

IDEA AND PERSPECTIVE

Towards a predictive model of species interaction beta diversity[‡]

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Abstract

Species interactions are fundamental to community dynamics and ecosystem processes. Despite significant progress in describing species interactions, we lack the ability to predict changes in interactions across space and time. We outline a Bayesian approach to separate the probability of species co-occurrence, interaction and detectability in influencing interaction betadiversity. We use a multi-year hummingbird–plant time series, divided into training and testing data, to show that including models of detectability and occurrence improves forecasts of mutualistic interactions. We then extend our model to explore interaction betadiversity across two distinct seasons. Despite differences in the observed interactions among seasons, there was no significant change in hummingbird occurrence or interaction frequency between hummingbirds and plants. These results highlight the challenge of inferring the causes of interaction betadiversity when interaction detectability is low. Finally, we highlight potential applications of our model for integrating observations of local interactions with biogeographic and evolutionary histories of co-occurring species. These advances will provide new insight into the mechanisms that drive variation in patterns of biodiversity.

Keywords

Bayesian, dissimilarity, evolutionary history, interaction beta-diversity, interaction turnover, network ecology, prediction, rewiring, scale, species turnover.

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INTRODUCTION

Patterns of species diversity are caused by multiple ecological, evolutionary and biogeographic processes acting across spatial, temporal and phylogenetic scales. Given this complexity, most attempts to explore the causes of ecological diversity focus on single trophic levels, ignoring the added complexity of species interactions. However, while it is well known that interactions will vary across time and space, (Winemiller 1990), we have only recently begun to model the spatial and temporal variation in species interactions (i.e. interaction beta-diversity; Poisot *et al.* 2015a; Tylianakis & Morris 2017). Attempts to understand this variation have yielded a myriad of results. In some cases, interaction beta-diversity appears to be driven by the change in species composition across sites (referred to here as species turnover), which depends largely on the environmental tolerances, phenology and dispersal ability of interacting partners (Miller-Struttmann & Galen 2014; Trojelsgaard *et al.* 2015; Kemp & Ellis 2017). Alternatively, co-occurring species may interact differently over space and time (referred to here as interaction turnover) as a result of changes in the costs and benefits of interactions (Vázquez *et al.* 2015). Given that distinct mechanisms, acting at different scales, lead to observed patterns of diversity (Mayfield & Levine 2010; Adler *et al.* 2013; Kraft *et al.* 2015), it has been challenging to develop models that embrace this complexity. Furthermore, despite significant methodological advances (Poisot *et al.* 2012; Jordano 2016), we lack a conceptual and statistical approach to rigorously evaluate spatial and temporal predictions of species interactions.

We build from recent developments (Bartomeus *et al.* 2013; Gravel *et al.* 2013, 2016; Poisot *et al.* 2015b; Weinstein & Graham 2017a,b) to model interactions as probability distributions using a hierarchical Bayesian framework (Wells & O'Hara 2013; Coblenz *et al.* 2017). This approach differentiates the predictors of interactions from the probability of detecting an interaction, and assesses the variation in emergent network properties using out-of-sample prediction. We focus on mutualistic interactions among plants and animals because they have played an important role in shaping biological diversity (Bascompte & Jordano 2007; Thomson 2010) and have been an important focus of theoretical development in network ecology (Bascompte *et al.* 2003; Rohr *et al.* 2014). We assess the predictive value of our approach using a 5-year time series of Ecuadorian hummingbirds and their food plants, which we divide into 5 years of training data, and 1 year of testing data. We show that analysing interaction networks without considering the uncertainty in interactions can cause us to misidentify the causes of interaction betadiversity. Finally, we discuss how our approach can be used to address hypotheses about the drivers of interaction betadiversity of mutualistic interactions which should yield new insights into the mechanisms underlying spatial variation in diversity.

From observation to prediction

Ecological networks describe the identity and frequency of observed interactions (Crea *et al.* 2016; Poisot *et al.* 2016; Rohr *et al.* 2016). First, field observations are used to establish which species interact, usually based on direct observation of

interactions or proxies of species visitation. Second, those interactions which were observed are combined into a single aggregate interaction matrix, based on the sum of the number of observations between species if sampling was even (CaraDonna *et al.* 2017), or the mean number of observations if sampling was uneven (Vizentin-Bugoni *et al.* 2016). Third, a matrix model, usually using a multinomial likelihood (Vázquez *et al.* 2009; but see Bartomeus *et al.* 2016), is fit to the observed interaction matrix to estimate the probability of interaction based on species identity (Gravel *et al.* 2013; Olito & Fox 2015). Finally, if there are multiple observation periods or locations, matrix-based dissimilarity metrics are used to separate species turnover and interaction turnover (note that the latter has also been referred to as 'rewiring') (Poisot *et al.* 2012; Kaiser-Bunbury *et al.* 2014).

Our aim is to combine the observation, model fitting and betadiversity steps described above into a single predictive approach that captures the variation in both the observation and ecological processes, estimates pairwise interactions and

tests model adequacy using out-of-sample data (Fig. 1). Transitioning from a descriptive to a predictive approach requires several changes to traditional matrix-based models. First, in order to determine the likelihood of detecting interactions that occur, observations must be repeated over some relatively short period of time, during which we believe the probability of interaction among a pair of species is constant. Without modelling both detections and non-detections, it is difficult to predict the likelihood of observing an interaction in a new observation period (Bartomeus 2013). For example, in our example dataset (Box 1), we filmed the same flower for multiple days, and use each day of filming as a replicate sample. Second, rather than using a matrix-based multinomial model to estimate interaction probabilities, we use pairwise estimates of species interactions. Pairwise estimates likely better describe interactions, which are the result of individual fitness determined by the balance between the cost and benefits of interacting with a specific partner (Brosi & Briggs 2013;

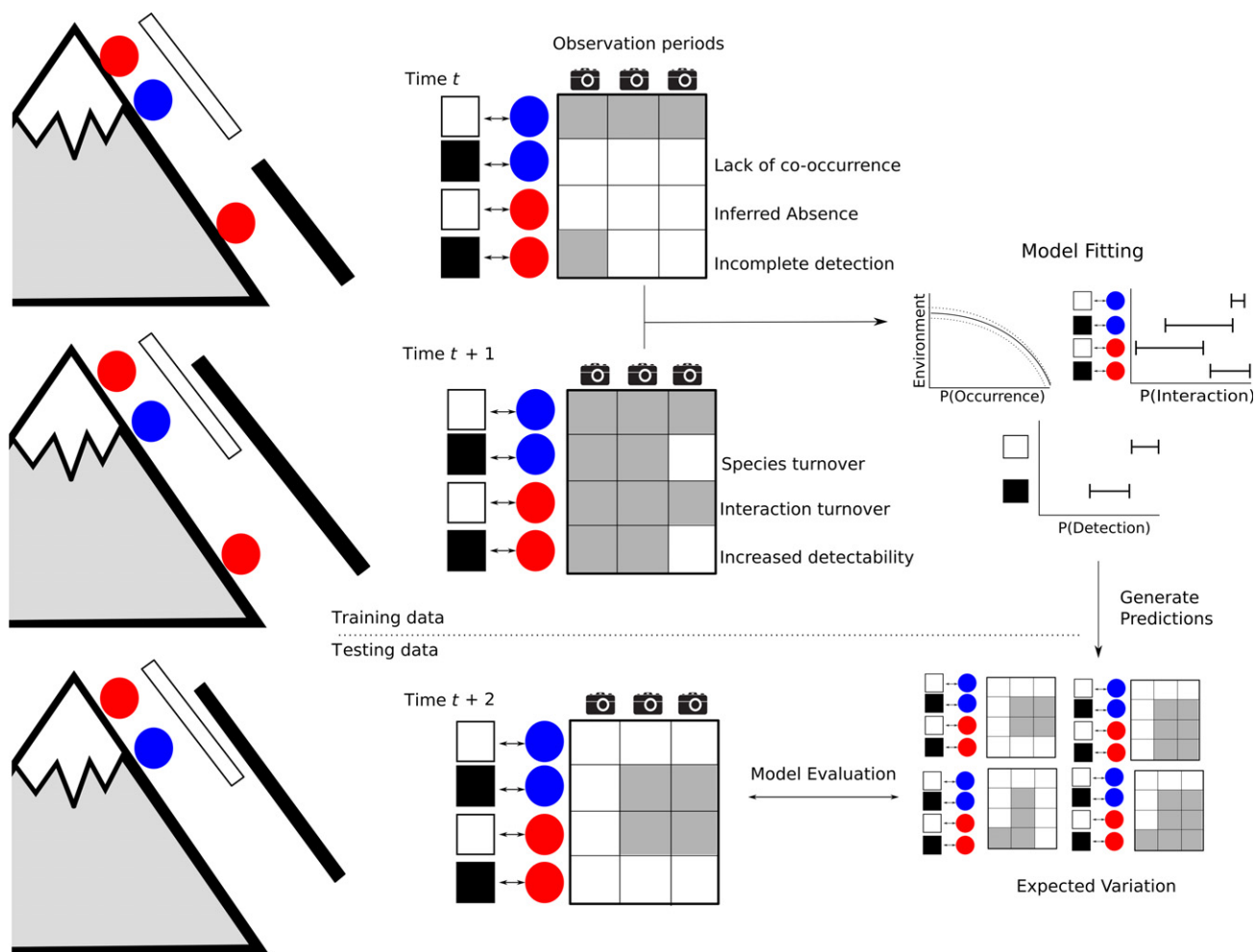


Figure 1 Conceptual overview of predictive models of species interactions. The circles (red and blue) and bars (white and black) represent the distribution of species across observation periods on an elevation gradient. During each period, interactions are either observed (grey) or not detected (white). Using repeat observations, we can estimate the detectability of interactions given that they occur. We can then incorporate environmental information, such as elevation, to separate non-interaction from lack of co-occurrence. For example, at time t species black overlaps with species red, but not species blue. However, in time $t+1$, all species overlap. By separately modelling the probability of occurrence, the probability of interaction and the probability of detection, we can generate predictions of interaction matrices. We then compare the expected variation in interactions to testing data withheld from model training.

Valdovinos *et al.* 2016; Schupp *et al.* 2017). In addition, a multinomial model is not suited for prediction because it uses the marginal sum of observations to fill the predicted matrix (Dormann *et al.* 2017). Since this number will naturally vary among observation periods, it is difficult to use in forecasting. Finally, to predict interaction betadiversity, the foremost challenge is assessing whether a new observation period has more variation than expected given the uncertainty in estimating the links among species. Each observed matrix of interactions is one realisation of the potential networks that could have been observed due to the spatial and temporal heterogeneity in detecting interactions (Poisot *et al.* 2015a). Therefore, it may be beneficial to consider the probability distribution of each interaction, and measure the (Box 1) change in these distributions over time and space Box 2.

BUILDING A PREDICTIVE MODEL OF SPECIES INTERACTIONS

While there has been significant quantitative development in measuring network properties, there has been less focus on predicting networks from field observations while accounting for the uncertainty that arises from stochasticity and incomplete detection (Blüthgen 2010; Jordano 2016). Previous attempts to predict species interactions have found low accuracy in estimating which interactions will occur in a new observation period, despite correctly predicting emergent network statistics (Olito & Fox 2015). Testing our models using prediction forces us to evaluate our ability to analyse complex biological systems, which will ultimately provide a more rigorous understanding of when and why interaction occur (Tylianakis & Morris 2017).

Modelling binary interactions as probabilistic events

To assess which species interact, ecologists often use repeated field observations as proxies for the fitness outcomes among species. It is useful to think of each interaction as a hypothesis ($H_{i,j}$), and each observation as a piece of data. From this perspective, we can use Bayes theorem

$$P(H_{i,j}|\theta) \approx P(\theta|H_{i,j}) * P(H_{i,j})$$

in which the support for the hypothesis given the data $P(H_{i,j}|\theta)$, called the posterior distribution, is proportional to the likelihood of the data $P(\theta|H_{i,j})$ multiplied by the prior distribution of the hypothesis $P(H_{i,j})$. Throughout this paper, we use a flat logistic prior, such that we make no prior statement in predicting which interactions could occur.

$$\text{logit}(P(H_{i,j})) = \text{Normal}(\mu = 0, \text{precision} = 0.386)$$

Our data (θ) are the detection (1) or non-detection (0) of each species in an observation period. For simplicity, we focus on binary interactions, since it allows us to easily estimate the proportion of links correctly predicted in the training data. See Weinstein & Graham (2017a,b) for examples using quantitative interactions.

The simplest model for the likelihood of the data $P(\theta|H_{i,j})$ is a random encounter, in which each species has an equal probability of interacting with each partner species

during each observation period. For example, for our hummingbird data (Box 1), the probability of observing a given hummingbird species (i) visiting a partner plant species (j) filmed by a camera (k), on a filming day (d) would be a draw from our flat prior distribution.

$$\text{logit}(Y_{i,j,k,d}) \sim \text{Normal}(\mu = 0, \text{precision} = 0.386)$$

In this random model, the expected probability of interaction would be 0.5, and the probability of a link would therefore be $1 - (1/2)^n$ for n days of camera filming. This model is a baseline for comparison to subsequent ecological models. If our ecological models cannot outperform this random model, we can infer that random interactions best explain our observed data (Krishna *et al.* 2008; Canard *et al.* 2014).

The next step is to replace the random encounter model with an interaction probability for each species pair. This is the species identity model, with a fixed intercept for each possible interaction.

$$Y_{i,j,k,d} \sim \text{Bernoulli}(p_{i,j})$$

The intercept $p_{i,j}$ can be interpreted as the per camera filming day probability of interaction. Species identity is useful because it captures the multi-dimensional niche without needing to specify a formal relationship between covariates. However, it limits the prediction of species interactions to species present in the training data.

Incorporating incomplete detection

Due to incomplete sampling, it is not possible to detect all interactions which occur (Blüthgen 2010; Olesen *et al.* 2011). Incomplete and uneven sampling limits our ability to compare the frequency and predictors of interactions across networks (Chacoff *et al.* 2012; Fründ *et al.* 2015). Past studies have used null models to compare the observed interaction matrix with permutations that maintain the abundance of one or both sets of species (MacLeod *et al.* 2016). However, choosing the correct null model can be extremely difficult, especially when attempting to disentangle the multiple mechanisms shaping species interactions (Dormann *et al.* 2017). Rather than focusing on the observed matrix, we can estimate the probability of detecting an interaction, given that it occurs, using hierarchical N-mixture models (MacKenzie *et al.* 2002; Royle 2006; Bartomeus 2013). The true interaction state (0 or 1) between species i and partner species j is considered fixed at each observation period k . Each sample during this period is an attempt to recover this true state based on species detectability (ω_i). By assuming there is some true state, and using repeat sampling events during this period, we can estimate the probability of detecting an interaction given that it occurs.

$$Y_{i,j,k,d} \sim \text{Bernoulli}(S_{i,j,k} * z_{i,j,k})$$

$$z_{i,j,k} \sim \text{Bernoulli}(\omega_i)$$

$$S_{i,j,k} \sim \text{Bernoulli}(p_{i,j})$$

In our example data, we model a fixed detectability for each hummingbird species intercept to capture the differences in

Box 1 Assessing probabilistic models using hummingbird–plant interactions

Data were collected along an elevational gradient from 1300 to 2500 m in the Maquipicuna Research Station and Santa Lucia Ecolodge in northwestern Ecuador (0.118 S, -78.612 W) between June 2013 and February 2018. The site contains primary and secondary montane cloud forest and has a cooler rainy season from November to May and a warmer dry season from June to October. We sampled flower abundance and hummingbird–plant interactions monthly along six 1-km transects every 200 m along the elevation gradient. To obtain hummingbird–plant interactions, we used time-lapse cameras placed 1–3 m from blooming flowers and identified images of the hummingbirds using the computer vision program MotionMeerkat (Weinstein 2015). For detailed information on data collection, see Weinstein & Graham (2017a,b). Our cameras recorded 1591 binary interactions across 20 hummingbird species and 44 plant species for a total of 253 observed links.

To test the predictive accuracy of the species identity, detection and occupancy models, we split the interaction data into two time slices. The training data contained 75% of the total data and the testing data contained 25% of the total data (Fig. 2). Models were built using the training data, and evaluated using the testing data. To test model adequacy, we used two evaluation metrics: 1) the prediction accuracy, defined as the proportion of correctly predicted interaction links – that is, both presences and absences; and 2) the connectance of the predicted networks vs. the connectance of the testing data. These measures of model fit represent our ability to predict which interactions occur and the emergent structure of the ecological community.

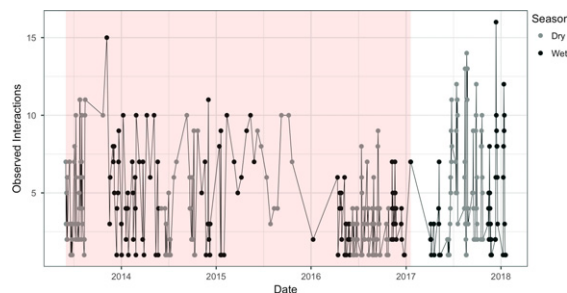


Figure 2 Time series of hummingbird–plant interactions from Northwest Ecuador. The data were split into training (pink) and testing subsets (white). To study seasonal interaction betadiversity, the data were divided into a wet season (grey), from November to May and a dry season (black), from June to October.

Our results show that a random encounter model predicts only about 20% of the interaction links and a nearly fully connected network (i.e. connections among 97.5% of species pairs) (Fig. 3a). While this model obviously correctly predicts which links occur, it fails to identify any of the links which do not occur. Replacing the random model with information on species identity improves accuracy to around 40%. Additional information on detectability raises the accuracy to over 60%, and subsequently incorporating species co-occurrence along the elevation gradient increases the accuracy to nearly 80% (Fig. 3a). The addition of species occurrence results in an increase in the estimated detectability of interactions because it accounts for observed absences that occur when a species does not occur at an observation location (Fig S1). All models overestimated the connectance of network from the testing data, but the final model most closely predicted its connectance (Fig 3b).

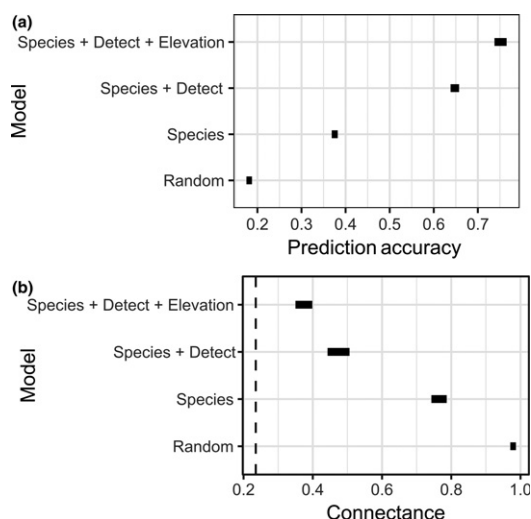


Figure 3 Evaluation metrics for the prediction of hummingbird–plant interactions from northwest Ecuador: (a) the prediction accuracy, calculated as the proportion of correctly predicted links, and (b) the network connectance of the predicted (bars) and the observed networks (dashed line). To generate the distribution predicted network connectance, we simulated 300 predicted networks and calculated the connectance of each network using the R package bipartite (Dormann *et al.* 2009). The 95th density interval is shown for each model.

encounter rates due to species abundance. The detectability of plants is not modelled since cameras are placed at flowers in bloom (see Box 2).

While there has been relatively little work on interaction detectability (Weinstein & Graham 2017a,b), studies outside of network ecology highlight that species detectability can vary because of differences in species size, colour, behaviour and movement (Garrard *et al.* 2013; McCarthy *et al.* 2013; Troschianko *et al.* 2017). Considering how such factors influence our ability to detect species interactions will rely on a greater understanding of species ecology and targeted experiments using repeated sampling across reasonably small temporal periods and geographic areas. For example, in plant–pollinator interactions, detectability could increase with territoriality, as the likelihood of repeat observations should increase at defended resources. In contrast, detectability may decrease as the frequency of replenishment of partner rewards decreases, due to the reduced benefit of repeat visits.

Incorporating species occurrence

To interact, species must co-occur. Therefore, inferred absence of an interaction may stem from either our ability to detect interactions that occur, as described above, or because one partner species is simply not present (Gravel *et al.* 2011; Cazelles *et al.* 2016). To estimate species co-occurrence, the probability of presence of each species during the observation period can be modelled as a function of an environmental variable(s) or habitat suitability (i.e. from a species distribution model). For example, in our dataset, cameras captured interactions along a wide elevation gradient ranging from 1300 to 2500 m. We can therefore model the probability of interaction as a function of the probability of occurrence of species i at the elevation of camera k ($\psi_{i,k}$), the probability of interaction between species i and partner species j ($p_{i,j}$), and the probability of detecting an interaction (ω_i), given that it occurs.

$$Y_{i,j,k,d} \sim \text{Bernoulli}(S_{i,j,k} * z_{i,j,k} * occ_{i,k})$$

$$z_{i,j,k} \sim \text{Bernoulli}(\omega_i)$$

$$S_{i,j,k} \sim \text{Bernoulli}(p_{i,j})$$

$$occ_{i,k} \sim \text{Bernoulli}(\psi_{i,k})$$

$$\text{logit}(\psi) = \alpha_i + \beta_i * \text{elevation}_k$$

This approach models the joint effects of occurrence and detectability using only our interaction data; however, these estimates rely on a strong environmental effect determining species presence. The estimate of β_i may be bolstered using independent data on environmental tolerances and habitat suitability. This is conceptually similar to approach proposed by Staniczenko *et al.* (2017), in which species distribution models are run independently for each species, then a graphical network structure of species interactions is generated either by inference from macroecological patterns of co-occurrence or from actual empirical data on interactions.

Applying this modelling to our example dataset, we find that including information on detectability and occurrence

increases the proportion of correctly predicted links (Fig. 3a), as well as improves predictions of network connectance in forecasts of species interactions (Fig. 3b). These results suggest that the inclusion of information on both species detections, as well as non-detections, will increase our ability to predict interactions across space and time.

EXTENDING OUR APPROACH TO INTERACTION BETADIVERSITY

Before we consider the ecological causes of interaction betadiversity, it is important to stress that every observation period will yield variation in the observed interactions. Using the posterior probability distributions from our statistical model of species interactions, we can generate the expected variation in networks among sampling periods, time intervals (e.g. seasons in our example Box 2) or geographic areas. For each set of predicted matrices, we can partition the total dissimilarity of interactions into the dissimilarity in observed links, and the dissimilarity in species occurrence (Poisot *et al.* 2012). We can then compare this expected dissimilarity to the observed dissimilarity in our testing data. If a new network falls outside of the expected variation, this suggests that additional ecological complexity is needed to explain the variation in species interactions. The three mechanisms that could shape interaction betadiversity are: (1) changes in fitness benefits leading to interaction turnover, (2) changes in species co-occurrence resulting in species turnover, (3) changes in detectability. If the addition of one, or multiple, of these mechanisms improves the prediction of out-of-sample data, we can infer that the variation in observed interactions is greater than expected based on training data.

Changes in fitness benefits leading to changes in interactions among co-occurring species

Species interactions can be conceptualised as the outcome of the quantity of interactions and the fitness-based quality of a given interaction (Vázquez *et al.* 2015; Schupp *et al.* 2017). For binary interactions, changes in the quality of interactions may be a function of the abiotic environment, such as increased foraging costs during a warmer season, or due to the biotic environment, such as the seasonal presence of competitors. For example, Magrath *et al.* (2017) found that seasonal pulses in honeybee abundance resulted in competing native bee species using fewer plant species in agricultural landscapes. Using our approach above, we could test if interactions among co-occurring species seasonally change by replacing

$$S_{i,j,k} \sim \text{Bernoulli}(p_{i,j})$$

with

$$S_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k})$$

$$\text{logit}(p_{i,j,k}) = \alpha_{i,j} + \beta_{i,j} * \text{season}_k$$

where $\beta_{i,j}$ is the effect of season on the temporal change in interactions (Box 2). A positive estimate of $\beta_{i,j}$ would mean that switching season had a significant influence on the probability of interaction. Applying this model to our example data,

Box 2 Testing seasonal interaction betadiversity

We tested the hypothesis that interactions among co-occurring species changed during seasonal pulses of flower availability. We found little support for seasonal species interacting differently after considering the expected variation in networks due to sampling (Fig 4a). Only 3 of 112 observed links had estimates of β_{ij} non-overlapping with zero. Of these three links, none had

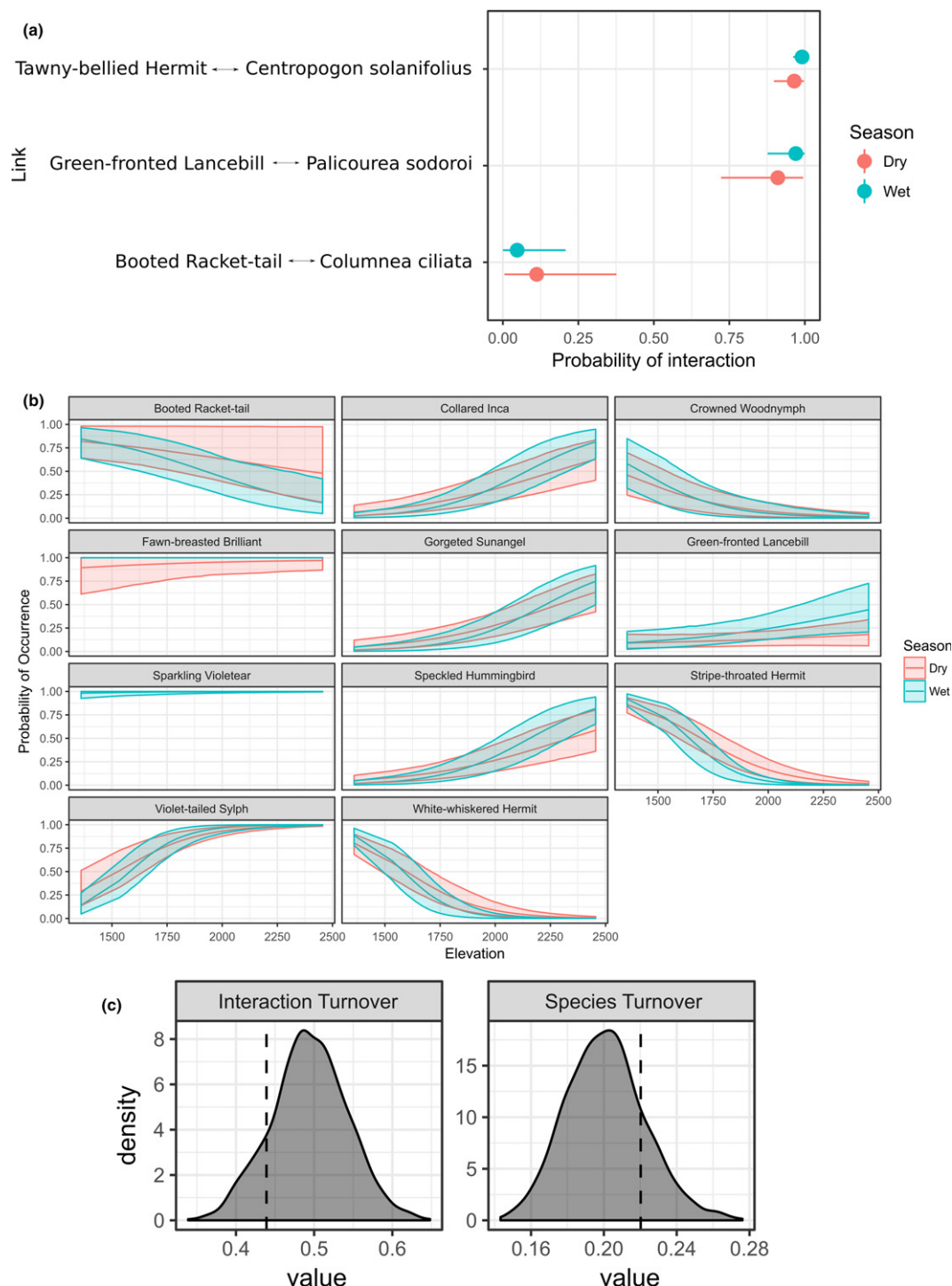


Figure 4 (a) The change in the probability of species interactions, (b) the probability of hummingbird occurrence, and (c) the two components of interaction betadiversity (i.e. among during wet and dry seasons). Only non-zero estimates of seasonal effect were shown. Using the seasonal model built on our training data, we compared the predicted variance in interactions in our testing data to the observed betadiversity of the testing data (dashed line).

Box 2 Continued

estimated probabilities of interaction that crossed $P_{i,j} = 0.5$ among wet and dry seasons. Therefore, while there is statistical significance, we do not see this as biologically important. Furthermore, the training data can accurately reproduce the observed seasonal changes in interactions among co-occurring species in the testing data with the vast majority of $\beta_{i,j}$ estimates centred on zero (Fig 4c). This result suggests that, while there is variation in the system, that variation can be better explained by sampling stochasticity than seasonal variation. While we cannot know how widely these results are mirrored in other systems, we encourage authors to consider sampling uncertainty when estimating changes in interactions among co-occurring species in ecological networks.

Applying our seasonal model to hummingbird occurrence, we find a similar pattern to that of seasonal changes in interactions among co-occurring species (Fig. 4b). Thirteen of 20 hummingbird species had a non-zero estimate of the seasonal effect of elevation on occurrence. However, plotting these changes showed that the seasonal changes in occupancy were minor and would not meaningfully impact their overlap with plant partners. Estimated elevation ranges aligned well with known elevation ranges, with the exception of Hoary Puffleg and Rufous-tailed Hummingbird. These two species had very few detections ($n < 5$) in our training data and our model was not able to converge on a probability of occurrence. This suggests that at very few detections, it will be difficult to separate occurrence from detection without additional independent data. Given how few interactions involve these two species, we do not believe this result has a major effect on our inference. As in the example above, our results show no meaningful change in hummingbird occurrence probabilities, suggesting that the observed differences in hummingbird species composition among wet and dry periods is best explained by sampling stochasticity.

Given our study design, we cannot infer seasonal changes in plant occurrence. Since cameras are only placed at flowers in bloom, we have no plant absence data, and therefore cannot model the temporal or environmental factors which might influence plant occurrence. Assessing interaction betadiversity in both sides of the network requires either independent measures of species occurrence, or a sampling strategy that allows both partners to vary in their occurrence within sampling periods.

we find that despite variation in the observed networks in our example data, the change in the probability of interaction is minimal (Box 2). This suggests that the seasonal variation in the network is explained by sampling completeness, despite having a large dataset. If this finding is maintained in other systems, it underlines the difficulty of assessing changes in interactions among co-occurring species given the low detection rates of many realised interactions.

Changes in species co-occurrence leading to interaction turnover

When species are absent, partners must choose new species with which to interact. We are therefore interested in when the probability of occurrence ($\psi_{i,k}$) approaches zero. Following the seasonal example in Box 3, we can add an interaction effect between elevation and season.

$$occ_{i,k} \sim \text{Bernoulli}(\psi_{i,k})$$

$$\text{logit}(\psi_{i,k}) = \alpha_i + \beta'_i * \text{elevation}_k + \beta''_i * \text{season}_k + \beta'''_i * \text{elevation}_k * \text{season}_k$$

The parameter of interest is β'''_i , which is interaction effect between season and elevation. Species which have a non-zero interaction effect show significant seasonal change in occurrence probability.

Changes in interaction detectability

Finally, the probability of interactions may be temporally constant, but our ability to detect those interactions may vary over time. For example, in times of low resources, animals may

expand foraging ranges, reducing detectability of the interactions during repeat observation periods. In plant–pollinator interactions, times of high flower availability may reduce detectability as interactions become more disperse (Poelchau & Hamrick 2012). To model the change in detectability, we can use a similar approach to the changes in probability of species interactions.

$$z_{i,j,k} \sim \text{Bernoulli}(\omega_i)$$

$$\text{logit}(\omega_i) = \alpha_i + \beta_i * \text{season}_k$$

This could be extended to any temporal scale (e.g. day, week, month) or spatial extent (e.g. site, region). However, we caution that to assess detectability, the repeat observations must occur within a time-frame at which the estimated probability of interaction is fixed. So, for example, if species interactions are hypothesised to be a function of Julian day, there would need to be multiple sampling events on the same day to maintain estimates of detectability.

FUTURE DIRECTIONS FOR INTERACTION BETADIVERSITY

We currently have a limited understanding of how and why interactions vary across geographic regions or seasons – whether as a function of the biotic community (Mayfield & Stouffer 2017), environment (Cazelles *et al.* 2016), geographic isolation (Boulangeat *et al.* 2012) or biogeographic history (Dalsgaard *et al.* 2013). We can address this limitation by gathering data from multiple sites and analysing them in a single analytical approach. By predicting interactions, we can uncover the abiotic and biotic mechanisms impacting the

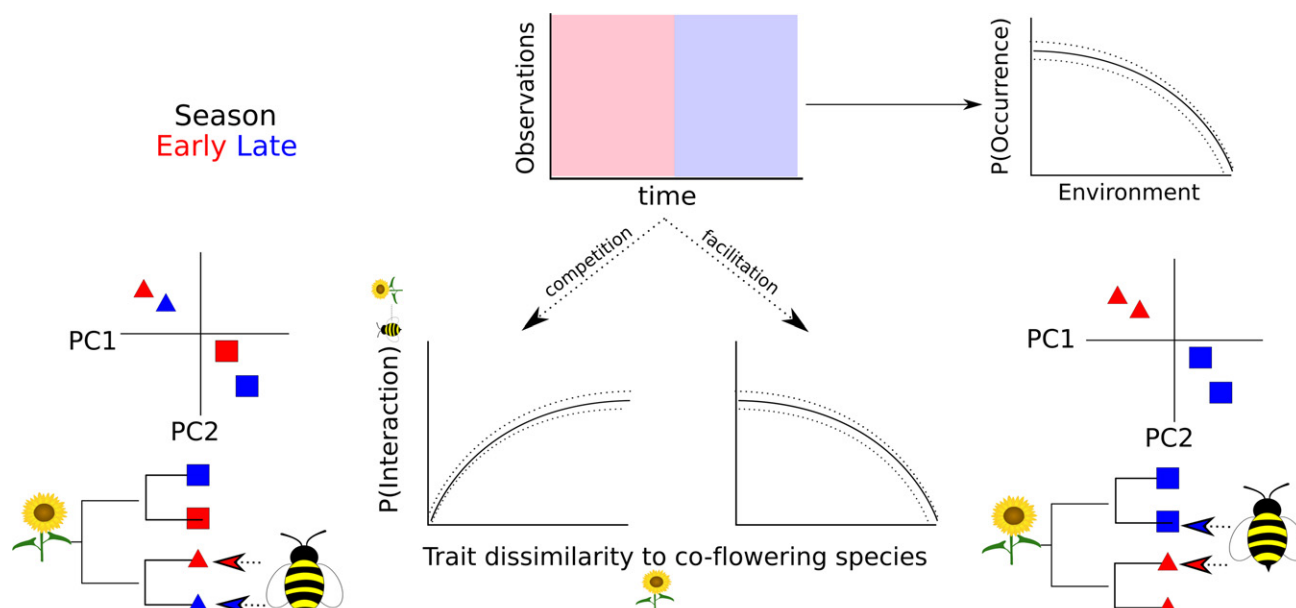


Figure 5 Potential patterns of trait dissimilarity of partners through time. Consider a clade of plants, in which flower morphology is relatively conserved. Species in each clade have distinct interaction niches, measured as a set of quantitative traits. If competition for a specialised pollinator leads to reduced phenological overlap among plant species, related species should bloom at different times, resulting in a positive relationship between trait dissimilarity among co-flowering and the probability of interaction (left side). Alternatively, facilitation among morphologically similar species may result in greater visitation by pollinators leading to a negative relationship between the probability of an interaction and trait dissimilarity to co-flowering species (right side).

changes in network structure across space and time. This approach will aid in forecasting interactions in new environmental contexts that arise from land-use and climate change (Tylianakis & Morris 2017). Below we discuss how our approach can contribute to various fields including functional, community, macro- and evolutionary ecology.

Functional ecology emphasises the physiological and morphological traits that influence species role in a community. While it can be challenging to identify which traits underlie interactions (Bartomeus *et al.* 2017), they may serve as a proxy for the fitness benefits incurred by one or both interaction partners (Stang *et al.* 2009; Bartomeus *et al.* 2016). For instance, trait-matching has been documented across many interacting organisms (Santamaría & Rodríguez-Gironés 2007; Stang *et al.* 2009; Maglianesi *et al.* 2014; Maruyama *et al.* 2014; Trojelsgaard *et al.* 2015; Bartomeus *et al.* 2016; Weinstein & Graham 2017b) with stronger interaction probability among well-matched partners assumed to be caused by the fitness advantage gained by foraging on well-matched resources (Liem 1980; Robinson & Wilson 1998). To model interactions a function of a similarity in traits, we could replace the species identity model with

$$\text{logit}(p_{i,jk}) = \alpha_i + \beta_j * |\text{Trait}_i - \text{Trait}_j|$$

Including functional traits when modelling the probability of interactions should provide the mechanistic basis for niche partitioning and guide experiments measuring the fitness effects of trait-matching. In addition, focusing on functional traits that mediate interactions, as opposed to using species identity as we have described thus far, will allow us to predict novel systems with new species.

In situations in which trait data are uninformative or unavailable, phylogenetic relatedness may serve as a proxy of similarity in interactions between related species (Webb *et al.*, 2002), provided unmeasured traits have phylogenetic signal (Weber & Agrawal 2012). For example, Brousseau *et al.* (2017) used a phylogenetic eigenvector approach (Diniz-Filho *et al.* 2012) to predict ground-beetle–prey interactions and found that the strongest models always included phylogeny. This approach could be used to include phylogenetic relatedness as a predictor for interaction betadiversity. Choosing the appropriate phylogenetic scale to interpret and analyse species interactions remains an important question; zooming in on a narrow set of taxa will miss the larger evolutionary history of interaction niches, whereas considering too broad scale will limit the predictive utility of the model (Graham *et al.* 2018).

Ecological assemblages are the result of a series of abiotic and biotic filters that govern species co-occurrence (Keddy 1992; Cadotte *et al.* 2009). Currently, it can be difficult to separate species responses to the abiotic environment from the biotic filters influencing species interactions (Kraft *et al.* 2015). Environmental factors limiting species occurrence can be identified by including these factors (i.e. either directly or summarised using species distribution models) in model formulation. For example, many studies of flowering plants report that interaction betadiversity is strongly influenced by environmentally driven asynchronous phenology of interaction partners (Elzinga *et al.* 2007; Rafferty *et al.* 2013; Miller-Struttmann & Galen 2014; CaraDonna *et al.* 2017). Exploring the probability of an interaction in the context of trait values of co-occurring flower species may provide insight into the

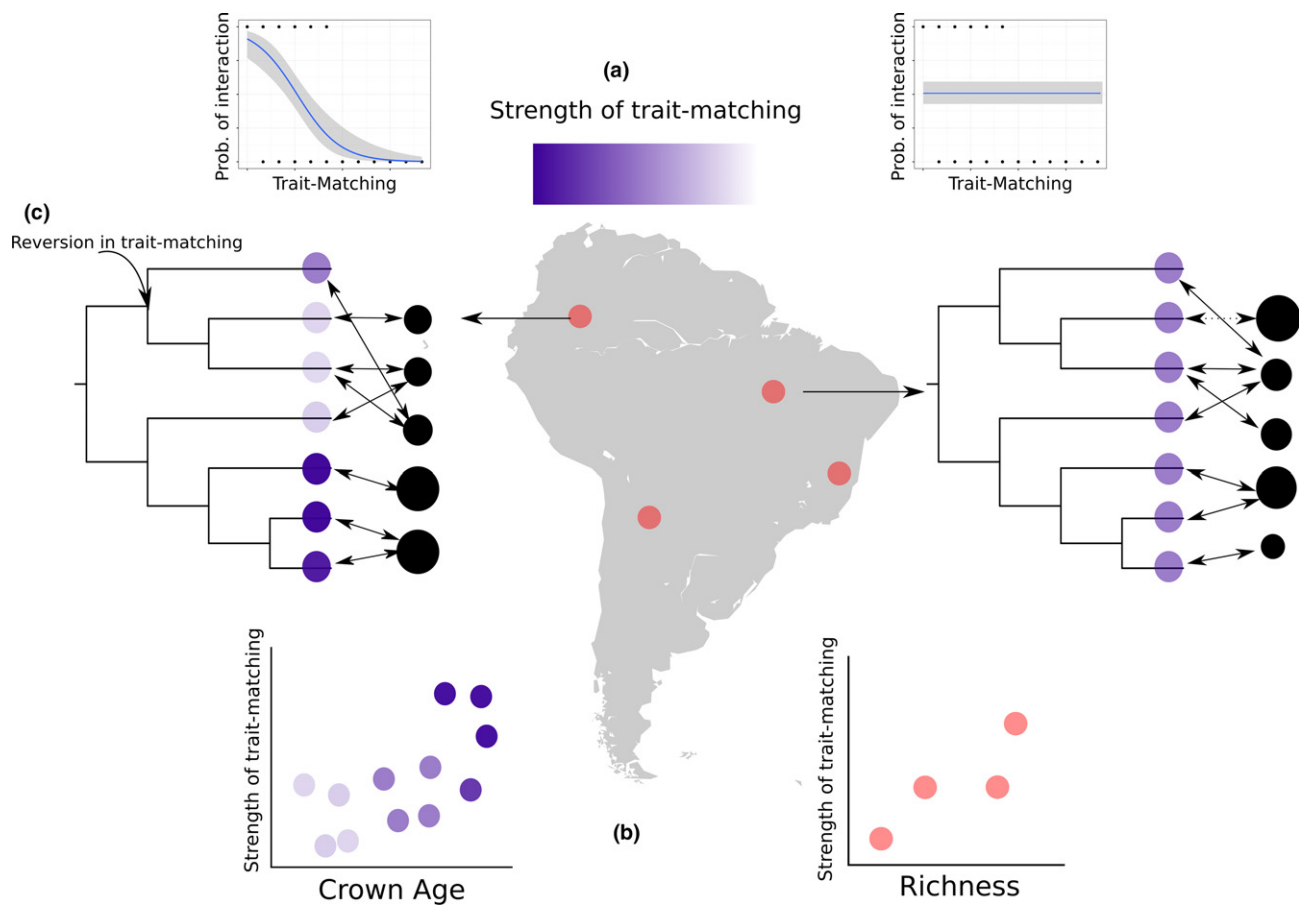


Figure 6 Connecting the local observations of species interactions with regional patterns of trait evolution and biogeography. The predictors of interactions, such as trait-matching, may be regionally variable (a) resulting in different relationships between the probability of an interaction and the strength of trait-matching. (b) By mapping the predictors of interactions on to phylogenies, we can reconstruct the evolution of interaction niches, and test the conservatism in evolution of interacting partners. The strength of trait-matching might also vary regionally based on variables such as (c) crown age or (d) species richness.

influence of competition or facilitation on assemblage structure (Levine & Hillerislambers 2009) (Fig. 5). If there is fitness advantage associated with minimal niche overlap among morphologically similar species, then plant species with similar morphology should bloom at different times. Alternatively, joint flowering of similar species may lead to facilitation if the risk of pollen contamination is low (Carvalho *et al.* 2014; Ye *et al.* 2014). By modelling the probability of occurrence as a function of both the environment and the presence of morphologically similar or related species, we can explore the roles of competition and facilitation in the occurrence, or reproductive capacity, of interacting species.

In addition to assessing overall patterns of species and interaction turnover, our focus on pairwise interactions allows us to identify the interactions and species characteristics that influence interaction betadiversity. For example, specialists, often defined as species that have few interaction partners, are considered more sensitive to environmental changes than generalists (Ashworth *et al.* 2004; Schleuning *et al.* 2015). However, Winfree *et al.* (2014) found that species abundance predicted species loss across disturbance gradients better than specialisation. There are few empirical tests that

simultaneously consider changes in both network structure and species composition; instead past studies have either evaluated the loss of rare species (Alarcón *et al.* 2008), species with specialised traits (Tinoco *et al.* 2017) or rare interactions (Vázquez & Simberloff 2002; Aizen *et al.* 2012; Berke & Knight 2012). We can explore if changes in the probability of interactions across gradients are the result of partner diversity or species abundance. For instance, we can explore if specialists that feed only on relatively scarce, well-matched resources, turnover across environmental gradients while simultaneously considering if interaction betadiversity is driven by species abundance. In this way, we can start to determine species-specific characteristics that influence variation in interaction probabilities and network structure across environmental gradients (Tylianakis & Morris 2017).

There is growing recognition in macroecology that emergent patterns may be caused by multiple factors (Ricklefs 2004; Matthews *et al.* 2014), and unravelling the predictors of species diversity will require better integration with local data (Marske *et al.* 2013). Macroecological analyses of networks show that specialisation and modularity increase with species richness, climate productivity and historic climate stability

(Dalsgaard *et al.* 2013; Martín González *et al.* 2015). However, network metrics often remain constant despite local changes in pairwise interactions (Olesen *et al.* 2011; Olito & Fox 2015; Carstensen *et al.* 2016; Kemp & Ellis 2017), suggesting that focusing on emergent structure alone may not uncover the mechanisms that govern species interactions (Olito & Fox 2015; Poisot *et al.* 2016). By evaluating the mechanisms influencing pairwise interactions, we can better understand the emergence of network properties and the relationships between partner diversity, biogeography and evolutionary history (Fig. 6). For example, when species richness is high, we might expect that greater niche partitioning is required to maintain this diversity. In this case, the predictive power of trait-matching should increase with species richness (Fig. 6d) which might be the driver behind network pattern of increased modularity. We might also expect greater trait-matching in older lineages, where there has been more time for specialisation or co-evolution (Fig. 6c). By comparing related groups across biogeographic regions, we can begin to understand macroecological patterns and drivers of interaction diversity.

Combining local data on the predictors of species interactions with phylogenetic comparative methods will uncover new patterns of the evolution of specialisation and interaction niches. By mapping the predictors of species interactions, such as the per species estimate of the strength of trait-matching, on to phylogenetic trees, we can begin to infer the importance of partner interactions in shaping evolution. In addition, we can evaluate if the evolutionary pattern of specialisation and interaction syndromes (Rosas-Guerrero *et al.* 2014; Fenster *et al.* 2015) is consistent across biogeographic regions. For example, older and more stable mutualisms may lead to greater trait-matching due to increased time for reciprocal co-evolution (Fig. 6b). Alternatively, trait-matching might be highest in young and recently isolated lineages, as has been observed during species radiations into new environments or exploiting novel resources (Schluter & McPhail 1992) (Fig. 6b). By simultaneously considering both evolutionary (i.e. clade age) and ecological (i.e. species richness, climate stability, productivity) correlates of trait-matching, we can begin to explore the multiple mechanisms leading to observed network structure across biogeographic regions.

The strategy presented in this paper allows for the greater integration of data because it estimates interactions on a pairwise basis, and can accommodate differences in sampling among sites. By splitting the probability of occurrence from the probability of interaction, we can separately assess mechanisms influencing each of the probabilities. This is important because the change in species occurrence is likely governed by different mechanisms than the change in species interactions (CaraDonna *et al.* 2017; Poisot *et al.* 2017). By splitting the probability of detection from the underlying true interactions among species, we can make predictions about the likelihood of observing interactions in new temporal or spatial samples. The worked example of our approach provides a methodological roadmap for the use of hierarchical models to study mutualistic interactions. While we realise that hummingbirds may be more specialised and easily identified than other species, such as syrphid flies or bees, we hope our approach

will inspire renewed efforts across different groups to understand the behavioural, ecological and evolutionary context of species interactions.

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AUTHORSHIP

CG and BW developed the conceptual ideas and wrote the MS.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.3gd34v2>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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