Eltonian niche modelling: applying joint hierarchical niche models to ecological networks

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Abstract

There is currently a dichotomy in the modelling of Grinnellian vs. Eltonian niches. Despite similar underlying data, Grinnellian niches are commonly modelled with species-distribution models (SDMs), Eltonian niches are modelled with ecological-network analysis. This separation stems from the much sparser data on species interactions, which has prevented the application of SDMs to Eltonian niches. Recently developed joint hierarchical niche models (JHNMs), however, overcome sparsity and improve predictions for individual species by considering non-independent relationships among co-occurring species. This unique ability makes JHNMs particularly suited for sparse datasets, such as ecological networks. Here, we propose to apply JHNMs to data on ecological networks, functional traits, and phylogenies to model species' Eltonian niches and exemplify the approach for frugivorous birds. Moreover, we demonstrate that JHNMs can even be used to predict interactions of species for which no empirical interaction data are available—solely based on their functional traits. This facilitates the prediction of new interactions in communities with altered composition, e.g. following climate-change induced local extinctions or species introductions. The high interpretability of our Eltonian JHNMs will provide unique insights into the mechanisms underlying species interactions and the potential impact of environmental changes and invasive species on species interactions in ecological communities.

Introduction

Species distribution models (SDMs) have become a ubiquitous tool in community and macroecology to study the relationship between environmental conditions and species' geographic ranges, with a growing number of methodological approaches (Guisan et al. 2017; Ovaskainen & Abrego 2020). SDMs commonly use the range of environmental conditions across sites where a focal species is known to occur to quantify the species' realized environmental niche or *Grinnellian niche*, which then can be used to predict its potential future distribution under altered environmental conditions (Elith & Leathwick 2009). In contrast, *Eltonian niches*—species' resource use and interactions with other species (Elton 1927)—have classically been studied via ecological networks, such as food webs (Bascompte & Jordano 2014; Dehling 2023), with recent approaches also combining networks with functional traits to describe species' Eltonian niches using multivariate statistics (Caron et al. 2022; Dehling et al. 2016, 2021, 2022a, b; Junker et al. 2013).

The current limited methodological overlap between the modelling of Grinnellian and Eltonian niches (but see Björk et al. 2018; Facon et al. 2021; Opedal & Hegland 2020) belies the fact that both approaches are based on data of a similar structure: a matrix of species occurrences (site × species for Grinnellian, species × species for Eltonian) combined with environment variables describing the sites where species occur (Grinnellian niche) or characteristics describing a species' resources or interaction partners (Eltonian niche), respectively. Superficially, the similar data structures should therefore make it straightforward to apply modelling approaches geared toward Grinnellian niches to the statistical modelling of Eltonian niches (Fig. 1). However, one major obstacle that has so far precluded this application lies in the availability of data. While data for modelling Grinnellian niches (i.e., species occurrences and environmental conditions) are often available from large-scale datasets, data for modelling Eltonian niches are generally still scarce due to the difficulty of sampling both species interactions and functional traits; this is known as the "Eltonian shortfall" (Peterson et al. 2011). As a result, data on species interactions are much less complete, especially for species that are rare or difficult to observe, which has made it very challenging to apply frameworks based on single-species SDMs to the modelling of species' Eltonian niches.

The recently introduced joint hierarchical niche models (most commonly formulated as joint species distribution models) aim to improve niche modelling by quantifying the niches of all species in a single model and considering non-independent relationships among co-occurring species, such as trait–niche relationships or species' phylogenetic relatedness (Ovaskainen & Soininen 2011). By "borrowing" data from ecologically or phylogenetically similar species, these models greatly improve predictions for individual species, especially for those species for which limited empirical data are available (Norberg et al. 2019; Ovaskainen et al. 2017).

This unique ability of joint hierarchical niche models makes them particularly suited for datasets that include species with incomplete sampling, which is usually the case for ecological networks (Jordano 2016).

Here, we propose to model species' Eltonian niches by applying joint hierarchical niche models to data from ecological networks, functional traits, and phylogenies. The approach builds upon the concept of describing a species' interactions via its Eltonian niche—characterized by the traits of its interaction partners (Dehling & Stouffer 2018; Dehling et al. 2022b; Elton 1927). Depending on the ecological process under study, a species' Eltonian niche is described by the traits of different types of interaction partners; for example, the prey of a predator, the hosts of a parasite, the flowers pollinated by a pollinator, or the fruit dispersed by a seed disperser. For simplicity, we will hereafter describe the Eltonian niche as the traits of the *resources* used by a *consumer*. We demonstrate our approach by using a joint hierarchical niche model to quantify the Eltonian niches of a community of frugivorous bird species (consumers) interacting with fleshy-fruited tree species (resources). This approach allows simultaneous niche modelling of multiple bird species while taking into account co-variation in resource use between them. In addition, the estimated interaction coefficients between consumer traits and resource traits can be used to test specific hypotheses about trait matching. Moreover, we demonstrate that joint hierarchical niche models can even be used to predict interactions between consumers and resources for which there are no empirical interaction data available—solely based on the matching of their functional traits—which makes it straightforward to model new species interactions in assemblages with altered species composition.

Material and Methods

Modelling Eltonian niches using joint hierarchical niche models

We based our Eltonian niche modelling on the joint species distribution modelling framework primarily developed for the Grinnellian niche (Niku et al. 2021; Ovaskainen et al. 2017; Warton et al. 2015), which usually takes the form of a multivariate, hierarchical generalized linear latent-variable mixed-effects model. The modelling of Eltonian niches requires data that are similar to those for the modelling of Grinnellian niches, but it involves the following changes (Fig. 1): instead of (i) a matrix describing species occurrences across sites (site $\times$ species) and (ii) a matrix describing the environmental conditions across sites (site $\times$ environment), Eltonian niche modelling uses (i) a matrix representation of an interaction network describing the consumers' interactions across resources (resource $\times$ consumer) and a matrix describing the traits across resources (resource $\times$ trait). The interaction network matrix can be represented either qualitatively (presence–absence) or quantitatively (number of interactions); we focus on the former in this study. Hence, the model assesses

the Eltonian niche of a consumer based on the traits of the resources that it uses. We exemplify our approach by modelling bird–plant frugivory interactions in the tropical Andes.

Networks

We used an interaction network between frugivorous birds and fleshy-fruited plants sampled in a montane rainforest in the Andes of south-east Peru (Manu Biosphere Reserve; 13.1°S, 71.6°W, 1500 m elevation; Dehling et al. 2014b). The network was sampled over a year with a total sampling effort of 960 h, and consisted of 4,988 interaction events between 61 bird and 52 plant species (further details on network sampling and robustness in Dehling et al. 2014b). The network includes interactions between 398 pairs of birds and plants. Our joint hierarchical model requires presence *as well as* absence data. For modelling Grinnellian niches, such data are usually readily available because absences in species occurrences are relatively well-known. In contrast, species interactions are much more difficult to record than occurrences, and the sampling of interaction networks are therefore notoriously sparse and opportunistic (Jordano 2016); presence (1) of interactions is often much more reliably sampled than the absence (0) of interactions. Treating all missing interactions as (structural) zeros represents an unrealistic assumption because rather than a true absence (e.g. either an impossible interaction or the active avoidance of a resource), missing interactions include many interactions that were simply not observed (Blasco-Moreno et al. 2019). To separate unobserved interactions from true absences for each species, we calculated the ratio between the plant's fruit diameter and the bird's bill width—a well-known trait-matching relationship in bird–plant interactions (Dehling et al. 2014b)—across all observed interactions in the empirical network (398 species pairs), and then used the inner 95th percentile of this ratio (range 0.2–1.5) as limits for unobserved, but possible interactions, which is a conservative estimate. Following Lai et al. (2021), we coded interactions considered possible as "NA" (2,370 species pairs) and interactions considered impossible as "0" (404 species pairs) in the network matrix. (Another analysis treating all missing interactions as absences, i.e., without NAs, yielded qualitatively similar results; Appendix 1, Table S1).

Plant traits

We included plant functional traits as predictors to assess how much of the variance in bird–plant interactions is determined by resource traits (i.e., by the birds' Eltonian niches). The functional traits for all plant species in the networks were collected in the field and included three morphological traits previously shown to influence the interaction between fleshy-fruited plants and frugivorous birds (Bender et al. 2018; Dehling et al. 2014b): fruit diameter (cm), plant height (m), and crop mass (g; the total amount of fruit offered by a

tree, calculated as mean number of fruits per plant × mean fruit mass). We also included a quadratic term for fruit diameter because niche optima are likely to be at intermediate values.

Bird traits and bird phylogeny

To potentially improve the joint modelling of the birds' Eltonian niches, we obtained data for bird functional traits and bird phylogeny to serve as additional co-variates with which to predict the birds' Eltonian niches (Ovaskainen et al. 2017). We used three functional traits shown previously to influence the foraging behaviour of birds (Bender et al. 2018; Dehling et al. 2014b): bill width (cm), Kipp's index (dimensionless; Dehling et al. 2014a), and body mass (g; Tobias et al. 2022). Kipp's index is a measure for the roundedness of the wing and measured on the folded wing as the ratio between the distance from the tip of the first secondary to the wing tip, and the full length of the folded wing. We built a phylogeny of all birds in the network as a consensus tree of 1,000 dated phylogenetic trees from birdtree.org (Jetz et al. 2012, 2014) using the phylogenetic backbone by Hackett et al. (2008).

Model fitting

Leveraging the aforementioned empirical data, we ran one model without including any bird co-variates (model 1), and three additional models with different combinations of bird co-variates: only bird functional traits (model 2), only bird phylogeny (model 3), and both bird functional traits and bird phylogeny (model 4; Table 1). For our analyses, we used the package Hmsc v3.0 (Tikhonov et al. 2020b) in R 4.21 (R Core Team 2022). For all models, we used the default priors in Hmsc (Ovaskainen et al. 2017). For each model, we ran four chains of Markov Chain Monte Carlo (MCMC) with 1,000,000 samples and a burn-in of 200,000 steps. We applied thinning (1,000 step intervals) and ended up with 1,000 posterior samples per chain (4,000 samples per model). We examined model convergence with effective sample sizes and potential scale reduction factors. To compare the different models, we calculated WAIC (Watanabe 2013), and we evaluated in-sample explanatory power by AUC and coefficient of discrimination (Tjur's R^2). To evaluate the out-of-sample predictive power of the models, we used two-fold cross-validation and calculated AUC and Tjur's R^2. We also used the computeVariancePartitioning function from the Hmsc package to assess the variance in bird–plant interactions determined by plant traits (associated with the regression slope β in models 1–4), the variance in the birds' Eltonian niches determined by bird traits (associated with γ in models 2 & 4), and the phylogenetic signal in Eltonian niches (associated with ρ in models 3 & 4) (Table 1, Appendix 2).

Predicting new or unobserved species interactions

To test the ability of our approach to model new or unobserved interactions based on proxies, we removed all observed interactions in the empirical network for three species that represent different bird lineages with different morphologies (Blue-necked Tanager *Tangara cyanicollis*, Passeriformes: Thraupidae, a common species; Andean Guan *Penelope montagnii*, Galliformes: Cracidae, an uncommon species; Crested Quetzal *Pharomachrus antisianus*, Trogoniformes: Trogonidae, a rare species). For these species, we changed all "1" to "NA" in the interaction matrix. Our reduced interaction network thus contained observed interactions between 58 bird species and the original 52 plant species. We then repeated model 2 (including bird functional traits) by re-fitting it on the data set consisting of the reduced interaction network, but complete consumer $\times$ trait (bird traits) and resource $\times$ trait (plant traits) data set. We chose model 2 to illustrate the modelling of species interactions from functional traits, which provides a more intuitive interpretation than modelling interactions from phylogenies. The Eltonian niches for the three removed bird species were thus predicted based only on their functional traits and the inferred Eltonian niches of the remaining bird species. We used correlations to compare the Eltonian niches of the three bird species modelled based on their observed interactions with those predicted based only on their functional traits.

Results

Modelling bird–plant interactions via Eltonian niches of birds

The explanatory power of all models (i.e., the explained variance in bird–plant interactions) was very high (AUC: 1, Tjur's R^2: 0.86–0.90; Table 1). Plant traits explained almost all the variance in the bird–plant interactions (Table 1). In turn, bird traits explained 90.3 (model 2), and 70.2 (model 4) percent of the variance in the birds' Eltonian niches (Fig. 3), and there was also a strong phylogenetic signal in the Eltonian niches (model 3: 95% credible interval 0.76–1, median 0.97; model 4: 0.70–1, median 0.95); that is, birds with similar morphology and birds that were more closely related to each other tended to have more similar Eltonian niches. The predictive power of all models was also high, but slightly lower than the explanatory power (AUC 0.65–0.70, Tjur's R^2: 0.65–0.70, Table 1). Unobserved empirical interactions that we determined as possible ("NA") tended to show a high predicted probability in the models, whereas those determined as unlikely were corroborated as unlikely in the models (Appendix 1, Fig. S1).

Trait matching between birds and plants

Model 2 and model 4 revealed similar sets of matching bird and plant traits that influenced the interaction between birds and plants (Fig. 3), including a positive relationship between fruit width and bill diameter, and a positive (model 4) or hump-shaped (model 2) relationship between body mass and fruit diameter (Fig. 3).

Predicting species interactions from functional traits

The Eltonian niches of the three bird species (*Tangara cyanicollis*, *Penelope montagnii* and *Pharomachrus antisianus*) predicted based only on their functional traits were very similar to the Eltonian niches modelled based on their empirical interactions in model 2 (correlation of interaction probabilities, *Tangara cyanicollis*, $R^2 = 0.99$, $p < 0.001$; *Penelope montagnii*, $R^2 = 0.94$, $p < 0.001$; *Pharomachrus antisianus*, $R^2 = 0.98$, $p < 0.001$; Fig. 2).

Discussion

Our example using bird–plant interactions demonstrates that joint hierarchical niche models can be used to infer species' Eltonian niches from ecological networks. The joint models revealed strong influences of plant traits, bird traits, and bird phylogeny on the birds' Eltonian niches. They also identified generalized interaction trends across a large number of consumer and resource species using a small number of matching traits. Furthermore, the unique ability of joint models to use data from one set of species when making predictions about the niches of new, out-of-sample species demonstrates a straightforward way to model previously unobserved interactions in the network.

Species interactions between frugivorous birds and fleshy-fruited plants were clearly captured by the birds' Eltonian niches (i.e., the range of trait combinations of the plant species with which each bird interacts), which in turn were strongly influenced by the morphology of the bird species. The strong interplay between bird and plant traits on the probability of bird–plant interactions is in line with the growing number of studies that demonstrate the influence of trait matching—the relationship between a consumer's traits and the traits of its resources—on species interactions (Caron et al. 2022; Dehling et al. 2014b, 2016; Eklöf et al. 2013; Peralta et al. 2020a, b; Sonne et al. 2020, Vizentin-Bugoni et al. 2014). For example, in plant–bird interactions, interactions are influenced by the match between fruit diameter and bill width, which determines whether a fruit can be used by a frugivore. However, so far, analyses on the influence of functional traits on species interactions have mostly been restricted to matching of individual trait pairs (Burns 2013; Dehling et al. 2014b) or the matching of trait combinations (Dehling et al. 2016), and even the latter are limited

to relating the morphology of a species (its own trait combination) to a single-point representation of its niche, for instance, a species' niche position (determined as the mean value of the trait combinations of their different interaction partners). Our proposed approach of simultaneously considering multiple traits in a single joint hierarchical model facilitates the consideration of the entire range of trait combinations that a consumer species uses and which, in their entirety, describe the species' Eltonian niche.

Modelling the probability of consumer–resource interactions via the joint modelling of Eltonian niches can help improve the modelling of responses for species with few observed interaction partners, for instance, for those species that are naturally rare or difficult to observe in the field. As we showed in our example, due to the strong relationship between the birds' functional traits and their Eltonian niches, it was even possible to predict interactions for species for which there are no empirical observations available—based entirely on the similarity in functional-trait values with the other bird species in the network. This demonstrates the power and main advantage of the joint modelling approach: empirical interaction networks are notoriously sparsely sampled (Jordano 2016), and—as revealed by studies comparing networks compiled from direct observations with networks sampled indirectly using molecular techniques (Pornon et al. 2017)—a large proportion of interactions in ecological networks are readily missed. The ability to predict unobserved interactions will lead to more complete data on species interactions which might lead to a better understanding of the drivers underlying interactions in ecological communities. Predicting new interactions from proxies is especially valuable when modelling new interactions between species that have never interacted before, e.g. in communities with altered composition due to climate-change induced range shifts or the introduction of exotic species. This facilitates assessing the potential impact of environmental changes and invasive species on ecological communities.

Improving niche models further by disentangling fundamental from realized niches

Even though the explanatory and predictive power of our models were high, an important task for improving the usability of niche models lies in disentangling the ecologically feasible interactions (fundamental Eltonian niches) from locally realized interactions (realized Eltonian niches). Due to the notorious sparseness of empirical networks and the uncertainty regarding the proportion of unobserved interactions, the approach required for fundamental Eltonian niches is different from the one for Grinnellian niches. For instance, Grinnellian niches are commonly modelled based on the environmental conditions found within a species' range (either continuous ranges or a set of point localities) and based on the assumption that these conditions are continuous in space. This has the advantage that even for the rarest species it is usually possible to

determine a range of environmental conditions (e.g., at least the seasonal variation in the type locality) that can be used to model its niche. Using the same approach and assumptions for interaction data is usually not possible because data on species interactions are much sparser—compared to geographic ranges, network data are more comparable to sparsely-sampled point occurrences. Assuming that a consumer can interact with all resources that show similar trait combinations as its observed resources—analogous to drawing ranges that connect known point occurrences—would likely work relatively well for abundant species because their resources are well represented in a sample; in contrast, it would probably underestimate the niches for species that are rare or difficult to observe, and for which therefore only few observations are available that are less likely to be a good representation of their niches.

In addition, as species interactions are usually studied on the level of species communities, this could lead to the assumption that all interactions between suitable co-occurring partners are realized; however, restrictions to species interactions might occur on smaller scales and could be difficult to sample in the field. For instance, at a certain site, a species might not use a potential resource as long as its preferred resource (e.g. the one to which it is best adapted) is abundantly available. Similarly, even though two suitable interaction partners are present in a local community, their interaction might ultimately depend on whether the home ranges (or growing sites) overlap or whether both species occur in sufficient numbers to encounter each other. In the absence of such detailed information, our approach of using empirical data and known trait relationships underlying species interactions to restrict absences to the extremely unlikely or impossible interactions, while treating possible, but unobserved, interactions as NA therefore served as a cautious and conservative compromise. The resulting high interaction probability for most of these unobserved interactions that we identified as possible suggest that treating those interactions as absences would have led to an underestimation of species' Eltonian niches. More-highly resolved networks on the level of individuals (Guimarães 2020; Hervías-Parejo et al. 2020; Rumeu et al. 2018; Wells and O'Hara 2013), potentially aided by the use of automatic detection (Weinstein 2015) or indirect sampling of interactions via molecular techniques (reviewed in Pringle & Hutchinson 2020), might facilitate the collection of more-highly resolved data on interactions that will lead to new insight into the restrictions on locally realized interactions.

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Table 1. Explanatory and predictive power, explained variance, and phylogenetic signal in Eltonian niches of four joint hierarchical models describing the interactions between 61 frugivorous birds and 52 fleshy-fruited plants. Eltonian niches of bird species are described by the functional traits of the plants with which the birds interact. The joint hierarchical models relate the birds' Eltonian niches to different combinations of co-variates (no co-variates, bird traits, bird phylogeny, bird traits + bird phylogeny). Percent variance explained describes the mean variance in bird–plant interactions explained by plant traits and the mean variance in Eltonian niches explained by bird traits. The phylogenetic signal in the birds Eltonian niches is given as the 95% interval and median value.

Model	**Co-variates**	**WAIC**	**Explanatory power**		**Predictive power**		**Percent variance explained**		**Phylogenetic signal**
			AUC	Tjur R^2	AUC	Tjur R^2	bird–plant interactions by plant traits	Eltonian niches by bird traits	bird traits
1	no co-variates	2.08	1	0.87	0.92	0.65	99.6	-	-
2	bird traits	2.24	1	0.86	0.95	0.70	99.5	90.3	-
3	bird phylogeny	1.69	1	0.90	0.95	0.66	99.8	-	0.76–1 (0.97)
4	bird traits + bird phylogeny	1.95	1	0.90	0.94	0.69	99.6	70.2	0.70–1 (0.95)

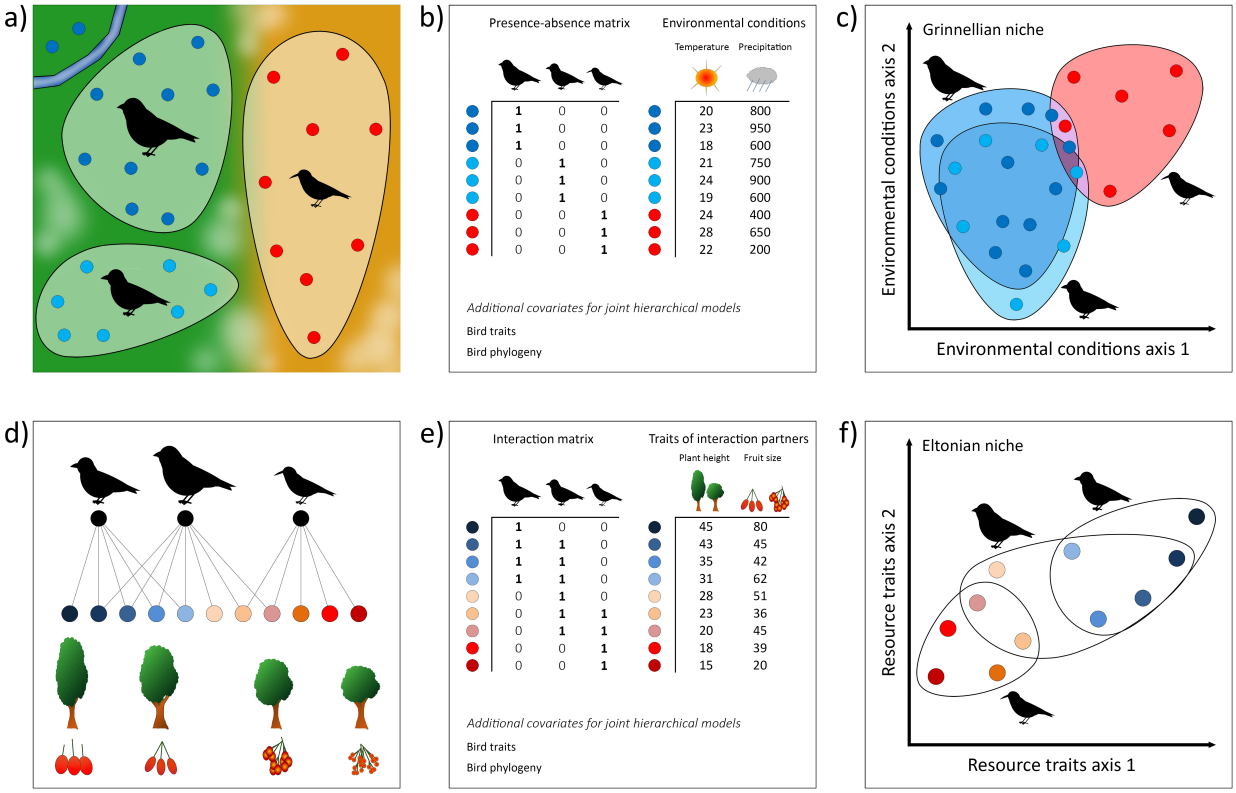

Fig. 1. Parallels between the modelling of Grinnellian and Eltonian niches. (a) Grinnellian niches are modelled by assessing the environmental conditions characterizing species' ranges, either across the entire range or at point samples of known occurrences. (b) Typically, the occurrence of species across the study area is recorded in a presence–absence matrix; the environmental conditions at the different sites are recorded as a site × environment matrix. Grinnellian niches are then modelled based on the environmental conditions found within a species' range. In joint hierarchical niche models, additional data such as the species' functional traits or their phylogenetic relationships can be taken into account to improve the modelling of Grinnellian niches. (c) Grinnellian niches can then be plotted in a multidimensional space representing the differences in environmental conditions found at the sites at which species occur. (d) In contrast, Eltonian niches are modelled by assessing species' resource use or interactions with other species, usually recorded in an interaction network, and the traits of the resources with which each species interacts. (e) Typically, the resource use of different consumers is recorded in a consumer × resource interaction network; the functional traits of resources are recorded in a resource × trait matrix. These two matrices are analogous to the presence–absence matrix and site × environment matrix in (b), respectively. Eltonian niches are then modelled based on the traits of the resources with which a consumer interacts. In joint hierarchical niche models, additional data such as the consumers' functional traits or their phylogenetic relationships can be taken into account to

improve the modelling of Eltonian niches. (f) Eltonian niches can then be plotted in a multidimensional space representing the differences in the traits of the resources used.

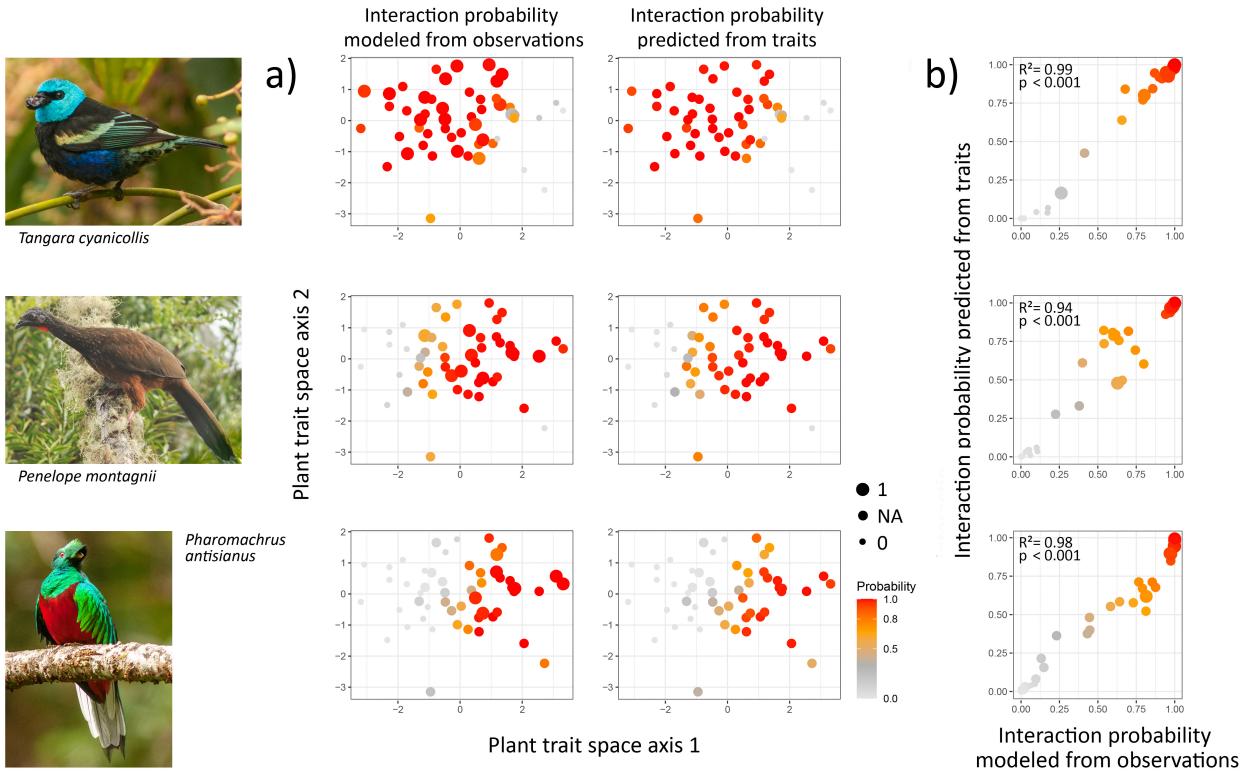

Fig. 2. Using joint hierarchical niche models to predict unobserved interactions based on proxies. (a) The Eltonian niches of three bird species in a multi-dimensional plant trait space (only first two axes shown). Plant species are projected into a multidimensional trait space using PCoA. Color of dots corresponds to the interaction probability between a bird species and a plants in the network. For each bird species, interaction probabilities were modelled once from observed interactions (left) and, after removing all observed interactions from the network, predicted based solely on their functional traits and the relationship between traits and Eltonian niches of the other bird species in the network (right). Interactions in the network were marked as observed (1), unobserved but likely (NA), and unobserved and unlikely (0; see Methods for details), differences are represented by dot size. (b) Correlations between the interaction probabilities modelled from observed interactions and those predicted based on birds' functional traits for the three bird species. Bird images by DMD.

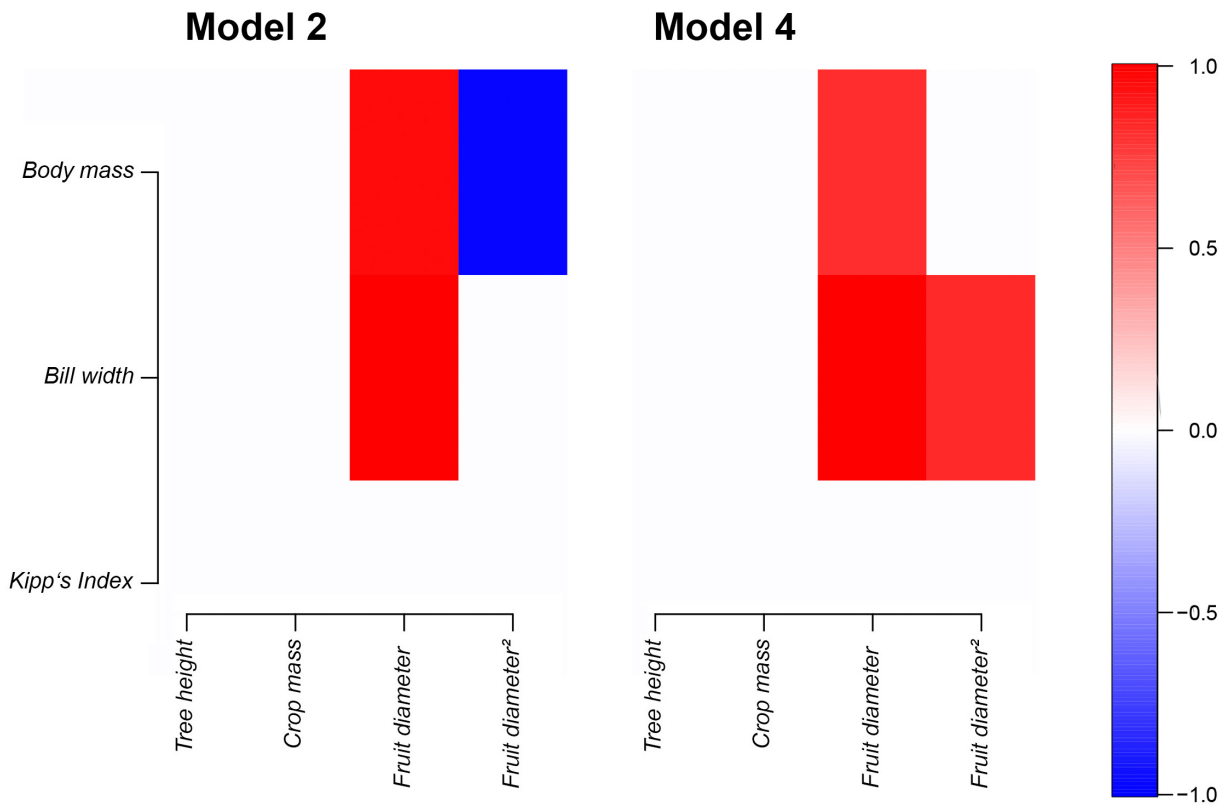

Fig. 3. Correlations (fourth-corner relationships) between bird traits and plant traits in an interaction network between frugivorous birds and fleshy-fruited plants (models 2 and 4). Bird traits include bodymass, bill width and Kipp's index; plant traits include tree height, crop mass, and fruit diameter (and its squared term).

Appendix 1

Table S1. Explanatory and predictive power, explained variance, and phylogenetic signal in Eltonian niches of four joint hierarchical models describing the interactions between 61 frugivorous birds and 52 fleshy-fruited plants. Eltonian niches of bird species are described by the functional traits of the plants with which the birds interact. The joint hierarchical models relate the birds' Eltonian niches to different combinations of co-variates (no co-variates, bird traits, bird phylogeny, bird traits + bird phylogeny). Percent variance explained describes the mean variance in bird–plant interactions explained by plant traits and the mean variance in Eltonian niches explained by bird traits. The phylogenetic signal in the birds Eltonian niches is given as the 95% interval and median value.

Model	**Co-variates**	**WAIC**	**Explanatory power**		**Predictive power**		**Percent variance explained**		**Phylogenetic signal**
			AUC	Tjur R^2	AUC	Tjur R^2	bird–plant interactions by plant traits	Eltonian niches by bird traits	bird traits
1	no co-variates	16.64	0.9	0.25	0.56	0.02	81.9	-	-
2	bird traits	16.63	0.9	0.26	0.60	0.03	83.4	42.2	-
3	bird phylogeny	16.59	0.9	0.24	0.55	<0.01	77.3	-	0.66–1 (0.91)
4	bird traits + bird phylogeny	16.53	0.9	0.25	0.54	<0.01	79.8	45.3	0.63–1 (0.91)

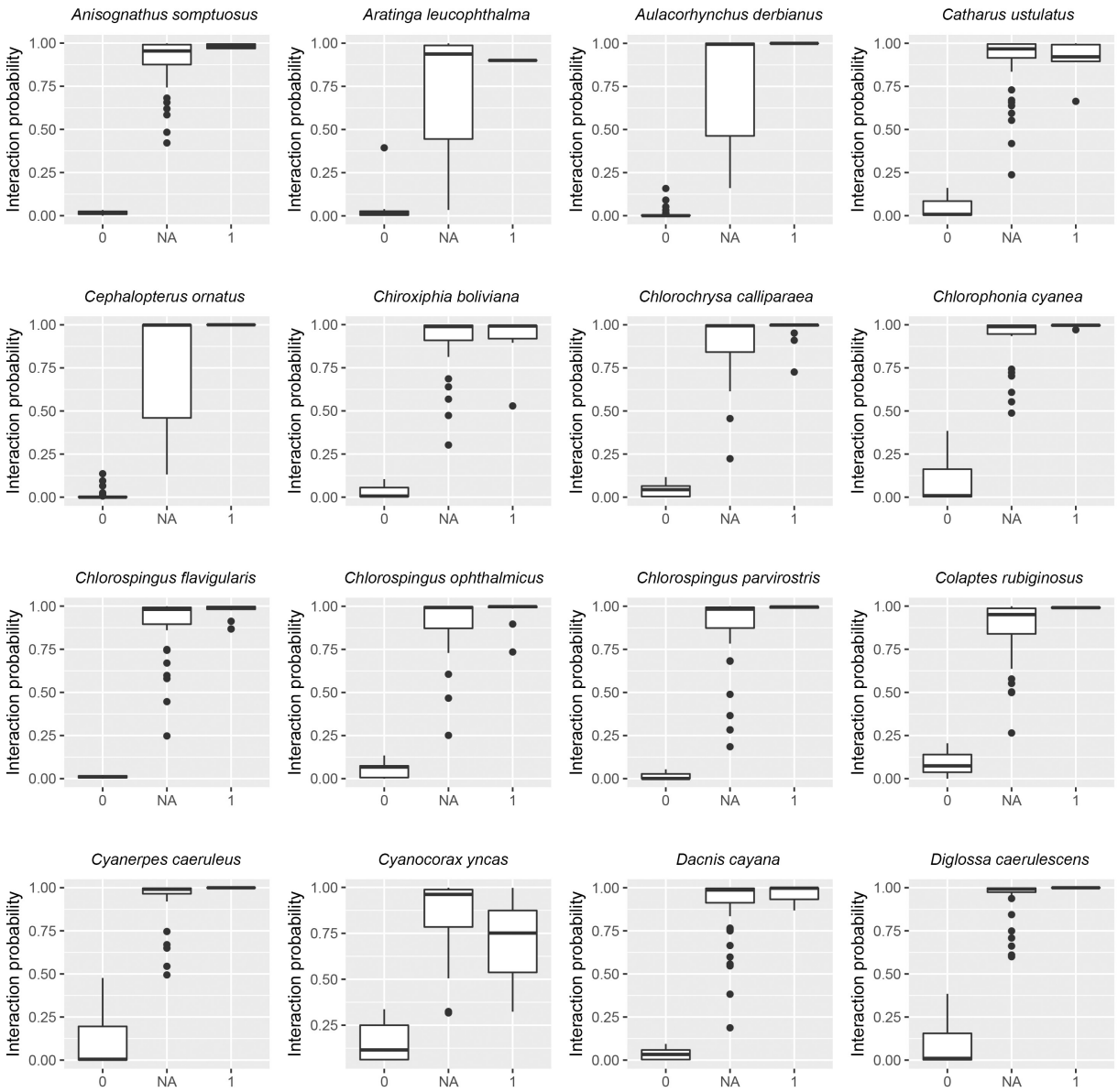

Fig. S1. Interaction probability for 61 bird species modelled with a joint hierarchical niche model (model 2) based on an empirical network of bird–plant interactions from the tropical Andes. Interactions in the network were marked as observed (1), unobserved but likely (NA), and unobserved and unlikely (0); see Methods for details.

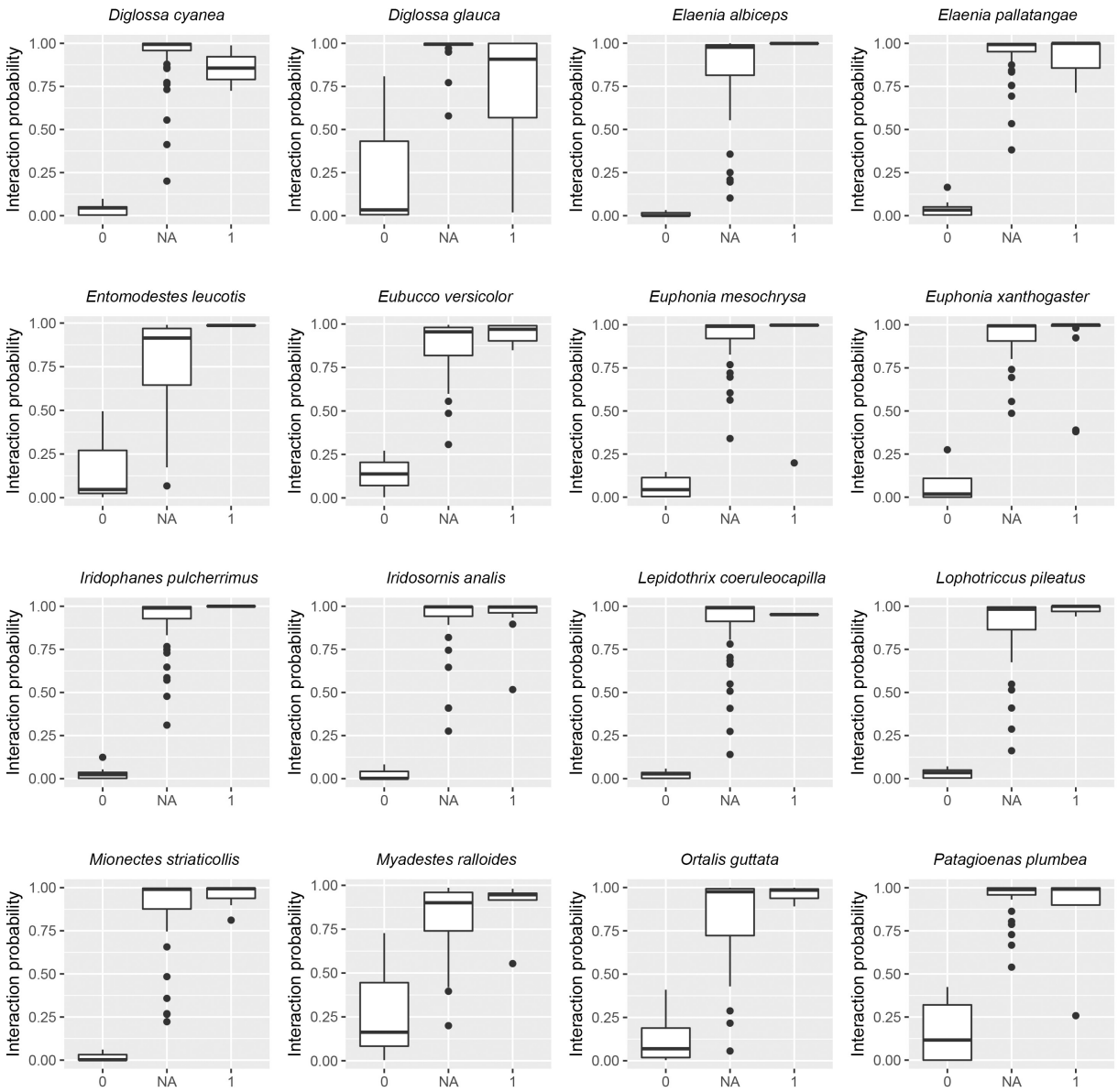
Diglossa cyanea
Diglossa glauca
Elaenia albiceps
Elaenia pallatangae
Entomodestes leucotis
Eubucco versicolor
Euphonia mesochrysa
Euphonia xanthogaster
Iridophanes pulcherrimus
Iridosornis analis
Lepidothrix coeruleocapilla
Lophotriccus pileatus
Mionectes striaticollis
Myadestes ralloides
Ortalis guttata
Patagioenas plumbea
Interaction probability
1.00
0.75
0.50
0.25
0.00
0
NA
1

Fig. S1. (ctd.)

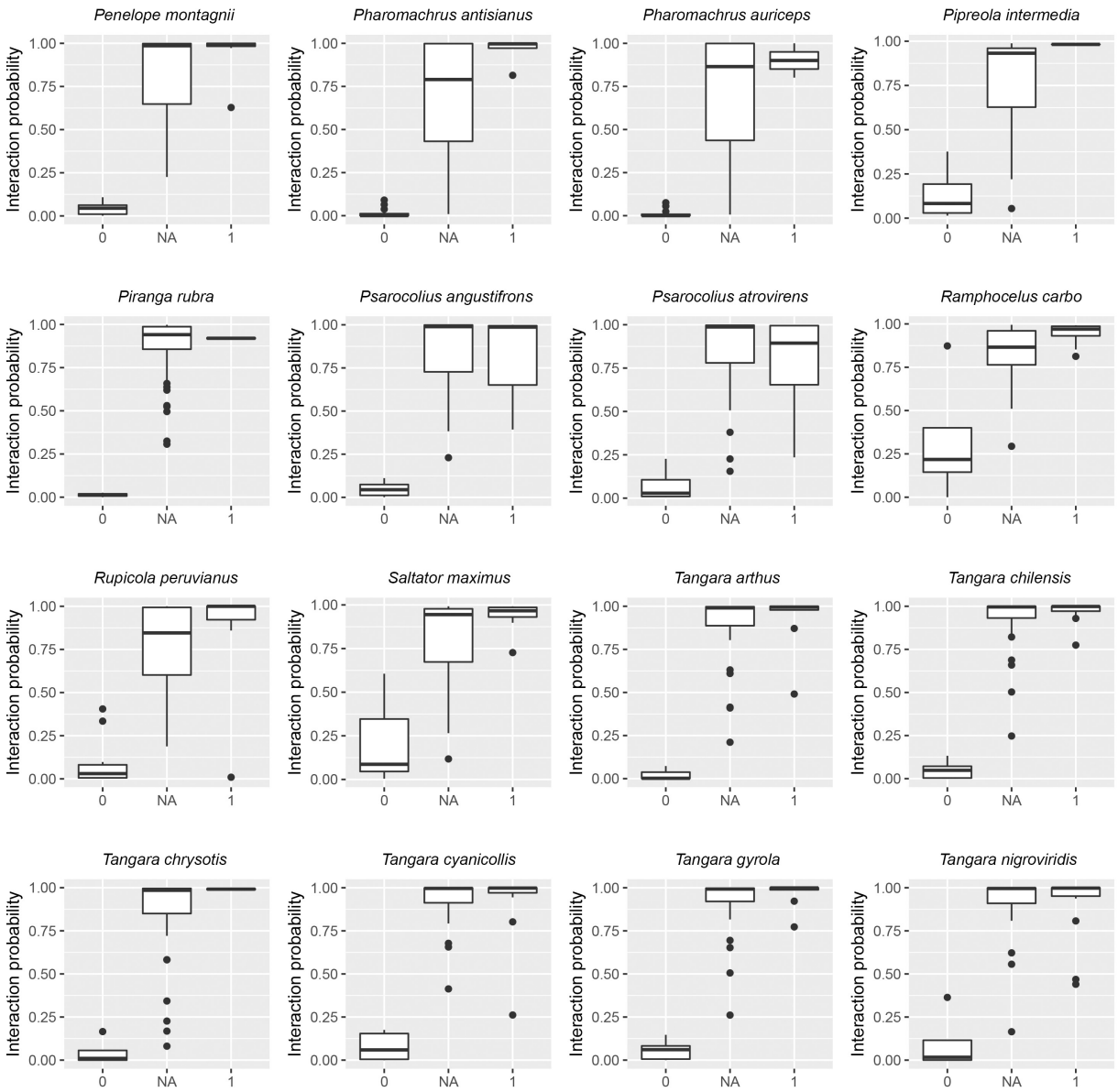
Penelope montagnii
Pharomachrus antisianus
Pharomachrus auriceps
Pipreola intermedia
Piranga rubra
Psarocolius angustifrons
Psarocolius atrovirens
Ramphocelus carbo
Rupicola peruvianus
Saltator maximus
Tangara arthus
Tangara chilensis
Tangara chrysotis
Tangara cyanicollis
Tangara gyrola
Tangara nigroviridis
Interaction probability
1.00
0.75
0.50
0.25
0.00
0
NA
1

Fig. S1. (ctd.)

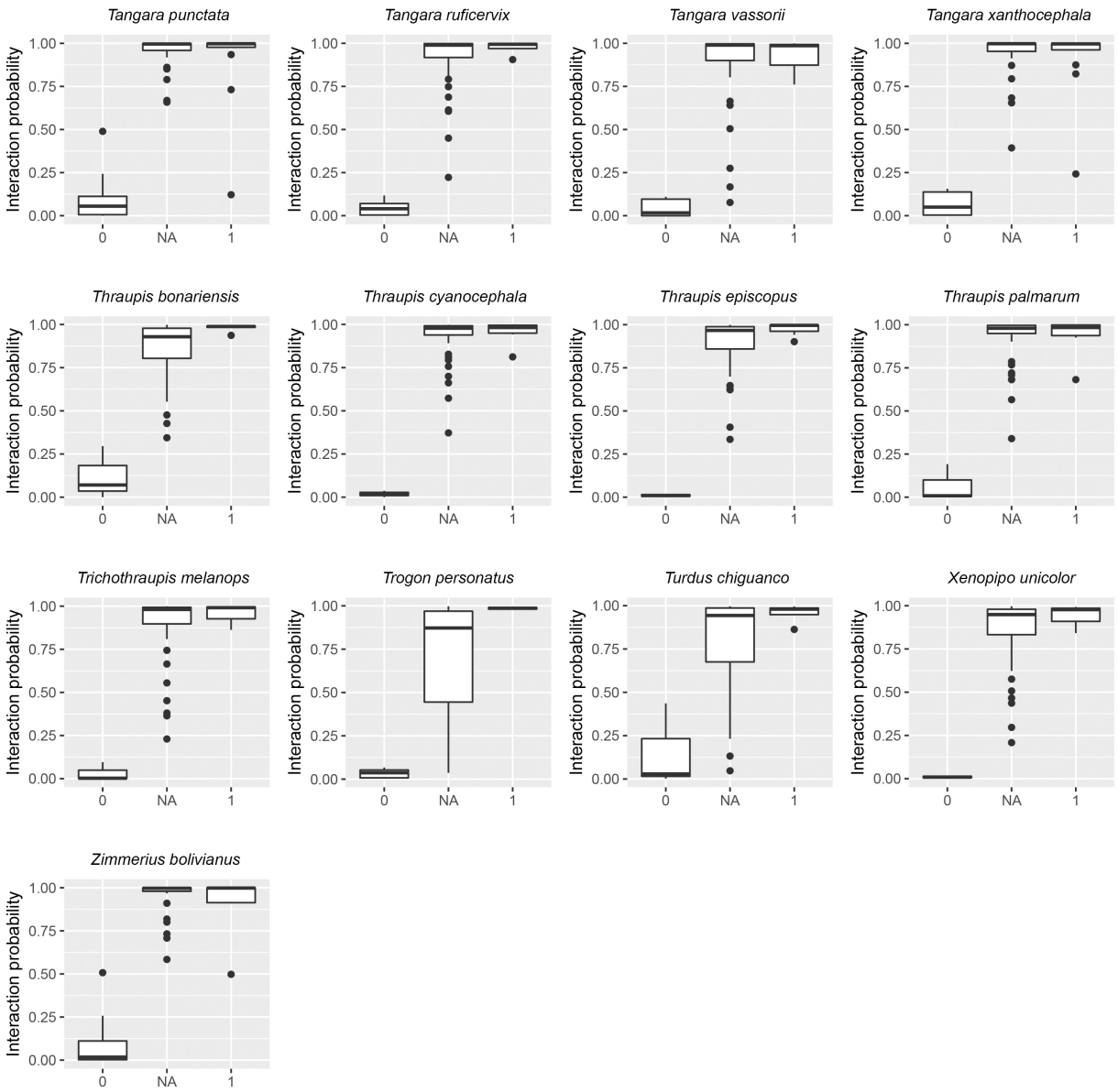
Tangara punctata
Tangara ruficervix
Tangara vassorii
Tangara xanthocephala
Thraupis bonariensis
Thraupis cyanocephala
Thraupis episcopus
Thraupis palmarum
Trichothraupis melanops
Trogon personatus
Turdus chiguanco
Xenopipo unicolor
Zimmerius bolivianus
Interaction probability
1.00
0.75
0.50
0.25
0.00
0
NA
1

Fig. S1. (ctd.)

Appendix 2

In our maximal model 4, we modelled the presence–absence of interaction, Y_{ij}, between plant (resource) species i and bird (consumer) species j in a joint hierarchical model as:

$$Y_{ij} \sim \text{Bernoulli}\left(\pi_{ij}\right) \tag{1}$$

$$\text{logit}\left(\pi_{ij}\right) = \alpha_i + \sum_{k=1}^{4} R_{ik}\beta_{jk} + \sum_{m=1}^{2} Z_{im}\omega_{jm} \tag{2}$$

$$\beta_{jk} \sim \text{Normal}\left(\sum_{l=1}^{4} C_{jl}\gamma_{kl},\ \mathbf{V}\right) \tag{3}$$

$$\mathbf{V} = \mathbf{V_0} \otimes \left[(\rho\mathbf{P} + (1-\rho)\mathbf{I})\right] , \tag{4}$$

where π_{ij} is the probability of interaction between plant species i and bird species j. The intercept α_i accounts for interspecific variation in average interaction probability across plant species, whereas β_{j1} (that corresponds to the intercept column $R_{i1} = 1\ \forall\ i$) accounts for interspecific variation in average interaction probability across bird species. The consumer-specific slopes $\beta_{j,k>1}$, which can be interpreted as the bird species' Eltonian niche, estimate bird species' responses to the three plant resource traits $R_{i,k>1}$. We also included two sets of plant- and bird-specific latent variables, Z_i and ω_j respectively, to account for co-variation in bird species' resource use. Next, we allowed the three bird consumer traits C_{jl} (plus an intercept column $C_{j1} = 1\ \forall\ j$) to moderate their Eltonian niche β_{jk} via the trait–trait interaction term, γ_{kl}. Lastly, the term $\mathbf{V}$ captures any unexplained variation in Eltonian niche not explained by bird traits, and is further partitioned into an overall variation unrelated to bird phylogeny, $\mathbf{V_0}$, and another component that is potentially influenced by bird phylogeny $\mathbf{P}$ by a proportional factor $0 < \rho < 1$; $\mathbf{I}$ is an identity matrix necessary for the estimation of phylogenetic signal in Eltonian niche.

In model 3, we omitted bird traits by removing the $\beta_{j,k>1}$ and $R_{i,k>1}$ terms. In model 2, we omitted bird phylogeny by setting $\mathbf{V} = \mathbf{V_0}$ (or equivalently $\rho = 0$). In model 1, we performed both of these omissions.