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3 Tricky partners: native plants show stronger interac-
4 tion preferences than their exotic counterparts
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20 **KEYWORDS**

21 Abundance – frugivory – mutualist network – neutrality – New Zealand – scaling – seed dis-
22 persal – birds

23 **ABSTRACT**

24 In ecological networks, neutral predictions suggest that species' interaction frequencies are
25 proportional to their relative abundances. Deviations from neutral predictions thus correspond
26 to interaction preferences (when positive) or avoidances (when negative), driven by non-
27 neutral (e.g. niche-based) processes. Exotic species interact with many partners with which
28 they have not coevolved, and it remains unclear whether this systematically influences the
29 strength of neutral processes on interactions, and how these interaction-level differences scale
30 up to entire networks. To fill this gap, we compared interactions between plants and frugivor-
31 ous birds at nine forest sites in New Zealand varying in the relative abundance and composi-
32 tion of native and exotic species, with independently sampled data on bird and plant abun-
33 dances from the same sites. We tested if the strength and direction of interaction preferences
34 differed between native and exotic species. We further evaluated whether the performance of
35 neutral predictions at the site level was predicted by the proportion of exotic interactions in
36 each network from both bird and plant perspectives, and the species composition in each site.
37 We found that interactions involving native plants deviated more strongly from neutral pre-
38 dictions than did interactions involving exotics. This "pickiness" of native plants could be
39 detrimental in a context of global biotic homogenization where they could be increasingly
40 exposed to novel interactions with neutrally-interacting mutualists. However, the realization
41 of only a subset of interactions in different sites compensated for the neutrality of interactions
42 involving exotics, so that neutral predictions for whole networks did not change systematical-
43 ly with the proportion of exotic species nor species composition. Therefore, the neutral and
44 niche processes that underpin individual interactions may not scale up to entire networks.
45 This shows that seemingly simplistic neutral assumptions entail complex processes and can
46 provide valuable understanding of community assembly or invasion dynamics.

47 INTRODUCTION

48

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

60 Second, interaction frequencies can be determined by factors that are inherent to the
61 species' identity. Numerous biological constraints might favor frequent interactions between
62 particular pairs of species, or restrain others such that they might avoid interacting altogether
63 due to morphological, phenological or behavioral incompatibilities (Jordano et al. 2003). For
64 example, the body size of consumer species is one of the predominant filters for trophic inter-
65 actions (Alcántara and Rey 2003, Brose et al. 2017, Grass et al. 2018). At the extreme, highly
66 specialized species such as parasites or obligate mutualists may interact exclusively within a
67 limited range of partners (e.g. ant-plant mutualisms as in Riginos et al. 2015). There are many
68 more examples of direct interaction filtering based on species and their traits (e.g. Dehling et
69 al., 2014), which are known to strongly constrain interaction structure (Cohen et al. 2003,
70 Stouffer 2010). More recently, the role of indirect interactions and ecological neighborhood
71 (*sensu* Donoso et al., 2017) have also been proposed to regulate interactions (Poisot et al.

72 2015), and notably found that indirect effects can be as important as direct interactions in
73 shaping the structure of mutualistic networks through coevolutionary processes (Guimarães et
74 al. 2017). Hence, deviations from interaction frequencies predicted based on species abun-
75 dances are common (Dáttilo et al. 2014, Vizentin-Bugoni et al. 2014, Isbell et al. 2017,
76 Bender et al. 2018, Peralta et al. 2020).

77 Consequently, the frequency of species interactions can be determined by two com-
78 ponents: first, a component that can be predicted based on relative abundances, which can be
79 considered to result from neutral processes (Volkov et al. 2003, Krishna et al. 2008, Vázquez
80 et al. 2009, Canard et al. 2014). In the extreme case, neutrality supposes that interactions are
81 systematically realized upon an encounter between two individuals of different trophic levels,
82 such that there is no filtering depending on species identity or traits (i.e. no niche differentia-
83 tion). The second component comprises interaction frequencies deviating from those predict-
84 ed by mass action (i.e. from neutrality), such that there is niche differentiation. An interaction
85 frequency that occurs more frequently than expected based on the relative abundances of a
86 species pair would thus correspond to an interaction preference, whereas an interaction that
87 occurs less often than expected depicts an avoidance (Staniczenko et al. 2013, García et al.
88 2014). This perspective allows us to test hypotheses regarding the frequency of interactions
89 while controlling for species relative abundances, by allowing interaction frequencies to be
90 partitioned into neutral and non-neutral determinants.

91 This partitioning is important, as it is likely that both neutral and non-neutral process-
92 es occur simultaneously to shape interaction frequencies within a community rather than be-
93 ing mutually exclusive (Chave et al. 2002, Leibold and McPeck 2006). In fact, the continuum
94 theory of network structure (Gravel et al. 2006) posits that neutral processes should govern
95 the nature and strength of given interactions between partners, whereas niche processes such
96 as niche-forbidden links (Jordano et al. 2003, González-Varo and Traveset 2016) should gov-

97 ern whether the encounter takes place at all. This perspective raises two key questions: 1) it is
98 unclear whether there are systematic differences in the relative intensities of niche vs. neutral
99 processes across species or systems, which could explain why some conform to neutral hy-
100 potheses better than others; 2) even if we understand why particular interactions may be driv-
101 en more by niche vs. neutral processes, it remains unclear whether such interaction-level dif-
102 ferences can be summed across a whole community. Specifically, it is necessary to under-
103 stand whether neutrality as a process affects all species of a community in a similar way, or if
104 it affects some species differently based on their identity and community composition.

105 In this study, we develop a framework (initialized by García et al. 2014 and built from
106 the logic of Staniczenko et al. 2013) that incorporates interaction preferences to understand
107 how the separate neutral and non-neutral components of interaction frequencies change be-
108 tween species and across networks. We apply this framework to interaction networks that
109 include recent introduction of exotic species into native assemblages, as these systems are
110 especially prone to alter their balance of neutral and niche processes (Nuismer et al. 2018,
111 Trøjelsgaard et al. 2019, Vizentin-Bugoni et al. 2019). Namely, coevolution between native
112 species often drives them to develop more extreme traits (Guimaraes et al. 2011, Mouillot et
113 al. 2013, Nagelkerke and Rossberg 2014), such that we hypothesize that interaction prefer-
114 ences and avoidances will be stronger between pairs of native species. In contrast, exotic spe-
115 cies are expected to have more generalist traits, which would allow them to interact with a
116 larger proportion of available species (Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008,
117 García et al. 2014). Thus, if they are sufficiently abundant, we hypothesize that interactions
118 involving exotic species will more closely match neutral predictions. Here, we focus on the
119 paired interactions between fleshy-fruited plants and frugivorous birds in a set of New Zea-
120 land forest sites with different relative abundances and compositions of native and exotic
121 species (García et al. 2014). We first investigate preferences at the interaction scale, to test

122 whether the exotic or native status of birds and plants predicts the contributions of each inter-
123 action to neutral or non-neutral processes. We then explore whether these results scale up to
124 whole networks to determine whether the relative importance of neutral vs. non-neutral pro-
125 cesses for each site is correlated with a gradient in the abundance of exotic bird interactions
126 or with bird or plant community composition in each site.

127

128 **METHODS**

129 **Study system and plant-frugivore networks.**

130 In a previous study, García et al. 2014 recorded frugivorous interactions between bird
131 and fleshy-fruited tree species from low-altitude, conifer-broadleaf forests in New Zealand.
132 They studied nine forest patches located around Wellington urban areas in the North Island (5
133 sites) and near Kaikoura in the South Island (4 sites, see SI Appendix 1 for a map with site
134 locations), that held a wide array of species from both trophic levels and encompassed a gra-
135 dient in the relative abundance of exotic birds and plants. In each site, a single sampling tran-
136 sect of approx. 1 km length was established along walking trails across the forest. On each
137 transect, from early February to late May 2012, which corresponds to the main ripening sea-
138 son of these fleshy-fruited species (Williams and Karl 1996), they conducted fortnightly fruit
139 counts (number of fruits on individual fruiting plants), along four sections of 100 m x 4 m
140 separated by at least 100 m one from each other. The absolute abundance of fruits was esti-
141 mated as the average number of fruits per sampling round (3-4 censuses per site) for each
142 plant species. They also estimated bird abundances through censuses carried out every 2-3
143 days at each site, between 8:00 and 16:00 (14-21 censuses per site). During the census, the
144 complete transect was walked, counting all individuals of the different bird species heard or
145 seen in a 10-m wide band at both sides of the walking trail. For each bird species at each site,

146 the absolute abundance was standardized by sampling time, and hence calculated as an en-
147 counter rate by means of the cumulative number of observations per 10 hours.

148 Interactions were recorded as the number of fruits consumed per bird and per plant
149 species surveyed as standardized observations which, importantly, were conducted independ-
150 ent of the estimation of species abundances. Observations of fruit consumption by birds were
151 made at each site while walking each complete transect at a constant speed (approx. 1-h).
152 Surveys were conducted immediately after the bird censuses, and lasted at least 15 min from
153 the end of the census (14-21 rounds per site). On each round, once a perching bird was de-
154 tected within a 5-m wide band at both sides of the walking trail, it was observed until it was
155 lost in the foliage. Each observation of a given bird eating was considered to be an event of
156 frugivory. For each site, the number of fruits consumed per bird and plant species was esti-
157 mated as the sum of fruit consumptions across all observation rounds. A plant-bird frugivore
158 interaction network was built for each of the nine study plots (see suppl. online material, fru-
159 givory_data.csv for a list of species, their interaction frequencies, relative abundances and
160 origin status).

161 Across all sites, interaction networks comprised 13 bird species (3 exotic and 10 na-
162 tive) interacting with 42 plant species (6 exotic and 36 native, see SI for a complete list of
163 species and interaction frequencies). Overall, we used data collected during 126 sampling
164 hours, during which 887 frugivory events were detected and 4655 fruits were consumed.
165 From the 13 bird species, we discarded the native species *Nestor meridionalis* because it oc-
166 curred only once in all sites, and was never observed consuming fruit. Despite the low exotic
167 to native species ratio, interactions involving exotic birds accounted for an average of 21%
168 (± 15) of all interactions across sites, and exotic birds interacted with an average of 32% (± 13)
169 of all plant species of a given site. Interacting with a wide spectrum of species can be a hint
170 of neutrality at the interaction scale, as we will see in the following section. The fruits of ex-

171 otic plants represented 5.9% of fruit consumptions, from which native and exotic birds ac-
172 counted for 4.98 and 0.92%. The percentage of fruit consumed by exotic birds per site ranged
173 from 9.3to 56.7%, and the percentage of fruits of exotic plants being consumed ranged from 0
174 to 13.7%.

175

176

177 **Estimating interaction preferences**

178 The framework from García et al. (2014) employs a Poisson regression to predict ob-
179 served interaction frequencies F_{ij} between two classes of species i and j based on their abun-
180 dances A_i and A_j :

$$181 \quad F_{ij} = e^{\log(C)+\log(A_i)+\log(A_j)+\log(\gamma_{ij})}, (1)$$

182 where F_{ij} follows a Poisson distribution, γ_{ij} corresponds to ‘interaction preferences’ (i.e. the
183 model residuals), and the constant C to an estimated intercept related to species’ overall
184 tendencies to interact. The leading component of the interaction
185 cies, $e^{\log(C)+\log(A_i)+\log(A_j)}$, corresponds to the mass-action term (Staniczenko et al. 2013),
186 which has been rearranged above to match the log link function of the Poisson regression. It
187 implies that the frequency of an interaction is directly proportional to the product of the rela-
188 tive abundances of each interaction partner, and thus $\gamma_{ij} = 1$ (zero in log scale) would corre-
189 spond to perfectly neutral expectations whereby all variation in interaction frequencies is ex-
190 plained by mass action. When one has censuses of bird and plant species’ relative abundances
191 (A_i and A_j) as well as independent estimates of fruit consumption to quantify interaction fre-
192 quencies F_{ij} , the only parameter to be inferred by this model is the intercept C , and interac-
193 tion preferences γ_{ij} emerge from the residuals in log space.

194

195 **Inclusion of missing interactions**

196 As is often the case in community ecology, our interaction matrices included many
197 zero values (two species not observed to interact), which are known to cause overdispersion
198 in Poisson models. In addition, absences of interactions complicate the discrimination of true
199 absences (i.e. when two co-occurring species never interact no matter their abundances) from
200 false absences (i.e. rare interactions less likely to be observed, e.g. Martin et al. 2005, Cirtwill
201 et al. 2019). True absences typically correspond to ‘niche forbidden links’ (Jordano et al.
202 2003) and can reveal niche- or morphologically-driven avoidances between species, whereas
203 false absences directly depend on species abundances, and have been conceptualized as ‘neu-
204 tral forbidden links’ (Canard et al., 2012). Previous studies using this framework
205 (Staniczenko et al. 2013, García et al. 2014) chose to discard these missing interactions. We
206 considered, however, that an absence of interactions between co-occurring species could car-
207 ry important information regarding the estimation of interaction preferences γ_{ij} (Martin et al.
208 2005). For example, the lack of interaction between two very abundant species could reveal
209 interaction avoidance, which would provide strong evidence for non-neutrality.

210 To incorporate zero-frequency (unobserved) interactions in our model, we extended
211 the framework from García et al. (2014) in equation (1) to use a zero-inflated negative bino-
212 mial model (ZINB, *zeroinfl* function, “pscl” package version 1.4.9, Zeileis et al. 2008, R Core
213 Team 2020) instead of a standard Poisson regression, for which the incorporation of the un-
214 observed interactions increased overdispersion. In ZINB models, parameters are estimated
215 from two components, based on different distributions.

216 The first component has a binomial distribution and corresponds to the probability of
217 observing a zero rather than an integer count. The second component has a negative bino-
218 mial distribution, and generates ‘counts’, among which zeroes may also occur. The purpose
219 for such a framework is to help differentiate ‘true’ zeroes – in our case the absence of interac-

220 tion between two abundant species, i.e. an avoidance – from ‘false’ zeroes, or the failure of
221 observing an interaction due to species rarity, the so-called ‘neutral-forbidden links’.

222 In other words, compared to a regular Poisson regression, the ZINB also has a log link
223 function, but re-adjusts the model parameters in the negative-binomial component—namely
224 the intercept, C_{nb} —based on the probability of observing a zero from the binomial compo-
225 nent. Following equation (1), we use this C_{nb} estimate to reevaluate the interaction prefer-
226 ences γ_{ij} :

$$227 \quad F_{ij} = e^{\log(C_{nb})+\log(A_i)+\log(A_j)+\log(\gamma_{ij})} \quad (2)$$

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

$$230 \quad \hat{F}_{ij} = e^{\log(C_{nb})+\log(A_i)+\log(A_j)}, \quad (3)$$

231 with \hat{F}_{ij} following a negative binomial distribution. This adjustment takes us a step further in
232 evaluating interaction preferences after controlling both for the mass-action effect (relative
233 abundances) and for the neutral forbidden links (incorporation of the zero-frequencies from
234 the observed data), which we will henceforth refer to as ‘neutral predictions’. In our analysis,
235 we used ZINB models with the observed interaction frequencies and species relative abun-
236 dances of each site to estimate the intercept C_{nb} for each site. In the following sections, we
237 then use C_{nb} in equation (3) to calculate interaction preferences at the interaction level and a
238 neutrality gradient at the network level for each site.

239

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

241 Neutral processes provide a mechanistic prediction of how frequently two species
242 should interact. As such, a deviation from this prediction results from alternative, non-neutral
243 processes that influence how often two species really interact. Within each site and for each

244 pairwise interaction, we estimated how well the relative abundances of species pairs predict-
245 ed their observed interaction frequencies by calculating each observed frequency's deviance
246 (d_{ij}) from neutral predictions, i.e. the deviance residuals from the generalized linear model in
247 equation (2). The mathematical calculation of these deviance residuals is explained in the SI
248 (Appendix 2).

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

257

258 **Are interactions involving exotic species more neutral?**

259 As mentioned previously, we hypothesize that the coevolutionary history could
260 strongly influence how often organisms interact, and that this signal can be measured in in-
261 teraction preferences and avoidances. We ran a linear mixed effects model (LME, *lme* func-
262 tion from the “nlme” package, Pinheiro et al. 2015), using $\log(d_{ij})$ as the response, two cate-
263 gorical variables, bird (native or exotic) and plant (native or exotic), as fixed effects, and an
264 interaction effect. We also added a site random effect to control for non-independence of in-
265 teraction frequencies across networks.

266

267 **Avoidances**

268 As noted earlier, deviance residuals d_{ij} are highest both when two rare species inter-
269 act frequently (i.e. strongly prefer each other) *and* when two abundant species seldom interact
270 (i.e. strongly avoid each other). Because it is biologically meaningful to distinguish prefer-
271 ences from avoidances and to help when visualize the deviances when plotting them (but not
272 for the analysis), we can create signed deviance residuals with $\text{sign}(F_{ij} - \hat{F}_{ij}) \times d_{ij}$, where
273 $\text{sign}(x) = 1$ if $x > 0$ and $\text{sign}(x) = -1$ otherwise. After this transformation, plotted values
274 at 0 still correspond to perfectly neutral interactions, all values less than 0 indicate avoidanc-
275 es, and all values greater than 0 indicate preferences.

276

277 **Scaling up to network level: Quantifying the importance of neutral processes in** 278 **each site**

279 The deviance residuals d_{ij} are a measure of the accuracy of the neutral predictions at
280 the interaction level. These predictions can further be combined within each site to evaluate
281 the global fit of the neutral model across the different sites. We calculated the global deviance
282 D_{ZINB} of the model from equation (3) as the sum of the d_{ij} in each site (see SI, Appendix 2
283 for mathematical details).

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

$$288 \quad \hat{F}_{ij}^{null} = e^{C_{null} + \varepsilon_{ij}}, \quad (4)$$

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

292 We then used a pseudo R^2 measure we defined as $N = 1 - \frac{D_{ZINB}}{D_{null}}$ to evaluate the per-
293 formance of the estimated interaction frequencies \hat{F}_{ij} (equation 3 model) compared with the
294 null \hat{F}_{ij}^{null} (equation 4). N is bounded between 0 and 1, where values approaching 1 indicate
295 that the total deviance D_{ZINB} of the equation 3 model is much smaller than D_{null} , suggesting
296 that including relative abundances to predict interaction frequencies results in a better estima-
297 tion of \hat{F}_{ij} and therefore that neutral processes are occurring. Conversely, values of N closer
298 to 0 would suggest similar values of D_{ZINB} and D_{null} , such that interaction frequencies are
299 similarly well predicted when ignoring species' relative abundances altogether, hence indicat-
300 ing that neutral processes are absent. Moreover, this approach allowed us to place each site
301 along a neutrality "gradient", whereby the local value of N quantifies the strength of neutral
302 processes relative to other non-neutral drivers.

303

304 **Exotic gradient and species composition to predict the neutrality gradient**

305 We tested several hypotheses involving species' origin to explain why neutral pro-
306 cesses might be stronger drivers of interaction frequencies in some sites and less so in others.
307 We investigated whether the neutrality gradient N could be explained by several measures of
308 exoticism in our networks. Hence, for each site, we calculated i) the percentage of exotic bird
309 interactions as the sum of interaction frequencies involving an exotic bird divided by the sum
310 of all interaction frequencies of that site; ii) the percentage of plants species interacting with
311 exotic birds, i.e. the number of plant species interacting with an exotic bird divided by the
312 total number of plants species in that site. These two measures were highly correlated ($r =$

313 0.75, p -value = 0.02) so we discarded the latter. We did not calculate the equivalent measures
314 from the exotic plant perspective (i.e. the proportion of exotic plant interactions or bird spe-
315 cies interacting with exotic plants) because of the absence of exotic plants in 2 of our sites.
316 Furthermore, since sites were located on the two islands with marked differences in their iso-
317 lation from urbanized areas, we also tested for a geographical correlation between sites by
318 testing an “Island” variable. We used two separate linear models to test whether the neutrality
319 gradient was related to the exotic bird gradient and to the island the sites were located (North
320 or South Island).

321 If the exotic gradient could be one way to explain the neutrality gradient N across
322 sites, so could species identities: some species might have stronger preferences while others
323 have none, regardless of the origin of their interaction partners. If so, the composition of both
324 bird and plant communities could also affect the relative importance of the neutral versus
325 non-neutral processes at a given site. We would expect communities of similar composition
326 to show similar values along the N gradient. Thus, we tested whether differences in the neu-
327 trality gradient N across sites were related to differences in their species composition. We
328 calculated Jaccard dissimilarities in the composition of plant and bird communities between
329 sites. We then used Mantel tests with the Kendall correlation to evaluate whether dissimilari-
330 ties in plant and bird species composition were correlated with the pairwise Euclidean dis-
331 tances between the sites based on the N values. Still using Mantel tests, we also tested wheth-
332 er plant community composition was correlated to bird community composition.

333

334

335 RESULTS

336 Are interactions involving exotic species more neutral?

337 The LME model testing whether the origin status of plant and bird species and their
338 interactive effect influenced their contribution to non-neutral processes showed that exotic
339 plants had significantly smaller the interaction deviances d_{ij} than native ones, as the latter
340 showed significant deviances from neutral predictions (Table 1). Conversely, the origin of
341 birds did not significantly affect the deviances of their interactions, nor did it impact the in-
342 fluence of plant origin on deviances through the interaction between the origin status of the
343 two. Nevertheless, the d_{ij} were highest for interactions between native pairs, and lowest for
344 the exotic ones (Figure 1), indicating that the relative abundances of native plants were not
345 overall as good at predicting interaction frequencies as were those of exotic ones. Moreover,
346 the frequency distribution of the signed d_{ij} for interactions involving native plants had more
347 extreme values of d_{ij} , especially on the preferences side, than did the distribution for exotic
348 plants (Figure 2). Contrastingly, the d_{ij} for interactions involving exotic plants displayed a
349 distribution of avoidances skewed towards weaker, increasingly neutral values. In both
350 groups, however, the proportion of avoidances was much higher than the proportion of pref-
351 erences (see also SI Appendix 3 for further details about avoidances).

352

353

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

355 From the interaction-level contributions of deviance residuals to non-neutral mecha-
356 nisms, we tested whether these patterns scaled up to the site level. We found that the global
357 deviance from the neutral model from equation (3) D_{model} was lower than that of the null
358 model D_{null} in all sampled networks : neutrality gradient N values were all between 0.9 and

359 1 (Figure 3). In each network, species relative abundances more accurately predicted interac-
360 tion frequencies than did the mean number of interactions (null model prediction), suggesting
361 that non-neutral mechanisms were weak relative to the abundance-driven ones.

362 Testing whether this neutrality gradient was related to the gradient of exotic bird in-
363 teractions or to the island effect did not reveal any significant relationships (Table 1, Figure
364 3). As such, neither the percentage of fruit consumptions by exotic birds nor the location of
365 the sites on the North and South Islands influenced how well bird and plant relative abun-
366 dances predicted interaction frequencies in a given site.

367 Finally, testing species identity effects revealed that shifts in the species composition
368 of birds were positively correlated with shifts in species composition of the plants (Mantel $r =$
369 0.32 , $p = 0.005$). The neutrality gradient N was, however, neither related to changes in plant
370 species composition ($r = 0.12$, $p = 0.144$) nor bird species composition ($r = 0.14$, $p = 0.094$)
371 across sites.

372

373 **DISCUSSION**

374 Here we provided a new framework to evaluate how neutral and non-neutral process-
375 es drive pairwise species interactions and whole networks. Our results revealed that interac-
376 tions involving native plants deviated most from neutral expectations, whereas the origin sta-
377 tus of birds did not strongly influence how species relative abundances predicted interaction
378 frequencies. Furthermore, these results did not scale up to entire networks: despite the differ-
379 ences in the strength of the neutral vs non-neutral drivers in each site (neutrality gradient N),
380 neither the gradient of the percentage of fruits consumed by exotic birds, nor species identity
381 effects explained these differences in a systematic way. Hence, our results suggest that neu-
382 tral predictions of pairwise interactions of exotic species could potentially be a good baseline

383 to estimate invasion dynamics or for conservation purposes, but that community-scale predic-
384 tions do not systematically emerge from these predictions.

385

386 **Mechanisms driving species interactions for native and exotic species**

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

394 Higher deviances (i.e., preferences or avoidances) of native plants from neutral pre-
395 dictions could result from coevolutionary constraints that evolve over long periods of coex-
396 istence, and shape species interactions (Legendre et al. 2002, Ives and Godfray 2006,
397 Bascompte and Jordano 2014). Some of the most extreme values of preferences observed in
398 the native-native pairs likely result from trait-matching processes, whereas extreme avoid-
399 ance values rather originate from forbidden links due to trait and/or phenological mismatches.
400 For example, the native Bellbird (*Anthornis melanura*) has a very high avoidance value of the
401 native Tawa tree (*Beilschmiedia tawa*), which has fruits that are too big for the Bellbird's
402 gape size (see also Kelly et al., 2010). These results are also congruent with Peralta et al.
403 (2020), who found in a recent study that trait-matching niche processes were stronger among
404 species that interact with fewer partners, and even more so among natives species than exot-
405 ics.

406 The fact that exotic plants interact more neutrally shows the opportunistic aspect of
407 exotic interactions (Peralta et al. 2020). Similarly, Sazatornil et al. (2016) found that neutral

408 hypotheses were better supported among assemblages of species originating from distinct
409 biogeographic areas. Moreover, if relative abundances successfully predict interaction fre-
410 quencies with exotic plants, then they are more likely to interact with the dominant disperser
411 species of the community, whether native or exotic. In native communities where species'
412 relative abundance distributions are more even and no such dominance is conspicuous, how-
413 ever, predicting which species will benefit most from interactions with exotics is more diffi-
414 cult.

415 In contrast to the plants, native and exotic birds did not differ in how they interacted
416 with plants: all birds interacted more neutrally with exotic plants and had higher preferences
417 and avoidances for native plants. This is surprising since birds would have been subjected to
418 coevolutionary constraints in the same way plants have, and we had expected to find mirror-
419 ing effects in plants and birds based on their origin status. Yet, there is a degree of exoticism
420 among birds. For example, Silvereyes (*Zosterops lateralis*), which we considered as a native
421 species, were introduced in New Zealand in 1856 and have not had much time to coevolve
422 with the native flora, such that previous studies (Williams and Karl 1996, Kelly et al. 2010)
423 argue that they behave intermediately between endemic and exotic birds in their relative con-
424 sumption of native and exotic fruits. Nevertheless, endemic birds that have had more time to
425 coevolve have likely been successful by using available resources opportunistically. This idea
426 is congruent with García *et al.* (2014) who found that networks with more exotic bird species
427 were less specialized, and that more neutrality depicts a higher flexibility of exotic species in
428 their choice of interaction partners.

429 From a conservation perspective, García et al. (2014) suggested that there is a certain
430 rescue effect from the exotic species that help to compensate for interactions between pairs of
431 declining species, which has been observed in other studies as well. For example, in the Ha-
432 wai'ian Islands, most of the understory rainforest species now depend the introduced birds for

433 dispersal after having lost most of their native dispersers (Foster and Robinson 2007,
434 Vizentin-Bugoni et al. 2019). It has been suggested that following a first phase during which
435 exotics are competing with native species for interactions, a secondary phase may occur
436 where specialist and rare species may indirectly benefit from having more mutualists within
437 their network, as long as the exotic newcomers do not accumulate all the interactions and
438 become invasive (Aizen et al. 2008, Bellingham et al. 2010, Tylianakis and Morris 2017). In
439 New Zealand, however, the net benefit of exotic birds on native forest regeneration remains
440 controversial (Burns 2012, MacFarlane et al. 2015) because even though they appear to be
441 suitable dispersers, interaction between exotic birds and native plants are never observed, and
442 evidence suggests that they instead spread seeds of weeds (Williams, 2006). Moreover, the
443 more neutral interactions of exotic plants suggests that, as native plants become more rare in
444 a given location, they will receive fewer mutualistic interactions from exotics, and this can
445 comprise a reproductive feedback to accelerate declining population size, potentially consti-
446 tuting or increasing an Allee effect (Courchamp et al. 1999).

447

448 **Neutral mechanisms at the network level**

449 The lack of relationship between the exotic gradient and the neutrality gradient showed that,
450 although pairwise interactions involving exotic plants were more neutral, they were also rar-
451 er, and this effect was compensated for at the network level. This compensation indicates that
452 communities with more exotic interactions were not overall more neutral. This could be ex-
453 plained if both neutral and non-neutral mechanisms are occurring simultaneously, producing
454 the occasional “opportunistic native” and “picky exotic” profiles. For example, the tendency
455 for certain plant species to attract all bird species regardless of their origin has been reported
456 for the native *Kahikatea* (*Dacrydium dacrydoides*, Beveridge 1964). In our study, in the
457 Puhi-Puhi River site, the relative abundance of the large *B. tawa* fruits was very low. Thus,

458 despite a high relative abundance of the kererū (*Hemiphaga novaeseelandiae*), an important
459 disperser of large fruit/seeds, we observed no interactions with *B. tawa* resulting in an avoid-
460 ance that was close to neutral.

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

475 As such, indirect effects, including those accounting for other types of interactions
476 (e.g. competition or facilitation) could participate greatly in determining the remaining varia-
477 tion - which could be associated with non-neutral processes – and incorporating them into
478 research on pairwise interactions is still in its early stages. Nonetheless, controlling for rela-
479 tive abundances while studying non-neutral processes remains necessary and provides in-
480 sights, as conveyed by many other studies (e.g. Canard et al. 2014; Al Hammal et al. 2015).

481 Altogether, we provide a simple framework to account for the influence of species'
482 relative abundances when testing other, non-neutral explanations of species interaction fre-

483 quencies. Our findings concerning the pickiness of native plants, compared with exotics, fur-
484 ther suggest that the blending of species communities via global biotic homogenization
485 (Lurgi et al. 2012, Gámez-Virués et al. 2015) may increasingly expose species to neutral in-
486 teractions with their mutualists. This could make rare species more vulnerable to this loss of
487 selectivity and to greater stochasticity in the identity of their interaction partner.

488 Our framework could easily be applied to other types of interactions, such as pollina-
489 tion or competition, provided that interaction frequencies and independent relative abundanc-
490 es are quantified. The next challenge in predicting interaction frequencies by controlling for
491 species relative abundances is to explicitly incorporate other agents which may be driving the
492 non-neutral component of interactions, and in our opinion, accounting for the abundances of
493 other species from the ecological neighborhood would provide an interesting and fruitful per-
494 spective.

495

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508

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670 **TABLES AND FIGURE LEGENDS**

671 **Table 1. Log-linear mixed effects model estimates of bird and plant origin effects on the interaction deviances d_{ij}** (i.e.

672 deviances from neutral predictions which can be either preferences or avoidances). Site was included as a random effect.

673 Significant effects are presented in bold. The intercept condition is exotic plant and exotic bird.

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	<i>Value</i>	<i>Std. Error</i>	<i>DF</i>	<i>t-value</i>	<i>p-value</i>
Intercept	-2.3997	0.2320	1145	-10.3442	0.0000
Native plant	0.8246	0.2243	1145	3.6772	0.0002
Native bird	0.2740	0.2797	1145	0.9795	0.3275
Native plant : Native bird	-0.1289	0.2918	1145	-0.4417	0.6588

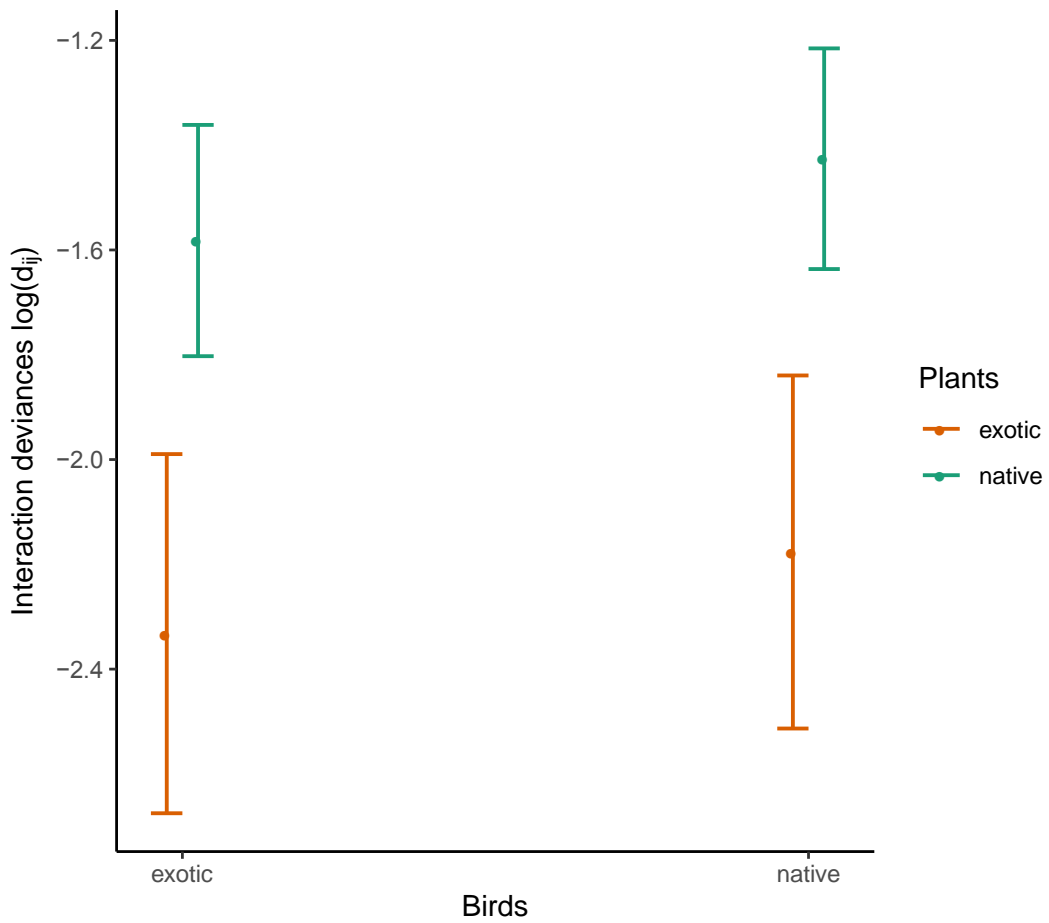
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Table 2: Regression coefficients for two linear models testing the network-scale relationship between the neutrality gradient N and i) the gradient of exotic bird interactions, and ii) the Island effect. The exotic gradient is the percentage of fruit 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).

$N = 1 - \frac{D_{model}}{D_{null}}$	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>Pr(> t)</i>
<i>Exotic Gradient</i>				
Intercept	0.9342	0.0130	71.948	2.64e-11
% fruits consumed by exotic birds	7.07e-4	5.13e-4	1.378	0.21
<i>Island effect</i>				
Intercept	0.9505	0.0108	87.944	6.47e-12
Island (South)	-0.0032	0.0162	-0.195	0.851

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686 **Figure 1: Interaction plot from the log-linear mixed effects model showing the effects of bird and plant origin on the**

687 **interaction deviances d_{ij} .** Predicated values of the interaction deviances are shown with 95% CI. Both exotic birds and

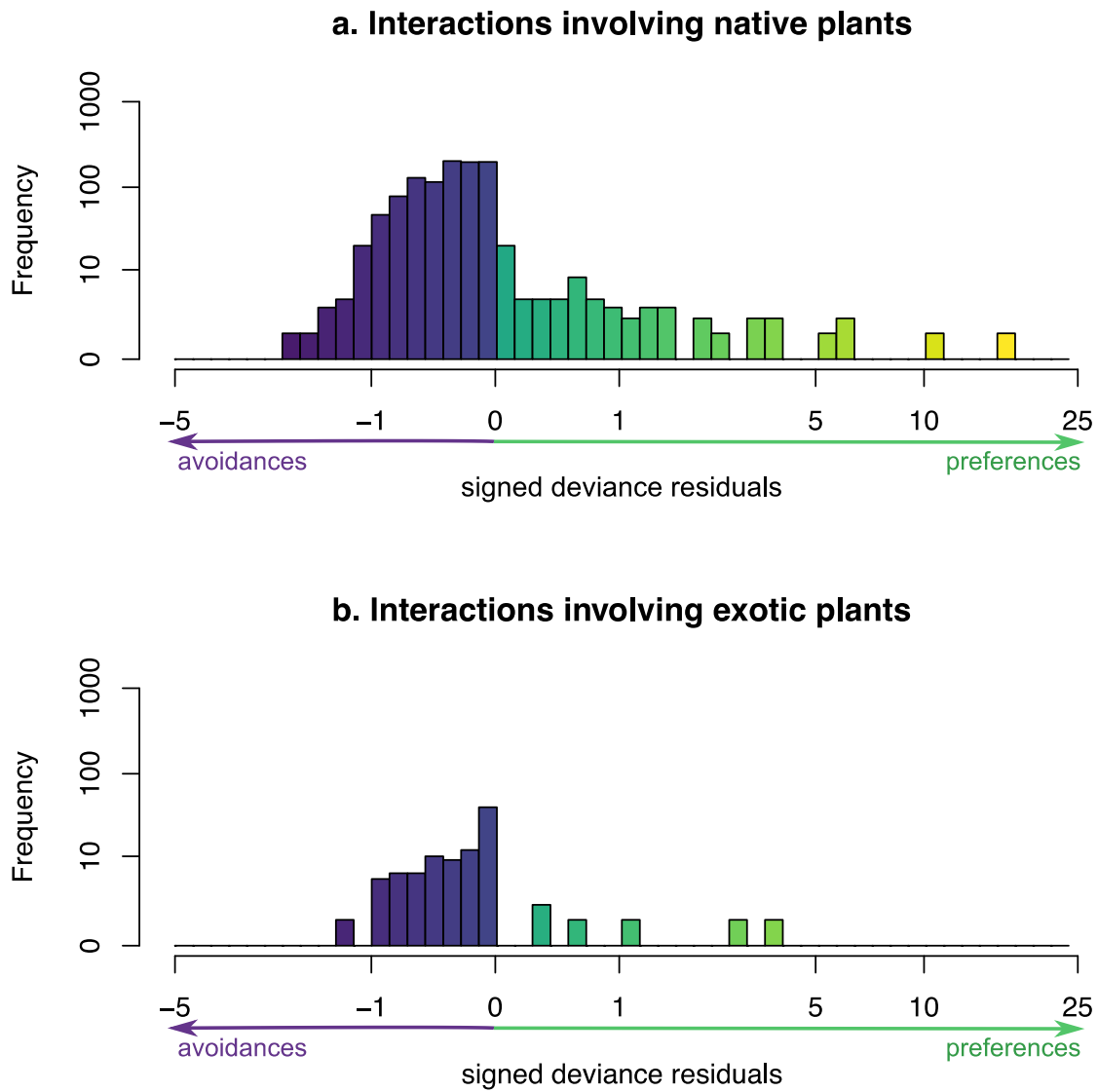
688 plants had smaller d_{ij} than their native counterparts, indicating more neutral interactions, but this effect was significant in

689 plants only. The interaction effect between bird and plant origin was not significant either (see Table 1 for further details).

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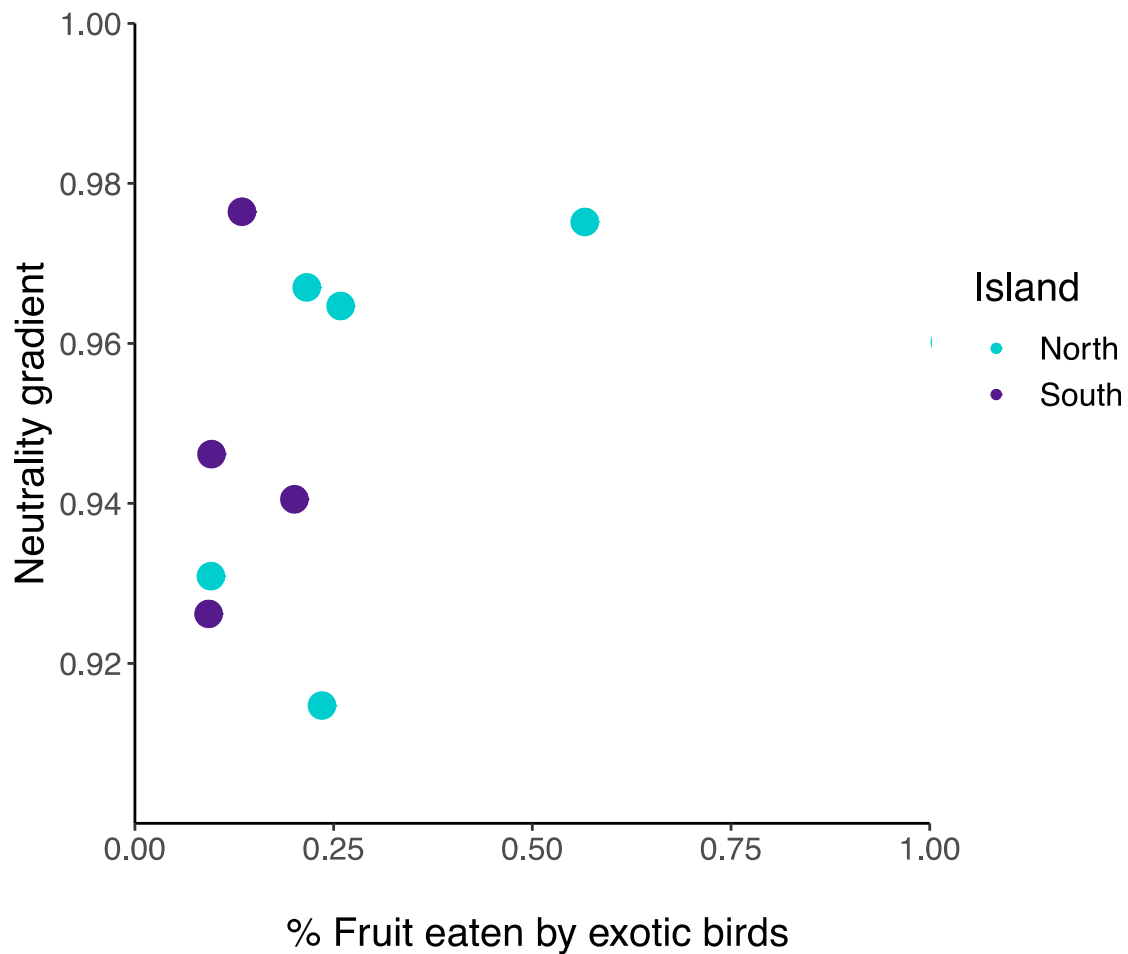
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692 **Figure 2: Frequency distributions of interaction preferences (positive values) and avoidances (negative values).** The
693 strength of preferences and avoidances increases according to the green and purple arrows, respectively. Values of 0 indicate
694 perfect neutrality (i.e. interaction frequencies that do not differ from expectations based solely on species abundances).



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Figure 3: Neutrality gradient versus 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 , i.e. the relative importance of neutral versus non-neutral 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 neither 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.