} \qquad \text{eqn 2}$$

In the general case, in which there is more than one pollinator species and more than two plant species, eqn (2) extends naturally and can be rewritten as follows:

$$\pi_{gj} = \frac{\exp(\beta' x_{gj} + \eta_{gj})}{\sum_{j=1}^{J} \exp(\beta' x_{gj} + \eta_{gj})} = \frac{\lambda_{gj} \exp(\eta_{gj})}{\sum_{j=1}^{J} \lambda_{gi} \exp(\eta_{gj})} \qquad \text{eqn 3}$$

for $g = 1, \dots, G$; and $j = 1, \dots, J$,

where $\lambda_{gj} = \exp(\beta' x_{gj})$. We further make the assumption that the exponential of the random group effects, $\exp(\eta_{gj})$, follows independent gamma distributions with both shape and scale (rate) parameters $\delta_g \lambda_{gj}$,

for some $\delta_g > 0$. Under these assumptions, Mosimann (1962) showed that the interaction probabilities for pollinator g follow a Dirichlet distribution (multivariate version of a beta distribution) with parameters $(\delta_g \lambda_{g1}, \delta_g \lambda_{g2}, \dots, \delta_g \lambda_{gJ})$. The term δ_g is used to quantify the overdispersion in the interaction counts.

The model has two main components: (i) the structural model, $\beta' x_{gj}$, which relates the plant attributes and/or (binary) linkage rules directly to the interaction probabilities, and (ii) the random effects, η_{gj}, which relate the pollinator traits with the model overdispersion. The coefficient associated with the kth covariate can be interpreted as follows: e^{β_k} is the odds ratio of a pollinator species interacting with a plant species relative to a second plant species with the same traits as the first, but for which the value of the kth covariate differs by one. The goal of fitting a DM regression is to unbiasedly estimate the regression coefficients in β' and the dispersion parameter δ_g using maximum-likelihood estimation.

DISPERSION STRUCTURE

The overdispersion associated with pollinator species g can be represented in several ways. The simplest case is constant overdispersion across all pollinator species: $\delta_g = \delta$. However, sometimes it may be reasonable to assume that overdispersion is a function of pollinator-specific traits: $\delta_g = f(z_g) = \exp(\gamma' z_g)$, where γ contains coefficients to be estimated by the model and z_g is an L-length vector of pollinator-specific characteristics (e.g. mean body size). Alternatively, overdispersion can be modelled as a function of the intra-class correlation coefficient, ρ_g, which represents the correlation among individual pollinators within species g (Guimarães & Lindrooth 2007). See Appendix S1. In the absence of dispersion, DM regression is equivalent to a standard multinomial logistic regression model.

SIMULATION STUDY DESIGN

We generated networks assuming one of four dispersion structures: none, constant ($\delta_g = \delta$), function of pollinator-specific covariates ($\delta_g = \exp(\gamma_0 + \gamma_1 z_g)$) and constant intra-correlation ($\rho_g = \rho$). There were four simulated covariates; three were Boolean operators that linked plant traits with pollinator traits per Santamaría & Rodríguez-Gironés (2007), giving $X = (x_1$: barrier trait, x_2: complementarity trait with narrow range variability, x_3: complementarity trait with medium-range variability, x_4: plant species relative abundances), where x_k is a $G \times J$ matrix with entries x_{gjk}, $k = 1, \dots, 4$. The associated regression coefficients used in the DM models were $\beta_1, \beta_2, \beta_3$ and β_4, respectively, which were then used to generate artificial networks. We analysed these networks using DM regression to facilitate evaluation of its performance for settings in which the true parameter values were known.

PARAMETER SETTINGS

The number of pollinator species was regressed on the number of plant species (on the square-root scale; Santamaría & Rodríguez-Gironés 2007) for pollination networks in the Interaction Web Database (Guimarães, Galdini Raimundo & Cagnolo 2011); see Appendix S6. Using this regression formula, artificial networks were generated with $J = 20$, 40 or 120 plant species and $G = 53$, 78 and 127 pollinator species, respectively. The values of β, δ, γ and ρ were selected to allow exploration of the parameter space, using parameter ranges based on an ad hoc pre-analysis (results not shown) that suggested the following. Coefficient values (β_k) between $(-1, 5)$, δ^{-1} values between $(0, 12)$, dispersion coefficient values (γ) between $(-4, 2)$, and ρ values between

(0, 1) generated networks that were neither too sparse nor too highly populated. Accordingly, parameter values were sampled from independent uniform distributions over low, medium and high subintervals of these respective ranges: $\{(-1, 1), (1, 3), (3, 5)\}$ for each β_k; $\{(0, 4), (4, 8), (8, 12)\}$ for δ^{-1}; $\{(-4, -2), (-2, 0), (0, 2)\}$ for each of γ_0 and γ_1; and $\{(0, 0.33), (0.33, 0.67), (0.67, 1)\}$ for ρ.

For each dispersion structure, networks were generated using parameter values set at the above levels according to a factorial design. Consider the no dispersion scenario. Low, medium and high values for each of the four β_k's were sampled, and then, all combinations of the coefficients at the different levels were used to generate $3^4 = 81$ networks according to a DM regression. This design was then replicated 10 times resulting in 810 networks in total. The constant and intra-correlation dispersion (δ^1 and ρ) scenarios included an additional dispersion parameter, resulting in $3^5 \times 10 = 2430$ networks each. Similarly, when dispersion was a function of pollinator covariates, there were two additional dispersion coefficients, resulting in $3^6 \times 10 = 7290$ networks in total. All scenarios were repeated for each of the three network sizes.

COVARIATE AND COUNT GENERATION

Covariates x_1, x_2 and x_3 represented linkage rules per Santamaría & Rodríguez-Gironés (2007). Let V_g and W_j be the mean trait values for the gth pollinator species and jth plant species, respectively, and ψV_g and ψW_j be their respective ranges in variability. V_g and W_j were generated from independent uniform distributions over (0, 1) and ψV_g and ψW_j were generated from independent uniform distributions over (0, 0.25) or (0, 0.5) for the narrow- and medium-range complementarity traits, respectively. Variability was ignored for the barrier trait. As such, the complementarity and barrier trait values were constructed using the following Boolean operators, respectively, as follows:

$$x_{gjk} = \begin{cases} 1, \text{if } |V_g - W_j| < 0.5(\psi V_g + \psi W_j) \\ 0, \text{otherwise} \end{cases} \quad k = 1, 2 \quad \text{and}$$

$$x_{gj3} = \begin{cases} 1, \text{if } V_g > W_j, \\ 0, \text{otherwise} \end{cases},$$

where x_{gjk} is the kth covariate for the g–jth pollinator–plant pair. Covariates x_4 and z_1 represented relative species abundances for plant and pollinator species, respectively, and were generated using the inverse cumulative distribution function method (Devroye 1986) to sample from the species abundance distribution (Ravasz *et al.* 2005). Conditional on the row sums, cell counts y_{gj} were generated from a Poisson distribution with rate $\lambda_{gj} = \exp(\beta' x_{gj})$. See Appendix S3.

All networks were generated in R (R Development Core Team, 2011), and the following network metrics were calculated: connectance, links per species, mean number of shared partners, NODF, weighted NODF, interaction strength asymmetry, specialization asymmetry, generality, vulnerability, linkage density, interaction evenness, relative diversity[1], H'_2, and mean paired difference index (PDI) for both species levels (Dormann *et al.* 2009; Poisot *et al.* 2012). DM regression was also fit in R (Crea 2014) to each network and Monte Carlo estimates (Robert & Casella 2010) of relative biases (RB) were computed as follows,

$$\text{RB} = \frac{100}{R} \times \sum_{r=1}^{R} \frac{\left(\hat{\beta}_k^{(r)} - \beta_k\right)}{\beta_k}$$

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[1]Relative diversity = exp $(H_2)/(G \times J)$, where H_2 is Shannon's interaction diversity.

where $\hat{\beta}_k^{(r)}$ is the estimate of the kth regression coefficient from the rth generated network and β_k is the true parameter value used to generate the rth network. Percentage coefficients of variation were computed as follows:

$$\text{CV} = \frac{100}{\beta_k} \times \sum_{r=1}^{R} \frac{\left(\hat{\beta}_k^{(r)} - \beta_k\right)^2}{R - 1}.$$

Percentage relative biases and percentage coefficients of variation <100 are associated with good performance. Pearson chi-square goodness-of-fit statistics were also used to evaluate DM regression and its robustness to misspecification of dispersion structure.

DESCRIPTION OF CANTERBURY DATA

Insect pollinator sampling was carried out using flight intercept and pan traps over 5-day periods every month for 1 year in the Canterbury plains region, on the South Island of New Zealand. Six replicate sites were selected within four different land-use types. Data were pooled across land-use type and time because the primary interest was in the range of plant–pollinator interactions across the landscape. All insects captured were stored in a laboratory freezer (−80°C) until further processing. Pollen transport networks quantified the number and identity of pollen grains on the insects' bodies. Pollinator effectiveness was established via published literature or unpublished studies conducted in the same geographic area.

Plant and pollinator traits were compiled using existing published and unpublished data sets from the Canterbury region (Eklöf *et al.* 2013; Hudson *et al.* 2014). Plant traits included (i) life span: short (annual/biennial) or long (perennial); (ii) flower type: single flower or small cluster; inflorescence spike, raceme, panicle/cyme/thyrse, umbel/corymb, inflorescence capitulum/head or inflorescence catkin; (iii) ease of access to nectar: openly available or partly hidden; and (iv) flowers per inflorescence: tens, hundreds or thousands. Pollinator traits included (i) average body length (mm); (ii) average body width (mm); (iii) average body breadth (mm); (iv) species behaviour: social or solitary; and (v) larval feeding preference: nectar/pollen or decaying vegetation/animal/dung.

CONSTRUCTION OF CANTERBURY POLLEN TRANSFER NETWORK

In total, there were $G = 16$ pollinator species, $J = 15$ plant species and $N = 485$ interactions collected from 337 individual pollinator specimens. A plant–pollinator species pair was deemed to have interacted if at least one pollen grain from that plant species was detected on the body of an individual from that pollinator species. For example, if there were ten individuals of *Apis mellifera* that carried any pollen grains from *Raphanus* sp., then we recorded ten interactions between *Apis mellifera* and *Raphanus* sp. in our network, regardless of how many grains were found on each individual. Counts in the resulting 16×15 pollen transfer network represent the *minimum* number of interactions required to explain the observed transfer of pollen to the pollinator species (Appendix S4). A stepwise selection method, based on examination of *P*-values from Pearson chi-square goodness-of-fit statistics, and Akaike's information criterion (AIC) were used to determine which plant traits and pollinator traits (for overdispersion) were most compatible with the data.

Results

SIMULATION STUDY: NETWORK STATISTICS

In general, simulated networks exhibited a diverse range of network structures, regardless of the assumed dispersion. Under no dispersion, or dispersion in terms of δ, increasing trends in median were observed for vulnerability, generality, linkage density, links per species and mean number of shared partners (both levels), while little to no trend was observed for the median of other metrics. Interestingly, under constant intra-correlation, median connectance, NODF and weighted NODF tended to decrease and the median values were smaller overall relative to other dispersion structures; other metrics showed little to no trend. For brevity, only four metrics are shown in Fig. 2; see Appendix S5 for all other metrics.

Connectance ranged from 0·02 to 0·97 across all generated networks, with the highest values and least variability arising from generated networks assuming no dispersion. These findings are compatible with Dormann *et al.* (2009), who reported connectance between 0·37 and 0·55 for similar sized networks, and with Vázquez *et al.* (2009a) who found low connectance in published empirical networks. NODF ranged from 0 to 92,

with a slight increasing trend with network size. Relative diversity ranged from 0·00 to 0·74 across all generated networks, with little to no trend as network size increased. Note that in the empirical networks available in the bipartite package in R, NODF ranged from 7·7 to 84·9 and relative diversity ranged from 0·01 to 0·17. Finally, linkage density ranged from 1 to 93, with increasing values and variability seen with increasing network size. This metric is the average of vulnerability and generality and is known to be low in empirical networks (Bersier, Banasek-Richter & Cattin 2002; Tylianakis, Tscharntke & Lewis 2007). Dormann *et al.* (2009) suggested that linkage density slightly increases with network size and reported values between 0 and 40 for similar sized networks.

SIMULATION STUDY: DM MODELS

In general, when networks were analysed assuming the correct dispersion structure, DM regression could recover the regression coefficients with low bias (Tables 1 and 2), as evidenced by most of the percentage relative biases being far below 100%. A closer look at the biases showed that most of the highly biased estimates were associated with either coefficients that were close to zero ($-0.5 < \hat{\beta}_k < 0.5$) and/or high intra-cor-
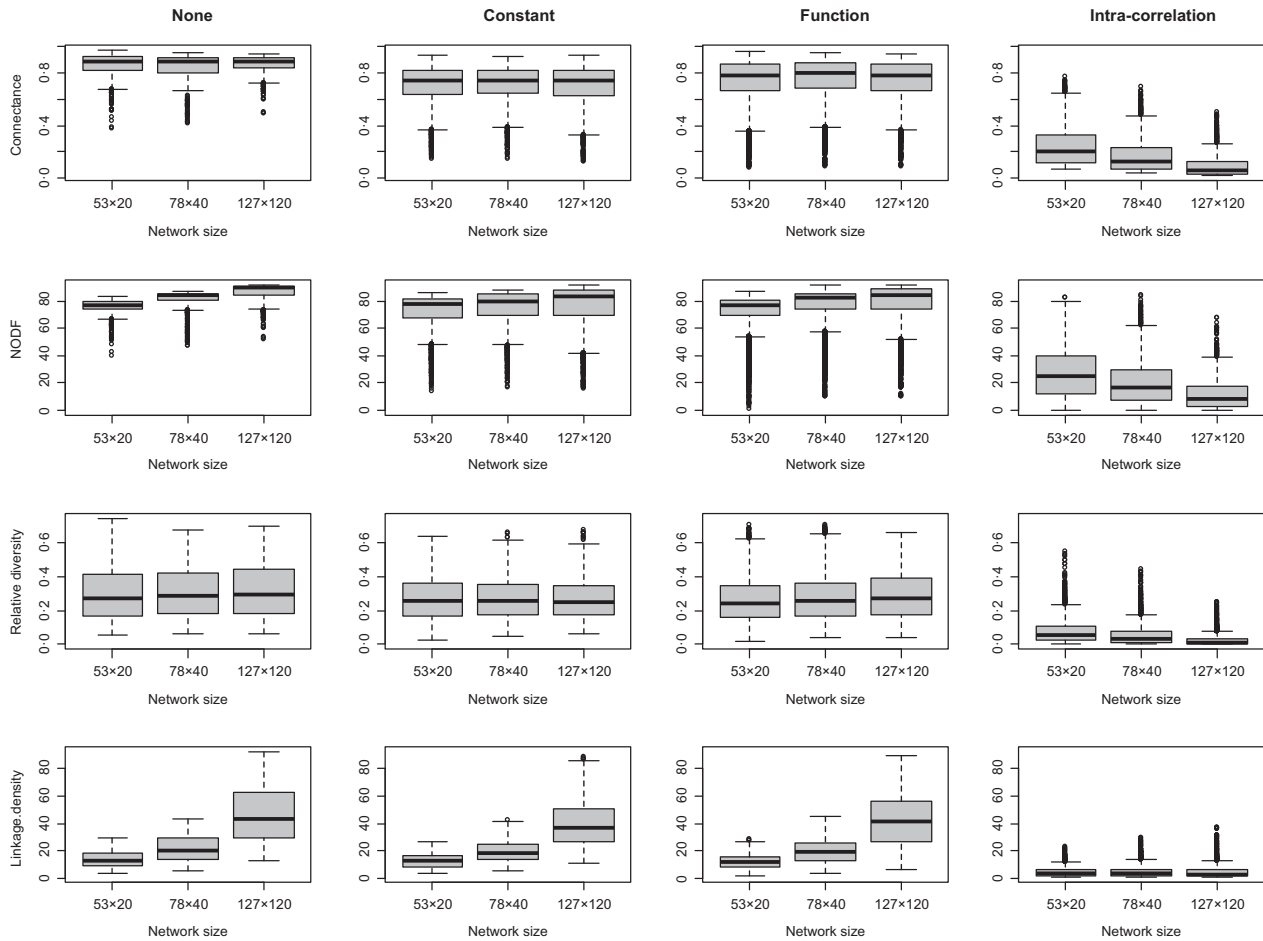

Fig. 2. Network metric distributions of simulated networks by network size and dispersion structure. None: $\delta_g = 0$; Constant: $\delta_g = \delta$; Function: $\delta_g = f(z_g)$; Intra-correlation: $\rho_g = \rho$.

Table 1. (Percentage relative bias) and [percentage coefficient of variation] of $\hat{\beta}$

Network size	True dispersion	Modelled dispersion*		
		None[1]	Constant[2]	Intra-correlation[3]
Percentage relative bias				
53 × 20	None	(6·8, 3·4, 3·41, 39·96)	(7·17, 3·6, 3·62, 42·71)	(6·98, 4·48, 3·79, 41·38)
	Constant	(9·86, 5·66, 8·47, 15·14)	(7·93, 4·86, 7·01, 12·92)	(8·69, 5·35, 7·82, 14·44)
	Intra-correlation	(1241·05, 137·34, 100·25, 747·69)	(523·99, 59·05, 42·98, 139·41)	(522·35, 58·66, 41·67, 188·43)
78 × 40	None	(1·22, 1·19, 3·85, 8·74)	(1·26, 1·24, 4·14, 9·17)	(1·29, 1·29, 4·23, 9·34)
	Constant	(3·64, 12·07, 2·39, 32·62)	(2·86, 10·07, 2·05, 30·18)	(3·47, 10·85, 2·23, 32·84)
	Intra-correlation	(115·89, 62·73, 68·69, 1419·86)	(50·31, 29·41, 30·22, 469·91)	(36·63, 24·84, 26·53, 366·75)
127 × 120	None	(2·52, 1·06, 0·68, 6·6)	(2·46, 1·07, 0·67, 6·99)	(3·01, 1·04, 0·78, 7·55)
	Constant	(3·62, 1·95, 1·52, 27·44)	(2·72, 1·62, 1·22, 27·25)	(3·51, 1·72, 1·41, 25·92)
	Intra-correlation	(38·32, 37·02, 45·35, 5481·41)	(31·39, 14·75, 19·05, 4710·98)	(13·19, 11·13, 15·01, 2221·9)
Percentage coefficient of variation				
53 × 20	None	[29·59, 11·55, 14·59, 325·23]	[30·51, 11·95, 15·54, 337·56]	[29·95, 23·21, 15·95, 329·48]
	Constant	[35·27, 14·13, 29·31, 42·15]	[26·02, 10·74, 23·68, 32·33]	[25·42, 11·05, 23·77, 33·91]
	Intra-correlation	[6311·23, 509·79, 360·9, 12142·99]	[2420·52, 217·02, 133·62, 381·55]	[2497·91, 262·98, 148·36, 1976·09]
78 × 40	None	[2·58, 3·87, 21·88, 35·73]	[2·62, 3·98, 22·35, 35·35]	[2·78, 4·34, 23·04, 39·61]
	Constant	[8·8, 78·65, 5·33, 117]	[6·31, 62·95, 4·37, 102·43]	[7·08, 68·72, 4·41, 103·74]
	Intra-correlation	[517·83, 206·06, 198·58, 14640·54]	[105·21, 163·37, 70·61, 2309·82]	[120·03, 148·92, 72·7, 1801·92]
127 × 120	None	[10·3, 5·33, 2·28, 14·92]	[10·19, 5·44, 2·23, 18·46]	[14·49, 4·05, 2·64, 17·92]
	Constant	[20·97, 6·44, 4·21, 96·21]	[13·49, 4·61, 2·84, 97·44]	[14·35, 4·63, 3·11, 77·4]
	Intra-correlation	[101·99, 108·03, 101·36, 46392·42]	[34·74, 30·76, 40·05, 40616·03]	[38·82, 32·12, 40·04, 17022·77]

*None: $\delta_g = 0$; Constant: $\delta_g = \delta$; Intra-correlation: $\rho_g = \rho$.
[1]For true dispersion, Intra-correlation: based on the 99·5% (53 × 20) and 99·6% (78 × 40) networks for which parameter estimates converged.
[2]For true dispersion, None: based on the 93% (53 × 20), 94% (78 × 40) and 96% (127 × 120) networks for which parameter estimates converged.
For true dispersion, Intra-correlation: based on the 99·7% (53 × 20 and 78 × 40) networks for which parameter estimates converged.
[3]For true dispersion, None: based on the 97% (53 × 20 and 78 × 40) and 96% (127 × 120) networks for which parameter estimates converged.
For true dispersion, Intra-correlation: based on the 99·9% (53 × 20) networks for which parameter estimates converged.

Table 2. (Percentage relative bias) and [Percentage coefficient of variation] of $\hat{\beta}$ for data generated with $\delta_g = f(z_g)$

Network size	Modelled dispersion*			
	None	Constant	Intra-correlation	Function[1]
Percentage relative bias				
53 × 20	(7·39, 9·48, 18·42, 16·3)	(5·85, 8·15, 14·91, 14·34)	(6·85, 8·86, 16·46, 15·98)	(5·83, 8·05, 15·33, 14·48)
78 × 40	(5·85, 32·99, 722·19, 16·04)	(4·83, 22·6, 458·84, 13·7)	(5·67, 24·71, 502·77, 14·83)	(5·11, 21·68, 485·65, 14·02)
127 × 120	(1·99, 1·92, 3·76, 20·23)	(1·58, 1·63, 2·82, 21·08)	(2·17, 1·81, 3·09, 19·68)	(2·36, 2·13, 13·1, 19·47)
Percentage coefficient of variation				
53 × 20	[25·03, 35·71, 142·11, 55·89]	[16·41, 30·74, 108·41, 47·99]	[17·97, 30·62, 115·62, 50·71]	[16·22, 30·72, 110·9, 47·56]
78 × 40	[21·11, 351·7, 7546·71, 66·27]	[16·74, 198·81, 3848·9, 51·61]	[18·49, 209·99, 4222·44, 52·14]	[25·06, 195·98, 4008·67, 56·62]
127 × 120	[6·61, 8·12, 30·03, 62·34]	[4·64, 6·13, 16·14, 67·42]	[5·32, 6·26, 16·61, 51·5]	[52·95, 28·03, 806·3, 58·87]

*None: $\delta_g = 0$; Constant: $\delta_g = \delta$; Function: $\delta_g = f(z_g)$; Intra-correlation: $\rho_g = \rho$.
[1]Statistics based on the 96%, 90% and 90% networks, respectively, for which parameter estimates converged.

relation ($\rho > 0.67$). When data were generated with no overdispersion, the estimates obtained by assuming otherwise tended to produce small relative biases for the binary covariates (linkage rules). Under constant intra-correlation, the average relative biases tended to be larger, but decreased for the binary covariates as network size increased. The relative bias of $\hat{\beta}_4$ (continuous covariate for plant species RA) was greater than that of the binary covariates and tended to increase with network size under constant intra-correlation.

Similar trends were seen in the percentage coefficients of variation for $\hat{\beta}$. If data were generated with no overdispersion, then all methods seemed competitive, though models assuming overdispersion tended to have smaller coefficients of variation. Further, the percentage coefficient of variation values were often close to or much >100% when the true β was close to zero or ρ was high. Overall, modelling dispersion in terms of δ_g or no dispersion seemed more robust to model misspecification compared to modelling dispersion in terms of ρ.

Less than 10% of the time, the chi-square statistics indicated a poor fit to the data (*P*-values <0·05) when networks generated with no overdispersion and correctly fit assuming no overdispersion. When those same networks were analysed assuming some overdispersion, the model fit was quite good (*P*-values >0·05). On the other hand, when networks were

generated with some overdispersion but were analysed assuming no overdispersion, the chi-square statistics indicated poor model fits more than 85% of the time. However, the chi-square statistics indicated poor model fits only 1–25% of the time when analysed correctly assuming some overdispersion. These findings suggest that models assuming some overdispersion are statistically more robust to misspecification of dispersion structure.

EMPIRICAL STUDY

We found that, for this system, all plant traits but life span were important for modelling plant and pollinator interactions (Table 3). Most markedly, the estimated odds ratio of a pollinator interacting with two floral species having the same attributes, except that one has an inflorescence with a spike, raceme, panicle/cyme/thyrsi and the other a single or small cluster of flowers, was 3·48 ($P < 0.001$). Interestingly, after adjustment for constant dispersion, no pollinator traits were statistically significant. We refit the model assuming no dispersion and found that the odds ratios associated with having thousands of flowers (0·49; $P = 0.001$), with inflorescence capitulum/head (2·93; $P < 0.001$) and with inflorescence catkin (0·17; $P < 0.005$) were more statistically significant compared to the respective odds ratios assuming constant dispersion. Further, the chi-square statistic suggested a good fit of the constant dispersion model to the data ($P = 0.797$), but a poor fit of the no dispersion model ($P < 0.001$).

The final model predicted slightly higher values for most network metrics (Table 4), particularly for connectance, NODF and linkage density. However, predicted values of other network metrics, including vulnerability, interaction evenness, relative diversity and mean PDI (lower level), were similar to the observed values of metrics. The predicted metrics were calculated assuming a network with the same number of interactions observed for each pollinator species as that actually observed in the study.

Table 4. Network metrics for Canterbury data

Network metric	Observed	Predicted
Connectance	0·463	0·622
NODF (nestedness)	74·487	83·556
H2'	0·0999	0·000
Linkage Density	6·454	8·495
Vulnerability	5·409	5·929
Interaction evenness	0·702	0·775
Relative diversity	0·195	0·278
Modularity (Q)	0·126	0·047
Mean PDI (higher level)	0·833	0·574
Mean PDI (lower level)	0·910	0·943

Discussion and conclusions

We modelled the relative contributions of linkage rules (simulation study) and of functional traits (empirical study) to the interaction probabilities that determine the topological features of plant–pollinator networks using DM regression (Guimarães & Lindroth 2007). Although the linkage rules we used were rather simplistic, more than one fixed effect could be used to describe a single linkage rule. Alternatively, higher level interaction terms could be included in the model, corresponding to the product of two rules (e.g. include a covariate for ($x_1 \times x_3$) in the model, where x_1 and x_3 represent two different rules). Regardless, the DM model was still able to generate networks that exhibited a diversity of network structures, with some very similar to those observed in real-world networks. However, the simulated networks were not designed to account for sampling bias, which is a known causal effect of observed network structure (Vázquez *et al.* 2009a). Since the goal of the simulation study was to evaluate the performance of DM regression in a setting where the true parameter values are known, the effect of these discrepancies on the results drawn from the study is expected to be minimal.

The bias and standard errors of parameter estimates were typically low, but increased when the values of β_k were too

Table 3. Odds ratios of plant–pollinator interactions for Canterbury data

Variable	Constant dispersion			No dispersion		
	odds ratio	95% CI	*P*-value	odds ratio	95% CI	*P*-value
Type of flower						
Single flower or small cluster	1·00			1·00		
Inflorescence spike, raceme, etc.	3·48	(1·69, 7·18)	0·001	5·02	(3·14, 8·02)	<0·001
Inflorescence capitulum/head	2·31	(0·89, 6·02)	0·086	2·93	(1·62, 5·29)	<0·001
Inflorescence catkin	0·24	(0·06, 0·97)	0·045	0·17	(0·05, 0·57)	0·005
Ease of access to pollen/nectar						
Easy access	1·00			1·00		
Partly hidden nectar	2·15	(1·32, 3·51)	0·002	2·35	(1·81, 3·05)	<0·001
Flower density per floral unit						
Tens of flowers	1·00			1·00		
Hundreds of flowers	1·88	(1·12, 3·13)	0·016	1·60	(1·20, 2·14)	0·002
Thousands of flowers	0·85	(0·46, 1·58)	0·611	0·49	(0·32, 0·75)	0·001
Dispersion						
Constant	2·95	(1·23, 6·72)	0·010	NA	NA	NA

close to zero or intra-correlation was high. Models that assumed no or constant overdispersion were statistically more robust to model misspecification relative to assuming other dispersion structures. However, the chi-square statistics suggested that assuming some overdispersion was less prone to overfitting. Estimates associated with continuous covariates showed larger bias, but this may not pose a problem in practice if covariates correspond to binary linkage rules.

Note that we did not encounter problems recovering structural zeroes in the generated networks because their presence was driven by the linkage rules included in our model. In practice, it is anticipated that either an important trait is left out of the analysis (e.g. too difficult to measure), or it is encoded incorrectly when constructing a covariate. Accordingly, one may expect to find data that is zero-inflated because the fitted model does not account for all observed zeroes. Understanding the behaviour of DM regression in the presence of zero inflation or sampling bias is an important modelling issue, but is outside the scope of this paper and the focus of future research. Nonetheless, the results of the simulation study provide useful information about the performance of DM regression as a statistical model and how to use the analysis results to infer an appropriate dispersion structure.

In the empirical analysis, the actual number of interactions made to collect the amount of observed pollen was unknown. Because the pollen from a given plant species found on an individual pollinator was assumed to be the result of a *single* plant interaction, the pollen transfer network likely underestimated the true number of interactions. However, since pollen grains were physically found on the body of the pollinator, it is more likely that the recorded counts would have led to a pollination event relative to counts in a visitation web (Alarcón 2010; Popic, Wardle & Davila 2013).

Since an individual pollinator may have had more than one type of pollen on its body, multiple interactions in the pollen transfer network were from the same individual pollinator. Visitation webs have a similar drawback since multiple visits in a visitation web may have been made by the same individual pollinator. If visitation web data were available for these data, then a pollen transport network (Alarcón 2010) could have been constructed, but the cost of collecting such data was beyond the financial scope of the empirical study.

Pollinators tended to forage on plant species with inflorescences and/or many flowers, likely due to increased visual attraction and greater floral rewards of larger floral displays (Torres & Galetto 1998). They were also more likely to visit flowers with partly hidden floral resources, perhaps reflecting the spatio-temporal resource availability within the study area and/or the composition, abundance and resource preferences of the pollinator community (Heinrich 1979; Willmer 2011). For example, taxa with long tongue lengths or unique flower handling behaviours may access hidden resources more effectively than others. In the absence of nectar-accessible flowers, pollinator preferences may shift to those that require greater handling time.

Eklöf *et al.* (2013) analysed a binary version of the Canterbury network and found that pollinator body width was the single trait that explained the largest fraction of links in the network. Other important traits included amount of nectar and flower type (see Table 1), resulting in 91% of the links in the binary network being explained by their model. The plant attributes we identified as significant are in line with Eklöf *et al.* (2013). Interestingly, we found flower type, not body width, to be the single trait with highest contribution to the interaction probabilities in the network. In fact, we found that only constant dispersion was needed to accommodate pollinator heterogeneity, rather than a pollinator species body size measure. However, it should be noted that Eklöf *et al.* (2013) did not consider overdispersion in their model, which may explain this discrepancy.

Analogous to the simulation study, the model assuming overdispersion provided a better fit to the data. Note that the coefficients associated with inflorescence catkin and with floral density 'thousands of flowers' were based on very few floral species (≤2) in each category, so corresponding confidence intervals for these parameter estimates under the constant dispersion model were wider than their no dispersion counterparts, resulting in less significant estimates. Hence, the constant dispersion model appears to be more robust to potential outliers.

The properties of the network predicted by DM regression were also in line with trends found in the literature. For example, Nielsen & Bascompte (2007) found that nestedness is relatively robust to sampling effort and Chacoff *et al.* (2012) found that the number of interacting species was typically underestimated and estimated to be as much as 55% for a visitation web based on two study sites observed over four flowering periods. Our predicted weighted nestedness was close to the observed nestedness, while the predicted connectance was approximately 1·5 times the observed connectance.

RELATION TO OTHER METHODS

Santamaría & Rodríguez-Gironés (2007) assumed that all plant and pollinator species that could interact did interact and that each rule contributed equally to the process. Although our covariates were similar to theirs, we applied differential weights (coefficients) to each rule using our probabilistic approach. We also included species relative abundances. The dimension search method of Eklöf *et al.* (2013) plots the lower trophic species in trait dimensions and seeks the fewest number of traits to explain all links in the network. Rohr *et al.* (2010) use logistic regression to model the odds of a link using body size ratios. When latent traits are included, Markov chain Monte Carlo (MCMC) methods are needed. Gravel *et al.* (2013) also use the allometric scaling relationship between predator and prey body sizes. All of these models use binary networks; dimension search and logistic regression do not accommodate overdispersion.

Vázquez, Chacoff & Cagnolo (2009b) modelled network interactions assuming counts follow a multinomial distribution with probabilities based on relative abundances, spatio-temporal overlap, phenotypic traits, phylogenetic signal

and sampling effects. Sorensen *et al.* (2011) used the Dirichlet-multinomial distribution to estimate standard deviations of interaction frequencies, and Wells & O'Hara (2012) incorporated both individual level and species-level data in a Poisson random effects model for interaction probabilities. The former model does not incorporate any covariate information, while the latter model requires Gibbs sampling to fit the model.

The focus of several researchers has been to study interaction networks at the macrolevel (Bartomeus 2013; Eklöf *et al.* 2013) and identify common trends in network structure across several networks. However, our focus here has been on individual networks. To use DM regression to model several networks, the relevant factors for each network would need to be determined and measured in order to fit the model. Then, the predicted values of the network metrics, or the contributions of the common factors, could be compared across the networks.

In summary, we have presented a novel approach to modelling interaction probabilities in a plant–pollinator network. This approach can quantify the contributions of diverse traits and/or linkage rules to pollination, thereby providing insights into the mechanisms that drive this ecological process. However, DM regression could also be used to model other ecological networks such as seeder–disperser or host–parasite relationships.

Acknowledgements

Data accessibility

Code to generate and analyse artificial plant–pollinator networks in R, per the simulation study, is available on GitHub (Crea 2014). The empirical Canterbury data have been archived in the PREDICTS data base (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems – www.predicts.org.uk) as of December, 2014 (http://dx.doi.org/10.5519/0018993).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. DM regression and relationship between δ and ρ.

Appendix S2. GCL and DM regression R program.

Appendix S3. Data generation.

Appendix S4. Quantitative pollen transfer network for Canterbury data.

Appendix S5. Network statistics.

Appendix S6. List of plant-pollinator networks from the Interaction Web Database (IWDB) used to specify network sizes for simulation study.