Tricky partners: native plants show stronger interaction preferences than their exotic counterparts

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Abstract. In ecological networks, neutral predictions suggest that species' interaction frequencies are proportional to their relative abundances. Deviations from neutral predictions thus correspond to interaction preferences (when positive) or avoidances (when negative), driven by nonneutral (e.g., niche-based) processes. Exotic species interact with many partners with which they have not coevolved, and it remains unclear whether this systematically influences the strength of neutral processes on interactions, and how these interaction-level differences scale up to entire networks. To fill this gap, we compared interactions between plants and frugivorous birds at nine forest sites in New Zealand varying in the relative abundance and composition of native and exotic species, with independently sampled data on bird and plant abundances from the same sites. We tested if the strength and direction of interaction preferences differed between native and exotic species. We further evaluated whether the performance of neutral predictions at the site level was predicted by the proportion of exotic interactions in each network from both bird and plant perspectives, and the species composition in each site. We found that interactions involving native plants deviated more strongly from neutral predictions than did interactions involving exotics. This "pickiness" of native plants could be detrimental in a context of global biotic homogenization where they could be increasingly exposed to novel interactions with neutrally interacting mutualists. However, the realization of only a subset of interactions in different sites compensated for the neutrality of interactions involving exotics, so that neutral predictions for whole networks did not change systematically with the proportion of exotic species or species composition. Therefore, the neutral and niche processes that underpin individual interactions may not scale up to entire networks. This shows that seemingly simplistic neutral assumptions entail complex processes and can provide valuable understanding of community assembly or invasion dynamics.

Key words: abundance; birds; frugivory; mutualist network; neutrality; New Zealand; scaling; seed dispersal.

Introduction

All species engage in multiple interactions with one another, which can be represented by ecological networks (Elton 1927, Polis 1991, Bascompte 2009). The frequency of each interaction can be governed by multiple factors, leading to considerable variation in interaction frequencies within and across communities (Vázquez et al. 2009). First, interaction frequencies can be driven by factors that are to some extent independent from species' identity, such as their local relative abundances. Indeed, abundant species should tend to interact more frequently than rare species, simply because the latter are less likely to encounter one another at random (Blüthgen et al. 2008, Vázquez et al. 2009, Canard et al. 2012). This indicates a proportional relationship between species' relative abundances and their interaction frequencies (García et al. 2014, Donoso et al. 2017), analogous to the mass action principle that determines the reaction frequency of chemical compounds (Staniczenko et al. 2013).

Second, interaction frequencies can be determined by factors that are inherent to the species' identity. Numerous biological constraints might favor frequent interactions between particular pairs of species, or restrain others such that they might avoid interacting altogether because of morphological, phenological, or behavioral

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incompatibilities (Jordano et al. 2003). For example, the body size of consumer species is one of the predominant filters for trophic interactions (Alcántara and Rey 2003, Brose et al. 2017, Grass et al. 2018). At the extreme, highly specialized species such as parasites or obligate mutualists may interact exclusively within a limited range of partners (e.g., ant–plant mutualisms, as in Riginos et al. 2015). There are many more examples of direct interaction filtering based on species and their traits (Dehling et al. 2014), which are known to constrain interaction structure strongly (Cohen et al. 2003, Stouffer 2010). More recently, the role of indirect interactions and ecological neighborhood (sensu Donoso et al. 2017) has also been proposed to regulate interactions (Poisot et al. 2015), and it was notably found that indirect effects can be as important as direct interactions in shaping the structure of mutualistic networks through coevolutionary processes (Guimarães et al. 2017). Hence, deviations from interaction frequencies predicted based on species' abundances are common (Dáttilo et al. 2014, Vizentin-Bugoni et al. 2014, Isbell et al. 2017, Bender et al. 2018, Peralta et al. 2020).

Consequently, the frequency of species interactions can be determined by two components: first, a component that can be predicted based on relative abundances, which can be considered to result from neutral processes (Volkov et al. 2003, Krishna et al. 2008, Vázquez et al. 2009, Canard et al. 2014). In the extreme case, neutrality supposes that interactions are systematically realized upon an encounter between two individuals of different trophic levels, such that there is no filtering depending on species identity or traits (i.e., no niche differentiation). The second component comprises interaction frequencies deviating from those predicted by mass action (i.e., from neutrality), such that there is niche differentiation. An interaction frequency that occurs more frequently than expected based on the relative abundances of a species pair would thus correspond to an interaction preference, whereas an interaction that occurs less often than expected depicts an avoidance (Staniczenko et al. 2013, García et al. 2014). This perspective allows us to test hypotheses regarding the frequency of interactions while controlling for species' relative abundances, by allowing interaction frequencies to be partitioned into neutral and nonneutral determinants.

This partitioning is important, as it is likely that both neutral and nonneutral processes occur simultaneously to shape interaction frequencies within a community rather than being mutually exclusive (Chave et al. 2002, Leibold and McPeek 2006). In fact, the continuum theory of network structure (Gravel et al. 2006) posits that neutral processes should govern the nature and strength of given interactions between partners, whereas niche processes such as niche forbidden links (Jordano et al. 2003, González-Varo and Traveset 2016) should govern whether the encounter takes place at all. This perspective raises two key questions: (1) It is unclear whether there are systematic differences in the relative intensities of

niche vs. neutral processes across species or systems, which could explain why some conform to neutral hypotheses better than others; (2) even if we understand why particular interactions may be driven more by niche vs. neutral processes, it remains unclear whether such interaction-level differences can be summed across a whole community. Specifically, it is necessary to understand whether neutrality as a process affects all species of a community in a similar way, or if it affects some species differently based on their identity and community composition.

In this study, we develop a framework (initialized by García et al. 2014 and built from the logic of Staniczenko et al. 2013) that incorporates interaction preferences to understand how the separate neutral and nonneutral components of interaction frequencies change between species and across networks. We apply this framework to interaction networks that include recent introduction of exotic species into native assemblages, as these systems are especially prone to alter their balance of neutral and niche processes (Nuismer et al. 2018, Trøjelsgaard et al. 2019, Vizentin-Bugoni et al. 2019). Namely, coevolution between native species often drives them to develop more extreme traits (Guimarães et al. 2011, Mouillot et al. 2013, Nagelkerke and Rossberg 2014), such that we hypothesize that interaction preferences and avoidances will be stronger between pairs of native species. In contrast, exotic species are expected to have more generalist traits, which would allow them to interact with a larger proportion of available species (Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, García et al. 2014). Thus, if they are sufficiently abundant, we hypothesize that interactions involving exotic species will more closely match neutral predictions. Here, we focus on the paired interactions between fleshy-fruited plants and frugivorous birds in a set of New Zealand forest sites with different relative abundances and compositions of native and exotic species (García et al. 2014). We first investigate preferences at the interaction scale, to test whether the exotic or native status of birds and plants predicts the contributions of each interaction to neutral or nonneutral processes. We then explore whether these results scale up to whole networks to determine whether the relative importance of neutral vs. nonneutral processes for each site is correlated with a gradient in the abundance of exotic bird interactions or with bird or plant community composition in each site.

METHODS

Study system and plant–frugivore networks

In a previous study, García et al. (2014) recorded frugivorous interactions between birds and fleshy-fruited tree species from low-altitude, conifer–broadleaf forests in New Zealand. They studied nine forest patches located around Wellington urban areas in the North

Island (five sites) and near Kaikoura in the South Island (four sites, see Appendix S1, Fig. S1 for a map with site locations), that held a wide array of species from both trophic levels and encompassed a gradient in the relative abundance of exotic birds and plants. In each site, a single sampling transect of approximately 1 km was established along walking trails across the forest. On each transect, from early February to late May 2012, which corresponds to the main ripening season of these fleshy-fruited species (Williams and Karl 1996), the researchers conducted fortnightly fruit counts (number of fruits on individual fruiting plants), along four sections of 100 × 4 m separated by at least 100 m one from each other. The absolute abundance of fruits was estimated as the average number of fruits per sampling round (3–4 censuses per site) for each plant species. They also estimated bird abundances through censuses carried out every 2–3 d at each site, between 08:00 and 16:00 (14–21 censuses per site). During the census, the complete transect was walked, counting all individuals of the different bird species heard or seen in a 10-m-wide band at both sides of the walking trail. For each bird species at each site, the absolute abundance was standardized by sampling time, and hence calculated as an encounter rate by means of the cumulative number of observations per 10 h.

Interactions were recorded as the number of fruits consumed per bird and per plant species, surveyed as standardized observations that, importantly, were conducted independent of the estimation of species' abundances. Observations of fruit consumption by birds were made at each site while walking each complete transect at a constant speed (approximately 1 h). Surveys were conducted immediately after the bird censuses, and lasted at least 15 min from the end of the census (14–21 rounds per site). On each round, once a perching bird was detected within a 5-m-wide band at both sides of the walking trail, it was observed until it was lost in the foliage. Each observation of a given bird eating was considered to be an event of frugivory. For each site, the number of fruits consumed per bird and plant species was estimated as the sum of fruit consumptions across all observation rounds. A plant–bird frugivore interaction network was built for each of the nine study plots (see Data S1: frugivory_data.csv for a list of species, their interaction frequencies, relative abundances and origin status).

Across all sites, interaction networks comprised 13 bird species (3 exotic and 10 native) interacting with 42 plant species (6 exotic and 36 native; see Supporting Information for a complete list of species and interaction frequencies). Overall, we used data collected during 126 sampling hours, during which 887 frugivory events were detected and 4,655 fruits were consumed. From the 13 bird species, we discarded the native species *Nestor meridionalis* because it occurred only once in all sites, and was never observed consuming fruit. Despite the low exotic to native species ratio, interactions involving exotic birds accounted for an average of 21% (±15) of all interactions across sites, and exotic birds interacted with an average of 32% (±13) of all plant species of a given site. Interacting with a wide spectrum of species can be a hint of neutrality at the interaction scale, as we will see in the following section. The fruits of exotic plants represented 5.9% of fruit consumptions, from which native and exotic birds accounted for 4.98% and 0.92%. The percentage of fruit consumed by exotic birds per site ranged from 9.3% to 56.7%, and the percentage of fruits of exotic plants being consumed ranged from 0% to 13.7%.

Estimating interaction preferences

The framework from García et al. (2014) employs a Poisson regression to predict observed interaction frequencies F_{ij} between two classes of species i and j based on their abundances A_i and A_j:

$$F_{ij} = e^{\log(C)+\log(A_i)+\log(A_j)+\log(\gamma_{ij})} \tag{1}$$

where F_{ij} follows a Poisson distribution, γ_{ij} corresponds to interaction preferences (i.e., the model residuals), and the constant C to an estimated intercept related to species' overall tendencies to interact. The leading component of the interaction frequencies, $e^{\log(C)+\log(A_i)+\log(A_j)}$, corresponds to the mass-action term (Staniczenko et al. 2013), which has been rearranged to match the log-link function of the Poisson regression. It implies that the frequency of an interaction is directly proportional to the product of the relative abundances of each interaction partner, and thus $\gamma_{ij} = 1$ (zero in log scale) would correspond to perfectly neutral expectations whereby all variation in interaction frequencies is explained by mass action. When one has censuses of bird and plant species' relative abundances (A_i and A_j) as well as independent estimates of fruit consumption to quantify interaction frequencies F_{ij}, the only parameter to be inferred by this model is the intercept C, and interaction preferences γ_{ij} emerge from the residuals in log space.

Inclusion of missing interactions

As is often the case in community ecology, our interaction matrices included many zero values (two species not observed to interact), which are known to cause overdispersion in Poisson models. In addition, absences of interactions complicate the discrimination of true absences (i.e., when two co-occurring species never interact no matter their abundances) from false absences (i.e., rare interactions less likely to be observed, e.g., Martin et al. 2005, Cirtwill et al. 2019). True absences typically correspond to niche forbidden links (Jordano et al. 2003) and can reveal niche or morphologically driven avoidances between species, whereas false absences directly depend on species' abundances, and have been

conceptualized as "neutral forbidden links" (Canard et al. 2012). Previous studies using this framework (Staniczenko et al. 2013, García et al. 2014) chose to discard these missing interactions. We considered, however, that an absence of interactions between co-occurring species could carry important information regarding the estimation of interaction preferences γ_{ij} (Martin et al. 2005). For example, the lack of interaction between two very abundant species could reveal interaction avoidance, which would provide strong evidence for nonneutrality.

To incorporate zero-frequency (unobserved) interactions in our model, we extended the framework from García et al. (2014) in Eq. 1 to use a zero-inflated negative binomial model (ZINB, *zeroinfl* function, "pscl" package version 1.4.9; Zeileis et al. 2008, R Core Team 2020) instead of a standard Poisson regression, for which the incorporation of the unobserved interactions increased overdispersion. In ZINB models, parameters are estimated from two components, based on different distributions.

The first component has a binomial distribution and corresponds to the probability of observing a zero rather than an integer count. The second component has a negative binomial distribution, and generates "counts," among which zeroes may also occur. The purpose for such a framework is to help differentiate true zeroes—in our case the absence of interaction between two abundant species, that is, an avoidance—from false zeroes, or the failure of observing an interaction because of species rarity, the so-called neutral forbidden links.

In other words, compared to a regular Poisson regression, the ZINB also has a log-link function, but readjusts the model parameters in the negative binomial component—namely the intercept, C_{nb}—based on the probability of observing a zero from the binomial component. Following Eq. 1, we use this C_{nb} estimate to re-evaluate the interaction preferences γ_{ij}:

$$F_{ij} = e^{\log(C_{nb}) + \log(A_i) + \log(A_j) + \log(\gamma_{ij})}. \tag{2}$$

Moreover, the estimated interaction frequencies between pairs of species i and j, in turn are defined by

$$\hat{F}_{ij} = e^{\log(C_{nb}) + \log(A_i) + \log(A_j)} \tag{3}$$

with $\hat{F}_{ij}$ following a negative binomial distribution. This adjustment takes us a step further in evaluating interaction preferences after controlling both for the mass-action effect (relative abundances) and for the neutral forbidden links (incorporation of the zero frequencies from the observed data), which we will henceforth refer to as neutral predictions. In our analysis, we used ZINB models with the observed interaction frequencies and species' relative abundances of each site to estimate the intercept C_{nb} for each site. In the following sections, we then use C_{nb} in Eq. 3 to calculate interaction preferences

at the interaction level and a neutrality gradient at the network level for each site.

Contributions to (non-)neutral processes at the interaction level

Neutral processes provide a mechanistic prediction of how frequently two species should interact. As such, a deviation from this prediction results from alternative, nonneutral processes that influence how often two species really interact. Within each site and for each pairwise interaction, we estimated how well the relative abundances of species pairs predicted their observed interaction frequencies by calculating each observed frequency's deviance (d_{ij}) from neutral predictions, that is, the deviance residuals from the generalized linear model in Eq. 2. The mathematical calculation of these deviance residuals is explained in Appendix S1: Section S2.

The benefit of using deviance residuals rather than the commonly used Pearson residuals is that $d_{ij} > 0$, and in our data ranged from 10^{-5} to 10. Furthermore, total model deviance is the exact goodness-of-fit statistic that is minimized when fitting a generalized linear model such as our ZINB regression (Dunn and Smyth 2018). As such, deviance residuals d_{ij} correspond to each interaction's contribution to the nonneutral processes occurring at each site, whether in preferring or avoiding interactions with some of their partners. To approach normality in the distribution of deviance residuals, we log-transformed d_{ij} in the analysis described in the next section.

Are interactions involving exotic species more neutral?

As mentioned previously, we hypothesize that the coevolutionary history could strongly influence how often organisms interact, and that this signal can be measured in interaction preferences and avoidances. We ran a linear mixed-effects model (LME, *lme* function from the "nlme" package; Pinheiro et al. 2020), using log (d_{ij}) as the response, two categorical variables, bird (native or exotic) and plant (native or exotic), as fixed effects, and an interaction effect. We also added a site random effect to control for nonindependence of interaction frequencies across networks.

Avoidances

As noted earlier, deviance residuals d_{ij} are highest both when two rare species interact frequently (i.e., strongly prefer each other) and when two abundant species seldom interact (i.e., strongly avoid each other). Because it is biologically meaningful to distinguish preferences from avoidances and to help visualize the deviances when plotting them (but not for the analysis), we can create signed deviance residuals with sign $(F_{ij} - \hat{F}_{ij}) \times d_{ij}$, where sign($x$) = 1 if $x > 0$ and sign (x) = −1 otherwise. After this transformation, plotted

values at 0 still correspond to perfectly neutral interactions, all values less than 0 indicate avoidances, and all values greater than 0 indicate preferences.

Scaling up to network level: Quantifying the importance of neutral processes in each site

The deviance residuals d_{ij} are a measure of the accuracy of the neutral predictions at the interaction level. These predictions can further be combined within each site to evaluate the global fit of the neutral model across the different sites. We calculated the global deviance D_{ZINB} of the model from Eq. 3 as the sum of the d_{ij} in each site (see Appendix S1: Section S2 for mathematical details).

To estimate the relative importance of neutral mechanisms, we then compared the global deviance of the fitted model with that of a basic ZINB null model D_{null}. The latter predicts interaction frequencies for a given pair of interacting species simply based on the average number of interactions at a given site:

$$\hat{F}_{ij}^{\text{null}} = e^{C_{\text{null}} + \varepsilon_{ij}} \tag{4}$$

where $\hat{F}_{ij}^{\text{null}}$ follows a negative binomial distribution, C_{null} is the estimated intercept in log space, which corresponds to the log of the average interaction frequencies in each site, and ϵ_{ij} is the residual error.

We then used a pseudo R^2 measure we defined as $N = 1 - (D_{ZINB}/D_{null})$ to evaluate the performance of the estimated interaction frequencies F_{ij} (Eq. 3 model) ompared with the null F null (Eq. 4). N is bounded between 0 and 1, where values approaching 1 indicate that the total deviance D_{ZINB} of the Eq. 3 model is much smaller than D_{null}, suggesting that including relative abundances to predict interaction frequencies results in a better estimation of F_{ij} and therefore that neutral processes are occurring. Conversely, values of N closer to 0 would suggest similar values of D_{ZINB} and D_{null}, such that interaction frequencies are similarly well predicted when ignoring species' relative abundances altogether, hence indicating that neutral processes are absent. Moreover, this approach allowed us to place each site along a neutrality gradient, whereby the local value of N quantifies the strength of neutral processes relative to other nonneutral drivers. The R code used to calculate interaction preferences and avoidances and the neutrality gradient N can be found in Data S2: preferences_calculation.R.

Exotic gradient and species composition to predict the neutrality gradient

We tested several hypotheses involving species' origin to explain why neutral processes might be stronger drivers of interaction frequencies in some sites and less so in others. We investigated whether the neutrality gradient N could be explained by several measures of exoticism in our networks. Hence, for each site, we calculated (1) the percentage of exotic bird interactions as the sum of interaction frequencies involving an exotic bird divided by the sum of all interaction frequencies of that site; (2) the percentage of plant species interacting with exotic birds, that is, the number of plant species interacting with an exotic bird divided by the total number of plants species in that site. These two measures were highly correlated ($r = 0.75$, P value $= 0.02$), so we discarded the latter. We did not calculate the equivalent measures from the exotic plant perspective (i.e., the proportion of exotic plant interactions or bird species interacting with exotic plants) because of the absence of exotic plants in two of our sites. Furthermore, because sites were located on the two islands with marked differences in their isolation from urbanized areas, we also tested for a geographical correlation between sites by testing an "Island" variable. We used two separate linear models to test whether the neutrality gradient was related to the exotic bird gradient and to the island the sites were located (North or South Island).

If the exotic gradient could be one way to explain the neutrality gradient N across sites, so could species identities: some species might have stronger preferences whereas others have none, regardless of the origin of their interaction partners. If so, the composition of both bird and plant communities could also affect the relative importance of the neutral vs. nonneutral processes at a given site. We would expect communities of similar composition to show similar values along the N gradient. Thus, we tested whether differences in the neutrality gradient N across sites were related to differences in their species composition. We calculated Jaccard dissimilarities in the composition of plant and bird communities between sites. We then used Mantel tests with the Kendall correlation to evaluate whether dissimilarities in plant and bird species composition were correlated with the pairwise Euclidean distances between the sites based on the N values. Still using Mantel tests, we also tested whether plant community composition was correlated to bird community composition.

Results

Are interactions involving exotic species more neutral?

The LME model testing whether the origin status of plant and bird species and their interactive effect influenced their contribution to nonneutral processes showed that exotic plants had significantly smaller interaction deviances d_{ij} than native ones, as the latter showed significant deviances from neutral predictions (Table 1). Conversely, the origin of birds did not significantly affect the deviances of their interactions, nor did it impact the influence of plant origin on deviances through the interaction between the origin status of the two. Nevertheless,

the d_{ij} were highest for interactions between native pairs, and lowest for the exotic ones (Fig. 1), indicating that the relative abundances of native plants were not overall as good at predicting interaction frequencies as were those of exotic ones. Moreover, the frequency distribution of the signed d_{ij} for interactions involving native plants had more extreme values of d_{ij}, especially on the preferences side, than did the distribution for exotic plants (Fig. 2). Contrastingly, the d_{ij} for interactions involving exotic plants displayed a distribution of avoidances skewed towards weaker, increasingly neutral values. In both groups, however, the proportion of avoidances was much higher than the proportion of preferences (see also Appendix S1, Fig. S2 for further details about avoidances).

Can the exotic gradient or species composition predict the neutrality gradient?

From the interaction-level contributions of deviance residuals to nonneutral mechanisms, we tested whether these patterns scaled up to the site level. We found that the global deviance from the neutral model from the Eq. 3 D_{model} was lower than that of the null model D_{null} in all sampled networks: neutrality gradient N values were all between 0.9 and 1 (Fig. 3). In each network, species' relative abundances more accurately predicted interaction frequencies than did the mean number of interactions (null model prediction), suggesting that nonneutral mechanisms were weak relative to the abundance-driven ones.

Testing whether this neutrality gradient was related to the gradient of exotic bird interactions or to the island effect did not reveal any significant relationships (Table 2, Fig. 3). As such, neither the percentage of fruit consumptions by exotic birds nor the location of the sites on the North and South Islands influenced how well bird and plant relative abundances predicted interaction frequencies in a given site (Table 2).

Finally, testing species identity effects revealed that shifts in the species composition of birds were positively correlated with shifts in species composition of the plants (Mantel $r = 0.32$, $P = 0.005$). The neutrality
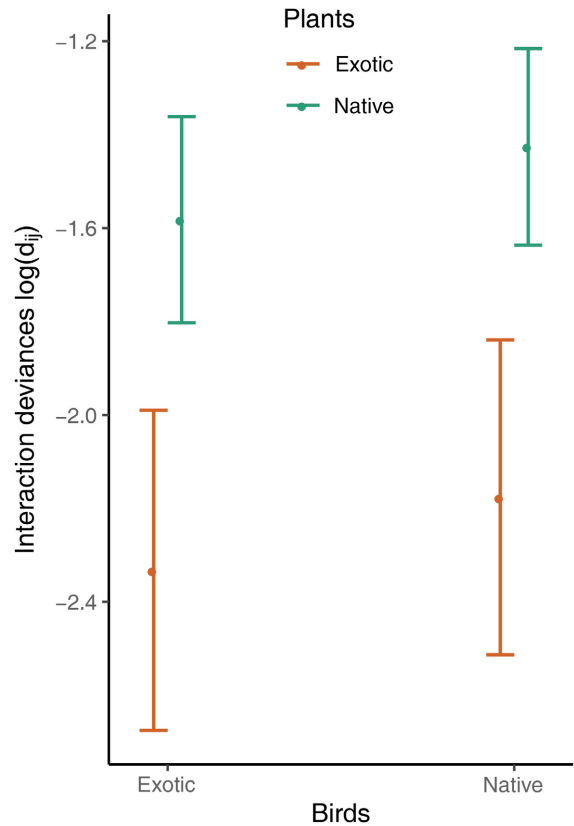

FIG. 1. Interaction plot from the log-linear mixed effects model showing the effects of bird and plant origin on the interaction deviances d_{ij}. Predicated values of the interaction deviances are shown with 95% confidence interval. Both exotic birds and plants had smaller d_{ij} than their native counterparts, indicating more neutral interactions, but this effect was significant in plants only. The interaction effect between bird and plant origin was not significant either (see Table 1 for further details).

gradient N, however, was not related to changes in plant species composition ($r = 0.12$, $P = 0.144$) or bird species composition ($r = 0.14$, $P = 0.094$) across sites.

DISCUSSION

Here we provided a new framework to evaluate how neutral and nonneutral processes drive pairwise species interactions and whole networks. Our results revealed that interactions involving native plants deviated most from neutral expectations, whereas the origin status of birds did not strongly influence how species' relative abundances predicted interaction frequencies. Furthermore, these results did not scale up to entire networks: Despite the differences in the strength of the neutral vs. nonneutral drivers in each site (neutrality gradient N), neither the gradient of the percentage of fruits consumed by exotic birds nor species identity effects explained these differences in a systematic way. Hence, our results

TABLE 1. Log-linear mixed-effects model estimates of bird and plant origin effects on the interaction deviances d_{ij} (i.e., deviances from neutral predictions that can be either preferences or avoidances).

	Value	SE	df	t value	P value
Intercept	−2.3997	0.2320	1,145	−10.3442	0.0000
Native plant	**0.8246**	**0.2243**	**1,145**	**3.6772**	**0.0002**
Native bird	0.2740	0.2797	1,145	0.9795	0.3275
Native plant: Native bird	−0.1289	0.2918	1,145	−0.4417	0.6588

Note: Site was included as a random effect. Significant effects are presented in bold. The intercept condition is exotic plant and exotic bird.
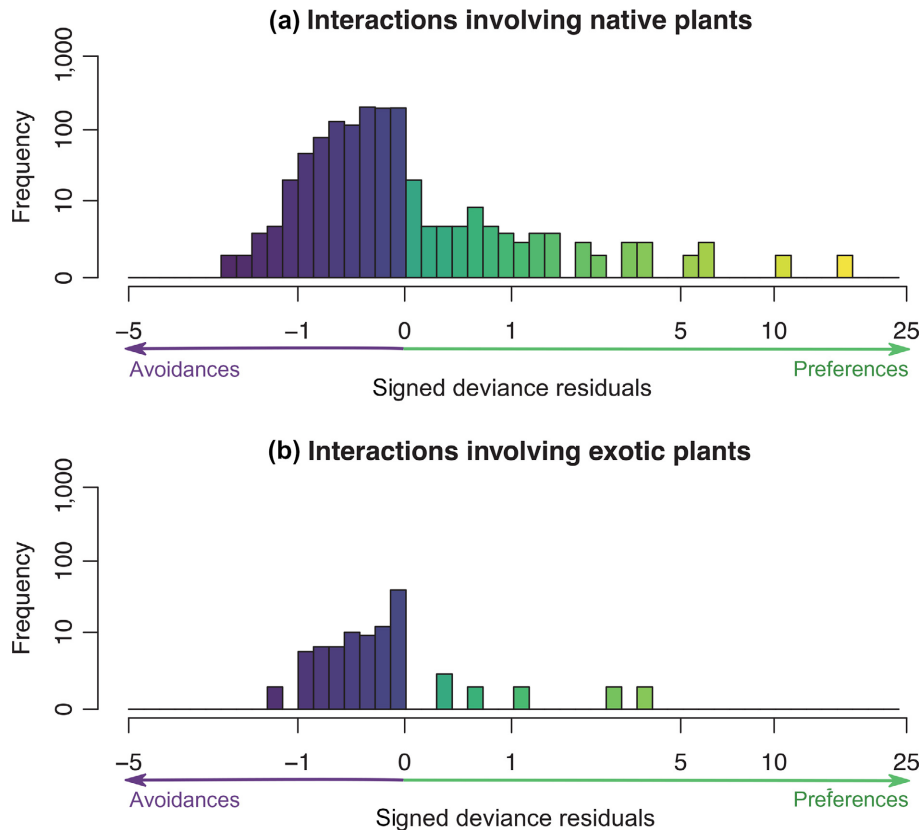
FIG. 2. Frequency distributions of interaction preferences (positive values) and avoidances (negative values). The strength of preferences and avoidances increases according to the green and purple arrows, respectively. Values of 0 indicate perfect neutrality (i.e., interaction frequencies that do not differ from expectations based solely on species' abundances).

suggest that neutral predictions of pairwise interactions of exotic species could potentially be a good baseline to estimate invasion dynamics or for conservation purposes, but that community-scale predictions do not systematically emerge from these predictions.

Mechanisms driving species interactions for native and exotic species

As a whole, our results at the interaction scale provide strong support for the hypothesis that neutral processes can drive how species interact in some ecological communities, including those with strong determinisms that could rule some species out from a panel of potential interaction partners (e.g., niche forbidden links). However, this is moderated by our finding that the predictive power of species' relative abundances differed according to whether interactions occurred with native or exotic plant species, such that neutral processes were better predictors of pairwise interactions when exotic plants were involved.

Higher deviances (i.e., preferences or avoidances) of native plants from neutral predictions could result from coevolutionary constraints that evolve over long periods

of coexistence, and shape species interactions (Legendre et al. 2002, Ives and Godfray 2006, Bascompte and Jordano 2014). Some of the most extreme values of preferences observed in the native–native pairs likely result from trait-matching processes, whereas extreme avoidance values rather originate from forbidden links because of trait and/or phenological mismatches. For example, the native Bellbird (*Anthornis melanura*) has a very high avoidance value of the native Tawa tree (*Beilschmiedia tawa*), which has fruits that are too big for the Bellbird's gape size (see also Kelly et al. 2010). These results are also congruent with Peralta et al. (2020), who found in a recent study that trait-matching niche processes were stronger among species that interact with fewer partners, even more so among native species than exotics.

The fact that exotic plants interact more neutrally shows the opportunistic aspect of exotic interactions (Peralta et al. 2020). Similarly, Sazatornil et al. (2016) found that neutral hypotheses were better supported among assemblages of species originating from distinct biogeographic areas. Moreover, if relative abundances successfully predict interaction frequencies with exotic plants, then they are more likely to interact with the
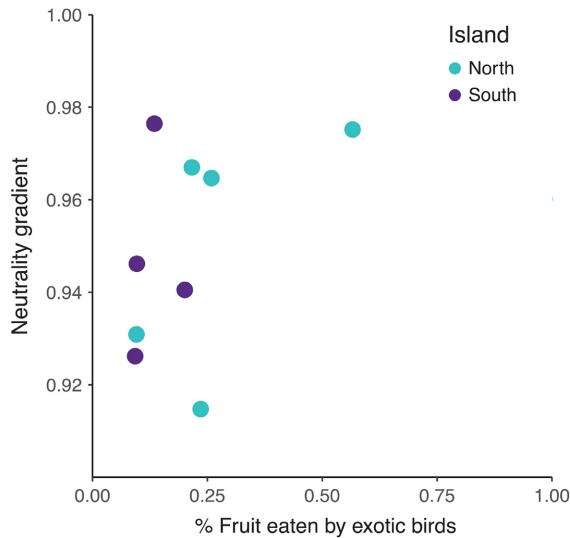
FIG. 3. Neutrality gradient vs. the gradient of exotic bird interactions. Each dot represents a site, color-coded according to the island where the plant–frugivore network was sampled. The neutrality gradient N, that is, the relative importance of neutral vs. nonneutral mechanisms in each site, is not statistically related to the percentage of exotic interactions from birds or the island sites are located in. Values of N approaching 1 are more neutral. Furthermore, N was not related to changes in plant species composition ($r = 0.12$, $P = 0.144$) or bird species composition ($r = 0.14$, $P = 0.094$) across sites.

dominant disperser species of the community, whether native or exotic. In native communities where species' relative abundance distributions are more even and no such dominance is conspicuous, however, predicting which species will benefit most from interactions with exotics is more difficult.

In contrast to the plants, native and exotic birds did not differ in how they interacted with plants: all birds interacted more neutrally with exotic plants and had higher preferences and avoidances for native plants. This is surprising, because birds would have been subjected to coevolutionary constraints in the same way plants have, and we had expected to find mirroring effects in plants and birds based on their origin status. Yet, there is a degree of exoticism among birds. For example, Silvereyes

(*Zosterops lateralis*), which we considered as a native species, were introduced in New Zealand in 1856 and have not had much time to coevolve with the native flora, such that previous studies (Williams and Karl 1996, Kelly et al. 2010) argue that they behave intermediately between endemic and exotic birds in their relative consumption of native and exotic fruits. Nevertheless, endemic birds that have had more time to coevolve have likely been successful by using available resources opportunistically. This idea is congruent with García et al. (2014), who found that networks with more exotic bird species were less specialized, and that more neutrality depicts a higher flexibility of exotic species in their choice of interaction partners.

From a conservation perspective, García et al. (2014) suggested that there is a certain rescue effect from the exotic species that helps to compensate for interactions between pairs of declining species, which has been observed in other studies as well. For example, in the Hawaiian Islands, most of the understory rainforest species now depend on the introduced birds for dispersal after having lost most of their native dispersers (Foster and Robinson 2007, Vizentin-Bugoni et al. 2019). It has been suggested that following a first phase during which exotics are competing with native species for interactions, a secondary phase may occur where specialist and rare species may indirectly benefit from having more mutualists within their network, as long as the exotic newcomers do not accumulate all the interactions and become invasive (Aizen et al. 2008, Bellingham et al. 2010, Tylianakis and Morris 2017). In New Zealand, however, the net benefit of exotic birds on native forest regeneration remains controversial (Burns 2012, MacFarlane et al. 2015) because even though they appear to be suitable dispersers, interactions between exotic birds and native plants are never observed, and evidence suggests that they instead spread seeds of weeds (Williams 2006). Moreover, the more neutral interactions of exotic plants suggests that, as native plants become more rare in a given location, they will receive fewer mutualistic interactions from exotics, and this can comprise a reproductive feedback to accelerate declining population size, potentially constituting or increasing an Allee effect (Courchamp et al. 1999).

TABLE 2. Regression coefficients for two linear models testing the network-scale relationship between the neutrality gradient N and (1) the gradient of exotic bird interactions, and (2) the island effect.

$N = 1 - \frac{D_{model}}{D_{null}}$	Estimate	S.E.	t value	Pr(>|t|)
Exotic gradient				
Intercept	0.9342	0.0130	71.948	2.64×10^{-11}
% fruits consumed by exotic birds	7.07×10^{-4}	5.13×10^{-4}	1.378	0.21
Island effect				
Intercept	0.9505	0.0108	87.944	6.47×10^{-12}
Island (South)	-0.0032	0.0162	-0.195	0.851

Note: The exotic gradient is the percentage of fruit consumptions by exotic birds (i.e., the sum of interaction frequencies involving an exotic bird divided by the sum of all interaction frequencies of that site).

Neutral mechanisms at the network level

The lack of relationship between the exotic gradient and the neutrality gradient showed that, although pairwise interactions involving exotic plants were more neutral, they were also rarer, and this effect was compensated for at the network level. This compensation indicates that communities with more exotic interactions were not overall more neutral. This could be explained if both neutral and nonneutral mechanisms are occurring simultaneously, producing the occasional opportunist native and picky exotic profiles. For example, the tendency for certain plant species to attract all bird species regardless of their origin has been reported for the native Kahikatea (*Dacrydium dacrydioides*, Beveridge 1964). In our study, in the Puhi-Puhi River site, the relative abundance of the large *B. tawa* fruits was very low. Thus, despite a high relative abundance of the kererū (*Hemiphaga novaeseelandiae*), an important disperser of large fruit/seeds, we observed no interactions with *B. tawa*, resulting in an avoidance that was close to neutral.

Furthermore, we did find a correlation between bird and tree community composition. This correspondence in the species composition of the different guilds of species, as well as the lack of scaling of neutral effects from the interaction to the network level, could imply a process of ecological fitting (Janzen 1985), which brings species into contact differently in different habitats and situations, without there being a speciation effect or a selected phenotype yet. For example, foraging for resources other than fruits (e.g., nectar) could lead bird species to switch their foraging strategy. As such, the importance of the other local species sharing interaction potential can be crucial. Donoso et al. (2017) evidenced in their study that the ecological neighborhood indirectly influenced pairwise interaction frequencies, mediated by the abundances of interacting birds, thereby also showing the context dependency associated with each ecological network. Furthermore, Guimarães et al. (2017) found that in multispecies mutualist assemblages, indirect effects could strongly influence trait evolution such that community-scale trait patterns, which govern species interactions, could result from the interplay of conflicting selection pressures.

As such, indirect effects, including those accounting for other types of interactions (e.g., competition or facilitation) could participate greatly in determining the remaining variation—which could be associated with nonneutral processes—and incorporating them into research on pairwise interactions is still in its early stages. Nonetheless, controlling for relative abundances while studying nonneutral processes remains necessary and provides insights, as conveyed by many other studies (Canard et al. 2014, Al Hammal et al. 2015).

Altogether, we provide a simple framework to account for the influence of species' relative abundances when testing other, nonneutral explanations of species' interaction frequencies. Our findings concerning the pickiness of native plants, compared with exotics, further suggest that the blending of species communities via global biotic homogenization (Lurgi et al. 2012, Gámez-Virués et al. 2015) may increasingly expose species to neutral interactions with their mutualists. This could make rare species more vulnerable to this loss of selectivity and to greater stochasticity in the identity of their interaction partner.

Our framework could easily be applied to other types of interactions, such as pollination or competition, provided that interaction frequencies and independent relative abundances are quantified. The next challenge in predicting interaction frequencies by controlling for species' relative abundances is to incorporate other agents that may be driving the nonneutral component of interactions explicitly, and in our opinion, accounting for the abundances of other species from the ecological neighborhood would provide an interesting and fruitful perspective.

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Supporting Information

Data Availability