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RESEARCH PAPER

Abundance and trait-matching both shape interaction frequencies between plants and birds in seed-dispersal networks

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Abstract

Abundance and trait-driven processes have both been identified as potential mechanisms in determining the occurrence of species interactions. However, little is known about how these two mechanisms interact to determine the relative frequencies of interactions between species, and thereby species-specific contributions to ecological functions. Here, we evaluate the effect of both species' abundance and trait-matching on the occurrence of plant-bird seed dispersal interactions in the Cantabrian Range (northern Spain). For two years at fourteen plots, we independently sampled the abundance and diversity of fleshy-fruited plants and frugivores, as well as the consumption of fruits by birds. We quantified trait-matching by applying a food-web approach based on the log-ratios of species traits relevant to seed dispersal and traits related to fruit-handling and foraging-stratum. We fitted multi-level models incorporating phylogenetic relatedness to identify phylogenetically independent effects of species abundance and trait-matching on interaction frequencies. Fitted models showed that species abundances of both plants and birds always had strong positive effects on interaction frequencies. Trait-matching effects associated with fruit-handling were weak, but consistent across years, whereas those derived from foraging stratum varied across years, according to strong interannual changes in species abundance. Our findings reveal that both species abundance and functional traits are required for a mechanistic understanding of species interactions, as well as for predicting species roles in ecosystems under global change.

Keywords: Fleshy-fruited plants; Legitimate seed dispersers; Neutral processes; Niche-driven processes

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Introduction

Mutualistic interactions are a crucial part of ecological communities with relevant effects on ecosystem functioning (Bascompte and Jordano, 2014). In particular, plant-animal mutualisms play an important role in many ecological functions, such as pollination and seed dispersal, which determine plant population and vegetation dynamics (Bascompte and Jordano, 2014). There is ample evidence that both abundance and trait-driven processes control plant-animal interactions. Abundance effects will arise under neutral models in which more abundant species are involved in more interactions by chance effects, whereas trait-driven effects will be based on niche models emphasizing morphological adaptations or exaptations (Bartomeus et al., 2016; Stang, Klinkhamer, and Meijden, 2006). Indeed, species abundance and traits have been found to predict general features of mutualistic networks (e.g. nestedness; Vizentin-Bugoni, Maruyama, and Sazima, 2014). However, we still know little about the determinants of interaction frequencies between species (Olito and Fox, 2015). This is important, as plant-animal interactions translate to the specific functional contributions of species to aggregate ecological functions (Bartomeus et al., 2016; Schleuning, Fründ, and García, 2015). Therefore, a better understanding of the drivers of species interaction frequencies, usually less studied than just the interactions, could help to identify the mechanisms regulating the effects of species diversity on ecosystem functioning (Schleuning et al., 2015).

Species interaction frequencies are assumed to result from neutral processes, where common species have higher number of interactions than rare ones because of a higher random encounter probability (Fig. 1A; Poisot, Stouffer, and Gravel, 2015). Moreover, the relevance of abundance effects on interactions could depend on the variability in plant and animal abundances through space and time (Poisot et al., 2015). Besides abundance, functional traits may also drive the emergence of interactions between co-occurring species (Fig. 1; Schleuning et al., 2015). In this sense, species interactions are favored when both plant and animal traits are compatible (Dehling et al., 2014), but are precluded when traits lead to physical restrictions or "forbidden links" (Olesen et al., 2011). Indeed, some studies have correlated the frequency of interactions with plant or animal traits (Stang et al., 2006; Garibaldi et al., 2015), and others have even estimated the degree of compatibility between plant and animal traits (e.g. González-Castro et al., 2015; Gonzalez and Loiselle, 2016). However, only a few studies of mutualistic interactions have approached trait-matching through food web models based on the use of consumer and resource trait ratios (e.g., body size; Gravel et al., 2016; Rohr et al., 2010). Such an approach allows to detect species preferences for specific partners based on their interacting consumer and resource traits (Fig. 1B; Rohr et al. 2010).

Despite the demonstrated effects of abundance or traits, few attempts have been made to study the relative contributions of fluctuating abundances and inter-specific trait-matching on pairwise interactions in concert (but see Sebastián-González et al., 2017; Peralta, Vázquez, et al., 2020). In some cases, trait-matching has been proposed as the prevailing force in high-diversity systems (e.g. tropical systems; Vizentin-Bugoni et al. 2014), where a high divergence of functional traits has led to a higher proportion of specialized species (in terms of interacting partners; Sonne et al. 2020). In other cases, abundance seems to rule plant-animal interactions in communities with low trait diversity and high phenological overlap between partners (Simmons et al., 2019), where local variation in species abundances influences the random chance for partners to interact (Donoso et al., 2017; Winfree et al., 2015). Thus, despite a

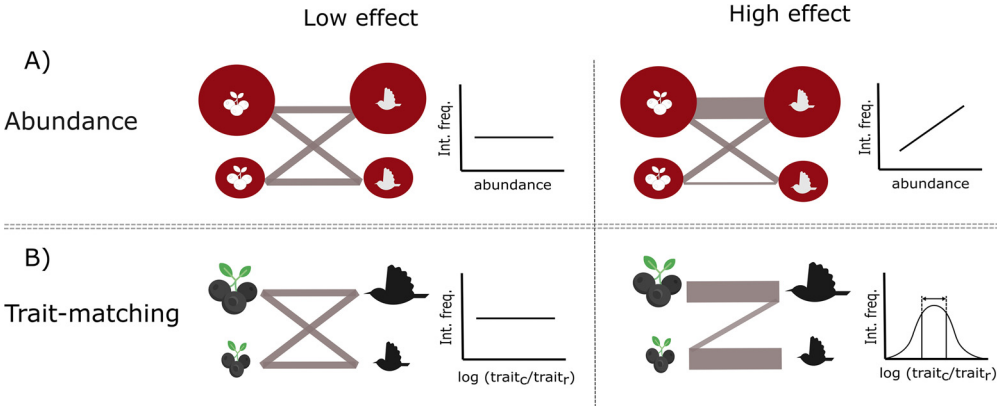

Fig. 1. Hypothetical relationships between species interactions and A) species abundances (represented proportionally by circle-size), with either low (top left) or high (top right) effects of abundance, or between species interactions and B) trait-matching between traits of consumer- (trait$_c$) and resource species (trait$_r$) (e.g., birds and fruits), with subsequent low (bottom left) and high (bottom right) effects of trait matching. A high effect of species abundances implies a positive association between abundance and interaction frequency (i.e. dominant species should interact more than rare species), whereas a high effect of trait-matching implies a hump-shaped relationship between the ratio of consumer and resource traits and interaction frequency, which reflects a maximum probability of interactions between species that possess an optimal ratio in trait values (sensu Rohr et a. 2010).

consensus that neither abundance nor trait-matching alone are sufficient to predict pairwise mutualistic interactions (Gonzalez and Loiselle, 2016; Olito and Fox, 2015), it is not yet clear how both drivers can jointly modulate species interactions.

Species features involved in plant-animal interactions (i.e. abundances, phenology, morphology, etc.) are conditioned by the evolutionary history of species (Herrera, 2002; Pellmyr, 2002). In fact, patterns of species co-occurrence may be affected by species phylogenies (Baeten et al., 2015), since closely related species could share life-history traits that influence their distribution and abundance (Baeten et al., 2015; Davies and Buckley, 2011). Moreover, closely related species may frequently share morphological and behavioral traits that are involved in the trait-matching between interacting partners (Tucker et al., 2018), leading to phylogenetic signals in the structure of plant-animal mutualistic networks and species interaction frequencies (Bascompte and Jordano, 2014). As such, the analysis of the effects of abundance and trait-matching on species interactions should take into account the phylogenetic relationships among species (Schleuning et al., 2014).

Here, we focus on mutualistic interactions within an assemblage of fleshy-fruited plants and avian frugivores in the Cantabrian Range (northern Spain). In this system, we have previously demonstrated the importance of fruit and bird abundance for the occurrence of plant-frugivore interactions (Donoso et al., 2017), as well as in the magnitude of the seed dispersal function derived from frugivory interactions (García, Donoso, and Rodríguez-Pérez, 2018). Moreover, we have highlighted the important role of plant and animal traits for the structure of seed-dispersal networks and the stability of seed-dispersal processes (García et al., 2018; Peña et al., 2020). As an important step forward, we here assess the relative contribution of species abundances and trait-matching on the frequency of plant-frugivore interactions. We expect that interaction frequencies depend on (a) species-specific abundances of both plants (fruit) and birds, and, (b) the trait-matching associated with species traits. Additionally, we evaluate whether these effects are consistent over time given the strong inter-annual variability of species abundances.

Materials and methods

Study system

The study was conducted in mid-elevation woodland pastures of the Cantabrian Range (northern Spain). The woodlands contain variable-sized fragments of primary forest and, more frequently, secondary forest embedded in an extensive matrix of open pastures. The secondary forest is typically dominated by fleshy-fruited plant species (Table S1.1 in Appendix 1), some of which have annual differences in their fruit production (i.e. masting effect), leading to strong variation in resource availability (e.g., *Ilex aquifolium*, a masting species; García et al. 2013). The ripening period for these fruits is from late summer to early winter, with species overlap in fruit production occurring from September to November. The main frugivores are passerine birds (García, 2016), which have different ecological effects on plants, from seed dispersal to pulp and seed predation (Simmons et al. 2018). Here, we focused exclusively on mutualistic interactions, that is, frugivores that act as legitimate seed dispersers through swallowing the entire fruits and dropping intact seeds by means of regurgitation or defecation.

The study area comprised two localities of Asturias (Sierra de Peñamayor, 43°18'09.5"N, 05°30'32.6"W; and Puerto de Marabio, 43°14'35.2"N, 6°05'41.6"W, 990−1250 m a.s.l.), chosen for their high availability of fruiting resources. In total, we delimited fourteen 150 m × 150 m study plots with a minimum distance between plots within each locality of 350 m. All plots represent a similar setting in terms of geomorphological characteristics, vegetation structure and composition, as well as anthropic management (extensive livestock raising), but were chosen to take into account a wide range of forest availability (range from 3 to 69%) to consider habitat heterogeneity. The sampling was carried out from 2012 to 2014, during two consecutive fruiting seasons (from September to February) corresponding to 2012-2013 and 2013-2014 (2012 and 2013 hereafter).

Bird abundance and fruit consumption

During the fruiting season, we estimated the abundance of birds by means of point-count censuses in each plot. To facilitate bird recordings, and due to logistical constraints, we systematically subdivided each plot into a grid of 36 cells each measuring 25 m x 25 m. Censuses were carried out at nine points regularly distributed within each plot, each census point being at the center of a set of four adjacent cells (i.e., an observation area of 50 m x 50 m). We considered distance-based differences in bird detectability within the observation area around each point-count were negligible. Nine census rounds per point-count, plot and annual fruiting season to be performed, resulting in a total effort of 94.5 h per year (1-2 censuses/month). Censuses were performed between 09.00 and 15:00 h, avoiding days of heavy rain and wind. In each census point, all birds heard or seen (with the help of 8 × 30 binoculars) in a set of four adjacent cells over a 5-minute period were registered. Each census round was carried out by a single observer in each plot. Four different observers were involved in the observations, alternating between plots. Bird abundance was estimated as the cumulative number of each bird species observed per plot per sampled year.

In each fruiting season, we recorded fruit consumption by birds by monitoring bird foraging activity. Observation

rounds were carried out by a single observer per plot, from 3-4 vantage positions chosen to cover different and complementary sections of each plot. The vantage points were positioned >50 m from patches of fruiting plants and chosen so that different fruiting plant species could be observed. Observers used 8 × 30 binoculars and stayed at distances ranging from 50 to 100 m from focal trees. Observations were performed from 9:00 to 15:00 h in 1-hour blocks. This sampling effort resulted in eight observation periods for each plot in 2012 and nine in 2013, reflecting a total effort of 112 h and 126 h, respectively. For every frugivory event (i.e., a bird picking fruits from fleshy-fruited plants), we recorded species identity and the number of fleshy fruits consumed per individual bird. We defined a pairwise interaction as one fruit of a given species removed by one bird species (i.e., irrespective of the frugivory event). Data from the different observation rounds of each plot per year were pooled. That is, pairwise interactions between species were defined as the cumulative number of fruits of plant species consumed by bird species in each plot in each year. Next, we built a set of local (i.e., plot-level) plant-bird matrices with all observations recorded per plot and fruiting season. Zero values were added to those plant-bird cells corresponding to species present in the plot and the year of observation (species abundance > 0), but without observations of fruit consumption. In this way, we included all potential combinations of interacting species present in each plot.

Fruit abundance

At the beginning of the fruiting season, we mapped each plot estimating the number of ripe fruits for all individuals of a species present within the plot. To ensure the accurate sampling of all available fruits of each fruiting season, we monitored fruit crops on two separate dates, which matched with the ripening peaks of different plant species. For this, we visually estimated the number of standing fruits (considering the arillated seeds in *Taxus baccata* and *Rubus fruticosus/ulmifolius* as single fruits for counting purposes) per individual tree or shrub by means of a semi-quantitative scale with six intervals (Fruiting Abundance Index or FAI, Saracco et al. 2004). Individual crop sizes were extrapolated from FAI ranks considering an allometric fit between the actual crop size and FAI (actual crop size = $1.765^{1.9249FAI}$; $R^2 = 0.80$; N = 136 individual plants; Martínez et al. 2014). Fruit abundance was quantified as the cumulative number of fruits of each species per plot and sampled year.

Species traits

We focused on plant and bird phenotypic traits relevant to frugivory and seed dispersal, in order to represent two levels of functional matching (Dehling et al., 2014). The first level of matching involved traits related to fruit-handling (hereafter "fruit-handling"): avian bill width and fruit diameter (Dehling et al., 2014). The second level of functional matching involved traits related to foraging behavior (hereafter "foraging-stratum"): avian wing shape and plant height (Dehling et al., 2014). Avian wing shape was estimated by Kipp's index (Kipp's distance, i.e. the distance from the tip of the first secondary to the wing tip measured on the folded wing, divided by wing length) and is related to bird mobility and the preferred foraging stratum (Pigot et al., 2020). All bird traits were measured on museum specimens (following Peña et al., 2020). Fruit species diameter was measured from 25 ripe fruits (five fruits from five different individuals) sampled in the plots in 2012. Plant height was measured as the average of visual estimates in at least 30 fruiting individuals of each species across study plots in 2012.

Trait matching and optimal ratio

We quantified the degree of trait-matching between species using an optimal match model based on a food web approach (Rohr et al., 2010). We modelled the occurrence of interactions between resource and consumer organisms as a function of the log-ratio of species traits (e.g., body size in Rohr et al. 2010). This approach assumes an optimal range of interaction probability, contingent on its relationship with the quadratic polynomial of the log-ratio (i.e., [log ($trait_{consumer}/trait_{resource}$) + log($trait_c/trait_r$)^2]). In the statistical model, a hump-shaped relationship between interaction probability and the log-ratio of consumer−resource traits is interpreted as an optimal phenotypic match between species (Fig. 1B, optimal ratio: log ($trait_c/trait_r$)^2). In other words, a certain range of values of traits enhances the probability of interaction between partner species. Within this framework, we represented the matching of fruit-handling as the ratio between bird bill width and plant fruit width, and foraging-stratum as the ratio between bird Kipp's index and plant height (see Appendix 3: Fig. S3). We thus examined fruit-handling and foraging-stratum in order to evaluate trait-matching between species for frugivory (Dehling et al., 2014).

Phylogenetic relationships

To identify phylogenetically independent effects of species abundances and traits on pairwise interactions, we incorporated the evolutionary relatedness of both plant and bird species. Firstly, we extracted the phylogenetic relationships among the fleshy-fruited plant species occurring in our study sites from the GBOTB.extended mega−tree (Jin and Qian, 2019), an updated and corrected version of the GBOTB.extended phylogeny (Smith and Brown, 2018). This is the largest dated phylogeny for seed plants available to date, and comprises all families of extant seed plants (Jin and Qian, 2019). The backbone tree was pruned for the set of species present using *phylo.maker* function of the V.

PhyloMaker package in R (Jin and Qian, 2019). For birds, phylogenetic relationships were based on a complete dated phylogeny from BirdTree.org (Ericson et al., 2006; Jetz, Thomas, Joy, Hartmann, and Mooers, 2012). We downloaded 10,000 backbone trees to generate the maximum clade credibility (Bayesian MCC) tree using TreeAnnotator (Drummond and Rambaut, 2007). For both birds and plants, we extracted the phylogenetic distance matrix among all species in the pruned phylogeny (Letten and Cornwell, 2015) using the function *cophenetic* implemented in the ape R package (version 5.3, Paradis and Schliep 2019).

Data analysis

In order to assess the roles of abundance and niche processes in determining interactions between plants and birds, we quantified the relative effects of abundance and trait-matching on interaction frequencies. Importantly, species abundance estimates were fully independent of the interaction data (Coux et al., 2020; González-Castro et al., 2015). Moreover, relative abundance and trait values were uncorrelated across species (all Pearson's correlation coeficients $r < 0.4$, $P > 0.05$; see Appendix 4). We used Bayesian Phylogenetic Generalized Linear Mixed Models (PGLMMs), implemented in the package brms (version 2.13.0, Bürkner 2017) as it allows the quantification of the effect of each predictor while controlling for phylogenetic interdependence. We fitted different models to evaluate the simultaneous effects of abundances and trait-matching for each sampling year (i.e., 2012 and 2013) separately.

Each model included fruit- and bird species abundance as well as the main and quadratic terms of trait-matching (separate models for fruit-handling and foraging-stratum). These models can be defined as:

$$Y_{ijk} = a_{i1}...+ a_{iK} + a_{j1}...+ a_{jK} + b_1 \text{ x } AB_{ik} + b_2 \text{ x } AB_{jk} + b_1 \text{ x } TM_{ijk} + b_1 \text{ x } TM_{ijk}\text{^}2$$

where Y_{ijk} is the interaction frequency for bird species *i* and plant species *j* in plot *k, a* the intercepts for each species and sample plot, *b* the slope parameters for abundance AB of bird species *i* and plant species *j* in each plot, and for trait-matching TM, which is the log ratio between the functional traits of bird species *i* and plant species *j*.

For each model, plant and bird species were included as random factors, in order to detect abundance or trait-matching effects irrespective of species identity. Moreover, we incorporated phylogenetic covariance matrices for both trophic levels to control for the influence of phylogenetic relationships among species. Plot identity was also included as a random factor. Interaction frequency was over-dispersed, with many zero values, and we therefore built models using a negative binomial error distribution. For all analyses, fruit and bird abundances were square-root transformed, and all explanatory variables were scaled to unit variance.

The posterior probability distributions were sampled using the No-U-Turn sampling algorithm (Hoffman and Gelman, 2014). Four independent Markov chains were run for 10,000 iterations. We discarded the first 3,000 samples during the burn-in period. We did not thin the posterior distributions as we detected no autocorrelation in our posterior draws. In such situations full chains have been suggested to provide more precise parameter estimates (Link and Eaton, 2012). Chain mixing and convergence were measured by *Rhat* (R^) statistics. This indicated convergence in all models, with *R^* being approximately equal to 1.0 for all parameters. We assigned non-informative priors to all parameters. We visualized posterior predictive checks using BayesPlot package in R (Gabry and Mahr, 2021). For each parameter, we report the 95% credibility interval, which describes the range of parameter values that fall within 95% of the posterior probability distribution. A credibility interval that overlaps zero indicates that one cannot assume that the effect is different from zero, and a larger absolute deviation from zero indicates stronger positive or negative effects.

We estimated the relative importance of independent fixed factors (i.e., abundance vs. trait matching) in the overall models by comparing the marginal R^2 (i.e., explained variance related to all fixed effects) of the overall model with that of its partial model, i.e. a model fitted excluding one of the fixed factors from the overall model (e.g., plant or bird abundances, trait-matching term). Thus, we divided the partial-model R^2 by the overall-model R^2 and used this ratio as a factor's contribution to the overall model.

Results

General overview

We observed a total of nine bird species which consumed 1304 and 1608 fruits in 2012 and 2013, respectively, from seven fleshy-fruited plant species (see Appendix 2: Table S2.1 and S2.2). In both years, *Turdus merula* was the dominant bird species (38% and 43% of bird abundance for 2012 and 2013, respectively), and the frugivore which also showed the highest interaction frequency (54% and 63% of total pairwise interactions, respectively), followed by *T. iliacus* (Fig. 2). *T. philomelos* and *Erithacus rubecula* showed a marked variation in abundance between years, although their interaction frequencies remained constant (Fig. 2; Table S2.2 in Appendix 2). Fruit abundances varied across years, being 1.8 times larger in 2013 than in 2012. This difference was caused by the masting of some species, especially *I. aquifolium*, which greatly increased in terms of both absolute and relative abundance (Fig. 2, Table S2.1 in Appendix 2). Despite inter-annual variability in total fruit abundance, *Crataegus monogyna* and *I. aquifolium* provided ca. 80% of all fruits and together were involved in 75% of all interactions in both years (Fig. 2).

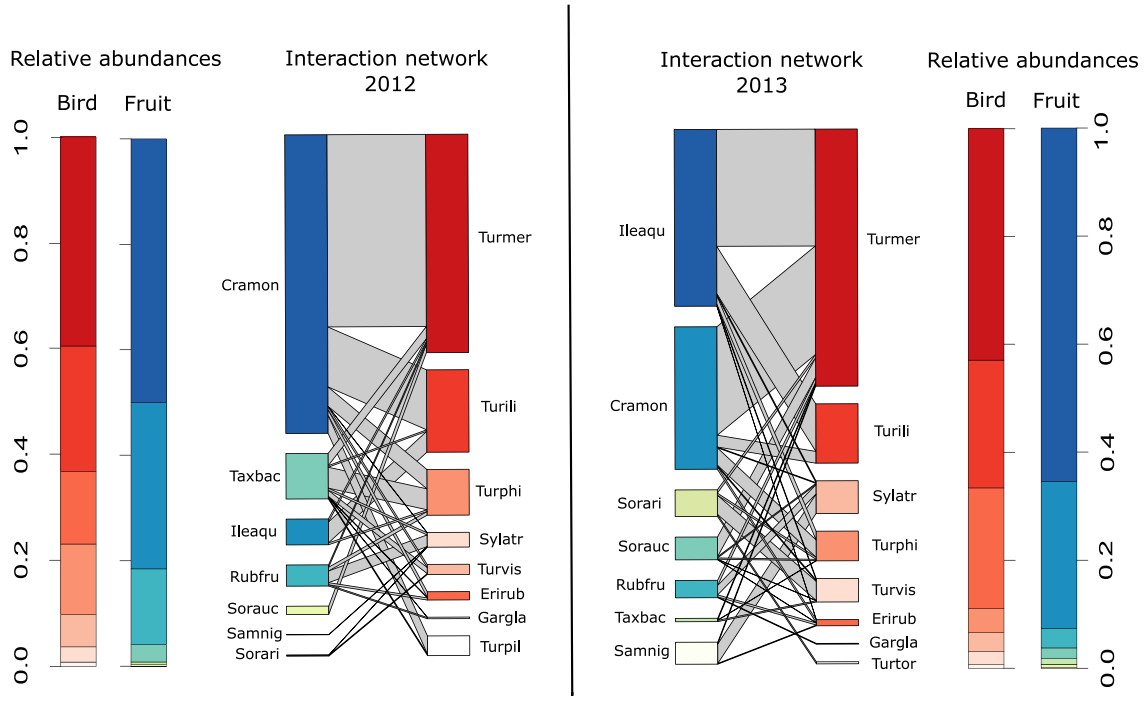

Fig. 2. Interaction networks between plants and avian seed dispersers in the Cantabrian Range (N Spain) corresponding to A) 2012 and B) 2013, represented by bipartite plots with bird species ordered by decreasing interaction frequency. Stacked bars show the relative abundances of plant (fruit; in red) and bird species (in blue) in a decreasing order of abundance and color. Species in bipartite plots are differentiated by color (the same as in stacked bars) and can be identified by the species acronyms (Cramon, *Crataegus monogyna*; Ileaqu, *Ilex aquifolium*; Rubfru, *Rubus fruticosus/ulmifolius*; Samnig, *Sambucus nigra*; Sorari, *Sorbus aria*; Sorauc, *Sorbus aucuparia*; Taxbac, *Taxus baccata*; Erirub, *Erithacus rubecula*; Gargla, *Garrulus glandarius*; Sylatr, *Sylvia atricapilla*; Turili, *Turdus iliacus*; Turmer, *Turdus merula*; Turphi, *Turdus phillomelos*; Turpil, *Turdus pilaris*; Turtor, *Turdus torquatus*; Turvis, *Turdus viscivorus*). Note that the identity of species by color-bars changes between years due to differences in species abundances.

Mechanisms driving pairwise interactions

We consistently found an effect of both species' abundance and trait-matching on interaction frequencies in all models. In both years, fruit and bird abundances were positively related to interaction frequencies (Fig. 3A-B). Moreover, the effect of fruit-handling was largely consistent across years (Fig. 3A), indicating an optimum relationship between interacting traits. In contrast, the matching related to foraging-stratum showed an effect on interaction frequency only in 2013 (Fig. 3B).

Overall, fruit and bird abundances showed greater contributions to the variation in interaction frequencies than trait-matching terms (Table 1). In particular, the partial models including exclusively fruit and bird abundances as predictors accounted for a larger amount of variation of interaction frequencies (> 75% across all models) than partial models combining fruit or bird abundance with trait matching terms (0.8%-47%; Table 1). The difference between these partial models was, moreover, consistent across years (Table 1). Regarding the different trait-matching terms, partial models based on fruit-handling accounted for limited amount of variation of interaction frequencies (models including fruit abundances: 12% and 10%; models including bird abundances: 1.0% and 0.8% in 2012 and 2013, respectively). Partial models based on foraging-stratum varied between years, with the model including fruit abundance showing higher contribution to the variation of interaction frequencies in 2012 than in 2013, and that including bird abundance showing higher contribution in 2013 (masting year) than in 2012 (Table 1).

Discussion

Here, we focus on fleshy-fruited plants and avian frugivores to show that both species abundance and trait-matching are important to shape the frequency of pairwise interactions in seed dispersal processes. The effect of species abundances on the occurrence of interactions was overall stronger than that of trait-matching in our study system. We also found that interannual variability of species abundances conditioned trait-matching effects related to foraging behavior.

Effect of species abundances and trait-matching on interactions

Our results showed effects of both species abundances and trait-matching on the frequency of interactions in seed

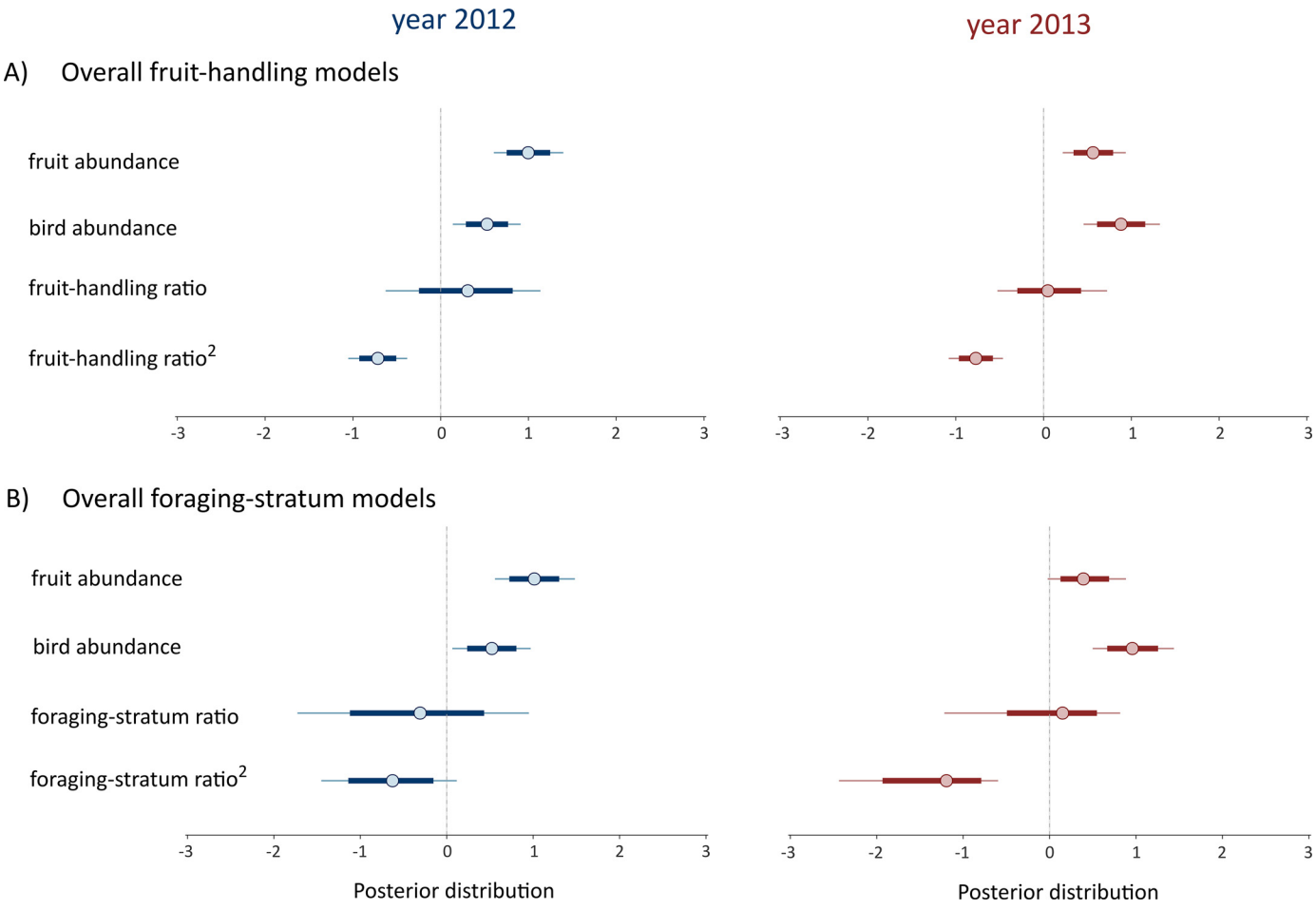

Fig. 3. Results of fitted PGLMM evaluating the effects of species abundances and trait-matching in the frequencies of plant-bird pairwise interactions in the Cantabrian Range. Each model includes different sets of predictors to represent the combined effect of both mechanisms. All models include plant (fruit) and bird abundances, and trait-matching terms [log ($trait_c/trait_r$) + log ($trait_c/trait_r$)^2] for fruit-handling (A) and foraging-stratum (B) related models; All models were fitted for each year, 2012 (left, in blue) and 2013 (right, in red) including the plot and species identity as random effects, as well as both phylogenetic covariance matrices from each trophic level. The vertical line at zero indicates the exact predicted values of estimates. Thus, a negative/positive value indicates the effect of each predictor on the frequency of pairwise interactions. Dots represent the predicted posterior median, and error bars the 95% and 70 % credible intervals (thin and thick lines, respectively).

Table 1. Relative contribution of abundance and trait matching terms to the occurrence of pairwise interactions, based on the ratio of marginal R^2 of partial to overall models. Partial models included subsets of two of the fixed predictors (i.e., plant abundance, bird abundance or trait-matching (TM) terms) included in the overall models. We fitted separate full models for trait matching related to fruit-handling and foraging stratum for each sampling year.

Overall model	Partial models	2012 Contribution (%)	2013 Contribution (%)
Fruit-handling	Plant abundance + TM	12.0	10.0
	Bird abundance + TM	1.0	0.8
	Plant + Bird abundances	76.0	78.0
Foraging-stratum	Plant abundance + TM	14.0	4.0
	Bird abundance + TM	4.0	47.0
	Plant + Bird abundances	90.0	77.0

dispersal networks, even after controlling for phylogenetic relatedness. Firstly, we identified species abundance as the main driver of plant-bird interactions, given that fruit and bird abundances accounted for a larger amount of variation in interaction frequencies than trait-matching (Table 1). Earlier studies have identified species abundances as a key driver in shaping pairwise interactions and global structure in networks of seed dispersal (Donoso et al., 2017) and pollination (Olito and Fox, 2015; Winfree et al., 2015), especially in temperate systems with low to medium levels of diversity (Sonne et al. 2020). Besides this strong species abundance effect, we here also detected a clear trait signal (Table 1), indicated by the consistent effects of the quadratic term of the bird-plant trait ratios. That is, there were specific trait values of interacting species leading to higher interaction frequencies (Fig. 1B). For instance, birds prefer fruits as large as they can swallow (i.e, $trait_c/trait_r < 1$, Fig. S3.1 in Appendix 3). These results support the existence of the trait-based preferences of interacting species for specific partners (Bascompte and Jordano, 2014; Maglianesi et al., 2014). Additionally, these also highlight that even in communities with little trait diversity (e.g., temperate systems), trait-matching conditions species' contribution to ecological functions (Schleuning et al., 2015). These results suggest that this food-web approach may be particularly suitable for identifying trait-matching effects in species-poor systems.

In our study system, interannual variability in species abundances is quite pronounced (Fig. 2), especially concerning the mast-fruiting species (Table S2.1 in Appendix 2). Despite this, we found consistent and positive effects of species abundances on interaction frequencies in both sampling years (Table 1). However, these interannual changes in abundance concurred with differences in the effects of fruit-handling and foraging stratum on interaction frequencies. That is, we found different patterns depending on the type of functional traits evaluated in terms of estimating trait-matching. In this respect, foraging-stratum effects seem to be more contingent on the animals' response to local and landscape features (see also Poisot et al., 2015; Sebastián-González et al., 2017) than fruit-handling effects. Namely, animal behavior, which strongly interacts with morphological traits such as avian wing shape to determine bird vegetation use, may be highly flexible in coping with fluctuating fruiting landscapes (García et al., 2013). For instance, in the *I. aquifolium* masting year (2013), large and conspicuous fruit patches were concentrated in forest remnants, which is reflected by the stronger foraging-stratum and bird abundance effects on interactions in this year (Fig.3B, Table 1). That is, thanks to their resource tracking ability, frugivores would adapt to strong variations in large-scale fruit distribution by searching more strongly for fruit-rich patches in masting years (see García et al., 2013). This behavioral flexibility of animals could underpin the differences in foraging patterns across years (see also Bender et al. 2017, Sebastián-González et al. 2017). On the other hand, previous studies have suggested organism size (i.e. a plant's flower/fruit and an animal's body) as a major trait involved in driving species performance in plant-animal mutualistic interactions (González-Castro et al., 2015). Indeed, this is also suggested by our results, with consistent between-years effects of fruit-handling (Fig. 3A), i.e. the level of trait-matching deriving from size-related features. Furthermore, from an evolutionary perspective, the consistent effect of fruit-handling may derive from the highly conservative character of size-related traits (Miner et al., 2005). Interestingly, our results suggest that different types of traits have more consistent and fixed effects (e.g., size-related traits) across years than other traits, which seem to depend on the ecological context (e.g., foraging behavior).

Implications for ecosystem functioning

Disentangling the main drivers of pairwise species interactions can provide clues to a better understanding of the relationship between biodiversity and ecosystem function in plant-animal assemblages. Theoretically, under the greater influence of abundance-driven processes, the magnitude of the ecological functions mostly depends on the role of dominant species, with species' functional contributions being proportional to their abundance (Winfree et al., 2015). Our results support the notion of the key importance of abundant species, as the main driver of species' contribution to seed dispersal (see also Donoso et al. 2017, García et al. 2018). Other studies have suggested that dominant species show a high degree of generalization in interaction networks (Fort, Vázquez, and Lan, 2016; Peralta, Perry, et al., 2020). In our case, a relatively species-poor plant-frugivore system, a few dominant species built a core of generalists that are highly interrelated among themselves (Fig. 2; Fig. S2 in Appendix 2). To sum up, species interactions and their contribution to functions may be mediated by relative species abundances (i.e., neutral forces), where dominant species are more likely to interact, which in addition, will contribute more to ecological processes by a sampling effect (Winfree et al. 2015).

Under a niche-partitioning scenario, the degree of trait complementarity between species can affect the magnitude of ecological functions (Garibaldi et al., 2015; Schleuning et al., 2015). In fact, species' contributions to the ecological functions derived from mutualistic interactions have been found to depend on trait-matching, particularly in specialist species (Bender et al., 2018; Peralta, Perry, et al., 2020). Although our study system is little specialized (García et al., 2018), we here empirically demonstrate the significant role of trait-matching in determining plant-frugivore interactions. This suggests that species with complementary traits can contribute additively to seed dispersal processes (see also García et al. 2018). These findings emphasize the importance of functional diversity for ecological processes, even in systems with high degrees of generalization.

Conclusion

The ongoing loss of diversity across trophic levels has the potential to disrupt species interactions and associated ecosystem functions. In this work, we show that data on species abundances predict largely interaction frequencies, but functional traits are also needed to understand species contributions to interaction networks. Our findings encourage to overcome the long-standing debate on abundance vs. trait-driven processes as main drivers of ecological interactions by applying an integrative approach that accounts for the additive effects of both mechanisms. The prediction of ecological interactions based on independent measures of both the abundance and traits of partner species is a promising way forward to forecasting ecological functions under anthropogenic global change.

Author contributions

D.G., M.S. and R.P. conceived and designed the study; D.G., J.R-P. and I.D. collected field data; R.P. and M.S. collected phylogenetic and trait data; R.P. performed the analyses with input from F.D.; R.P. wrote the first draft of the manuscript and, D.G. and M.S, contributed substantially to revisions. All authors reviewed the manuscript and approved the final version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.11.008.

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