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Exotic birds increase generalization and compensate for native bird decline in plant–frugivore assemblages

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Summary

1. Exotic species are thought to alter the structure of natural communities and disrupt ecosystem functioning through invasion. Nevertheless, exotic species may also provide ecological insurance when they contribute to maintain ecosystem functions after the decline of native species following anthropogenic disturbance.

2. Here, this hypothesis is tested with the assemblage of frugivorous birds and fleshy-fruited plants of New Zealand, which has suffered strong historical declines in native birds while simultaneously gaining new frugivores introduced by European settlers.

3. We studied the plant–frugivore assemblage from measures of fruit and bird abundances and fruit consumption in nine forest patches, and tested how this changed across a gradient of relative abundance of exotic birds. We then examined how each bird species' role in the assemblage (the proportion of fruits and the number of plant species consumed) varied with their relative abundance, body size and native/exotic status.

4. The more abundant and, to a lesser extent, larger birds species consumed a higher proportion of fruits from more plant species. Exotic birds consumed fruits less selectively and more proportionate to the local availability than did native species. Interaction networks in which exotic birds had a stronger role as frugivores had higher generalization, higher nestedness and higher redundancy of plants.

5. Exotic birds maintained frugivory when native birds became rarer, and diversified the local spectrum of frugivores for co-occurring native plants. These effects seemed related to the fact that species abundances, rather than trait-matching constraints, ultimately determined the patterns of interactions between birds and plants. By altering the structure of plant–frugivore assemblages, exotic birds likely enhance the stability of the community-wide seed dispersal in the face of continued anthropogenic impact.

Key-words: abundance, ecological insurance, frugivory, mutualistic networks, New Zealand, plant–animal interactions, redundancy, seed dispersal, *Turdus merula*

Introduction

Biological invasions, i.e. the human-assisted introductions of exotic species that disrupt native communities, are considered a major global threat to biodiversity and community interactions (Sala *et al*. 2000; Tylianakis *et al*. 2008). Despite this relevance, we are still far from identifying precisely how the disrupting effects of exotic species scale up to ecosystems (Simberloff 2011). More generally, the consideration of exotics as invaders should be judged based on their functioning within the ecosystems where they have been introduced (Davis *et al*. 2011), which often depends on their ability to exploit available resources. Many exotic animals are particularly successful in new communities, owing to their generalism, and eventually become invaders when they lead to the competitive exclusion of native

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species (Shea & Chesson 2002). Alternatively, exotics may help to fill the functional gap left by previous declines of native species (Didham *et al.* 2005). In fact, the empirical evidence of exotic species contributing positively to ecological functions is increasing (Schlaepfer, Sax & Olden 2011; Aslan *et al.* 2012). Unfortunately, an 'exotic insurance' hypothesis, within which human-introduced animals would relieve declining native ones in the maintenance of ecosystem functions, has seldom been tested at community-wide scales (Aslan *et al.* 2012).

Plant–animal mutualistic assemblages (e.g. plant-pollinator, plant-seed disperser) are suitable for the study of the functional consequences of exotic species (Traveset & Richardson 2006). This is mostly because, due to the high degree of generalization in these assemblages (i.e. animal species often do not interact with one but rather with multiple plant species, and *viceversa*), the impact of alien species is expected to ripple quickly through the whole community (Lopezaraiza-Mikel *et al.* 2007). Exotic species emerge as new consumers (animals), but also as new resources (plants), that can modify the structure of interaction networks as well as the derived ecological functions (Traveset & Richardson 2006; Thompson *et al.* 2012). For example, by over-attracting pollinators or seed dispersers, exotic plants may alter the reproduction of native ones, ultimately affecting the structure of the plant–animal networks (e.g. Lopezaraiza-Mikel *et al.* 2007; Heleno, Ramos & Memmott 2013; but see Vilà *et al.* 2009; Heleno *et al.* 2013). From the animal side, in plant–pollinator assemblages, exotics may also behave as super-generalists and quickly integrate into interaction networks, greatly modifying their architecture, stability and resilience to disturbances (Aizen, Morales & Morales 2008; Traveset *et al.* 2013). Despite the growing body of evidence, whether similar global effects of exotic animals occur in other kinds of mutualisms, such as plant-seed dispersal assemblages, still remains poorly demonstrated (Spotswood, Meyer & Bartolome 2012).

Here, we evaluate the role of exotic birds in the plant–frugivore assemblages of New Zealand forests. Since the mid-19th century, these assemblages have suffered a strong decay of native bird populations, but have gained new frugivores from the introduction of European passerines (Kelly *et al.* 2010). Frugivory in native communities seems to be partially determined by fruit-bird size-matching constraints (Burns 2013), but the diet breath of exotic birds should have favoured their integration in new plant–frugivore assemblages (Burns 2012). In this context, we hypothesized that the stronger the integration of exotic birds in the plant–frugivore assemblages, the higher their degree of generalization. We verify this hypothesis from three complementary approaches. First, we hypothesized that, in a predominantly generalist guild, the importance of species as frugivores would depend more on their abundance (with more abundant frugivores consuming more fruits and plant species than rarer ones) than on their traits (Vázquez, Chacoff & Cagnolo 2009). We therefore assessed frugivory patterns in relation to bird abundance and body size (the trait of interest), and the contribution of exotic species to these patterns. Second, we hypothesized that generalization should increase when frugivores consume fruits in a purely random fashion (i.e. there should be no underlying species-specific preferences, and frugivory should be proportional to the relative abundance of fruits and frugivores; Vázquez, Chacoff & Cagnolo 2009; Burns 2013). We thus compared the preferences for fruit consumption between native and exotic birds. Third, if exotics frugivores behave as generalists, we predicted an increased degree of generalization in exotic-dominated interaction networks (Traveset *et al.* 2013). We therefore evaluated the topological changes in local plant–frugivore networks along a gradient of frugivory by exotics.

Materials and methods

STUDY SYSTEM

Our study system was the low-altitude, conifer-broadleaf forest of New Zealand. This forest type contains a high proportion of trees (70%), shrubs and vines bearing fleshy cones (e.g. totara *Podocarpus totara* G. Benn. ex D. Don.), fleshy fruits (e.g. tawa *Beilschmiedia tawa* (A. Cunn.) Kirk), arilated seeds (e.g. titoki *Alectryon excelsus* Gaertn.) or sticky seeds (e.g. tarata *Pittosporum eugenioides* A. Cunn.), consumed by native birds that act as legitimate dispersers (Clout & Hay 1989; Dawson & Lucas 2000). The guild of frugivores entails a wide range of frugivore sizes (from <50 in waxeye *Zosterops lateralis* Latham to >500 g in kereru *Hemiphaga novaeseelandiae* Gmelin; Clout & Hay 1989) driving interspecific diet differences (Burns 2013). From the mid-19th century, native frugivorous birds have suffered strong population decays and even extinction, due to forest loss and introduced predatory mammals (Innes *et al.* 2010). Simultaneously, European birds (blackbird *Turdus merula* L., song thrush *Turdus philomelos* Brehm, and starling *Sturnus vulgaris* L.) have been introduced and have largely expanded, becoming new frugivores of native flora (Kelly *et al.* 2010).

Nine different study sites (Table S1, Supporting Information) were chosen to fulfil the following criteria: (i) to contain low-altitude forest patches dominated by bird-dispersed woody plants; (ii) to represent the wide array of bird and plant species present in both North and South Islands of New Zealand; and (iii) to encompass a gradient of relative abundance (and a corresponding concomitant frugivore role) of exotic birds. Sites hosted different proportions of mature and secondary-growth forest (e.g. mostly mature in Blue Duck Scientific Reserve; mostly secondary in Wrights Hill Reserve). Zealandia is a secondary forest reserve fenced to exclude introduced predatory mammals, where some frugivorous birds have been translocated and others have increased after fence establishment.

COUNTS OF BIRDS AND FRUITS

In each site, a single sampling transect of *c.* 1 km length was established along walking trails across forest. On each transect, we conducted periodical monitoring of birds and fruits from early February to late May 2012, encompassing the ripening peak of most fleshy-fruited species of conifer-broadleaf forests (e.g. Williams & Karl 1996).

Bird censuses were performed every 2–3 days at each site, between 8:00 and 16:00, in fortnightly sets on each island (14–21 censuses per site). During the census, the complete transect was walked at a constant speed (*c.* 1-h to complete 1 km), counting all individuals of the different bird species heard or seen in a 10-m wide band at both sides of the walking trail. To avoid multiple records of the same individual bird moving ahead, records of the same species made at <10 m and <5 min ahead of a given observation were discarded, unless they were clearly distinguishable from previous individual observation (e.g. two individuals being detected at the same time). 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. To standardize across species for further analysis, we calculated the relative abundance of a given species as the proportion of observations of the species from the total number of bird observations among all sites. Species relative abundances were also calculated at a local scale, as the proportion of observations of a species in a given site from the total number of bird observations in that site.

Fruit counts were carried out at each site every fortnight (3–4 censuses per site), along four sections of 100 m × 4 m separated by at least 100-m one from each other. The crop size of all fruiting plants present in each transect section was visually estimated by means of a semi-quantitative Fruit Abundance Index (FAI, 1: 1–10 fruits; 2: 11–100, 3: 101–1000, 4: 1001–10 000, 5: >10 000; García *et al.* 2013). FAIs were further translated into mid-interval values, and summed per species across sections. For each fruiting species on each site, the absolute abundance of fruits was calculated as the average number of fruits per sampling round. This parameter was considered a measure of the availability of fruits of each plant species for frugivorous birds across the fruiting season. In order to make comparable fruit abundance measures across species and sites for further analysis, we estimated the local relative abundance of a given fruiting species as the proportion of fruits of all species in each site comprised by that species.

FRUGIVORY

Observations of fruit consumption by birds were made at each site, while walking each complete transect at a constant speed (*c.* 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 at a 5-m wide band at both sides of the walking trail, it was observed with the help of 8 × 30 binoculars until it was lost in the foliage. Each observation of a given bird eating fruits (i.e. swallowing pulp with seeds or arilated seeds) was considered to be an event of frugivory. As we were interested in the role of frugivores as seed dispersers, we discarded those observations corresponding to birds preying only upon pulp and clearly discarding seeds. We recorded the number of fruits consumed during each frugivory event. We considered as consumed both fruits swallowed entirely and those partially swallowed after being chewed or crushed but containing seeds on swallowed pulp (e.g. *Macropiper* sp. fruitlets). For each site, we estimated the number of fruits consumed per bird and plant species as the sum of fruits consumptions across all observation rounds.

DATA ANALYSIS

Effect of species relative abundance and body size on frugivory

We quantified the frugivore role of each bird species as the proportion of fruits consumed (number of fruits consumed by a given species divided by the total number of consumed fruits) and the number of plant species consumed, estimated from the total pool of observations of fruit consumption by all birds across sites. We related the proportion of fruit consumed to the relative abundance of each bird species (from the total number of bird observations across all sites) and the specific body size (weight; Table S2, Supporting Information), by means of a Generalized Linear Model (GLM) with relative abundance and body size (and their interaction) as predictors and the proportion of fruit consumed as the response variable (binomial error distribution fitted using quasi-likelihood to account for overdispersion, logit link). A similar GLM was built for the number of plant species consumed as a response (Poisson error distribution, log link). Predictors were standardized and scaled in both GLMs, to compare their relative effects within each model (Quinn & Keough 2002). Kaka *Nestor meridionalis* Gmelin was removed from the models ($N = 12$ bird species), due to its behaviour as a statistical outlier: even though it was detected in censuses, no fruit consumption was detected for this species, and it showed a very low abundance but large body size. No correlation between relative abundance and body size was found (Spearman's correlation: $\rho = 0{\cdot}123$; $P = 0{\cdot}704$, $N = 12$), indicating a low risk of collinearity of these predictors.

FRUIT CONSUMPTION PREFERENCES

If species' rates of fruit consumption were a random or neutral process, the observed data would be perfectly predictable given abundance estimates for all species of fruits and of birds (Vázquez, Chacoff & Cagnolo 2009); that is, the expected interaction frequency f_{ij} between fruit i and bird j is given by $f_{ij} = a_i a_j$, where a_i and a_j are the two species' observed abundances. In reality, however, observed interaction frequencies can show considerable deviation from this mass-action hypothesis (Staniczenko, Kopp & Allesina 2013). One way to quantify the variation of each interaction from neutrality is by estimating all interaction frequencies as $f_{ij} = \gamma_{ij} a_i a_j$, and calling γ_{ij} that interaction's 'preference' (i.e. its deviation from neutral).Values of $\gamma_{ij} > 1$ indicate interactions that are observed more frequently than expected at random while values of $\gamma_{ij} < 1$ indicate interactions that are observed less frequently than expected at random (Staniczenko, Kopp & Allesina 2013).

Here, we have estimates of each species' local relative abundances; this adds an additional unknown parameter – equivalent to the product of the total abundance of all fruits with the total abundance of all frugivorous birds in each site – to the equation for estimating interaction frequencies. To estimate this unknown parameter and the interaction preferences, we rewrite the equation above to $f_{ij} = e^{\log A + \log ri + \log rj + \log \gamma ij}$. This version of the model is identical to a Poisson regression with the frequencies f_{ij} as the response variable, local relative abundances r_i and r_j as the predictor variables, $\log A$ as the best-fit intercept, and the values of $\log \gamma_{ij}$ as the model residuals. Following this model structure, we estimated the interaction preferences $\log \gamma_{ij}$ separately for each network using the *glm* function in R (Poisson error distribution, log link). The distributions of preference values were compared between exotic and native birds with a Welch's ANOVA and a Barlett's test, which tested respectively equality between means and variances.

NETWORK ANALYSIS

We also used a bipartite network approach, in which bird and plant species were considered as nodes, and paired plant–bird interactions were considered as links, to evaluate the global structure of the interaction assemblage (e.g. Blüthgen 2010). Interaction measures were exclusively based on fruit consumption data, and not on raw abundance measures of plants and birds. Thus, for each site, we represented the interaction frequencies of each plant–bird species pair with an interaction matrix whose cell entries were the total number of fruits consumed per bird species from each plant species. We used the number of fruits consumed as interaction measure, instead of, e.g. the number of feeding visits of a given bird species on a given plant species (e.g. Albrecht *et al.* 2013), as we were also interested in discussing the functional outcomes of frugivory from the plant's perspective, i.e. in terms of seed dispersal.

Three sets of topological metrics were estimated to characterize the structure of local interaction networks, with sample sizes similar to those typically used in plant–frugivore network studies (e.g. Schleuning *et al.* 2011; Albrecht *et al.* 2013; Plein *et al.* 2013). The first set accounted for simple metrics, related to the number and the diversity of species and interactions: *network size*, the total number of bird and plant species; *network asymmetry*, the balance between the number of bird and plant species relative to network size; *number of interactions*, the total number of interactions between frugivores and plants; *interactions per species*, the ratio between number of interactions and network size; *links per species*, the sum of the links divided by the number of species; *interaction diversity*, a Shannon Index-based measure of diversity estimated from interaction frequencies. The second set described network global complexity: *connectance*, the proportion of realized interactions from all potential interactions in the network; *weighted nestedness* (*WNODF*, measured as the weighted version of the Nestedness measure based on Overlap and Decreasing Fills, Almeida-Neto *et al.* 2008), the degree to which the interactions of less-connected species are a subset of those of more-connected species, *specialization* (H_2'), a measure of niche segregation between species, and an inverse measure of generalization (Blüthgen 2010); *interaction strength asymmetry*, a measure of the difference in the dependence of birds on plants vs. the dependence of plants on birds. Finally, a third set of group-level (birds vs. plants) metrics was calculated: *generality*, a weighted average number of plant species consumed per bird species; *redundancy (sensu* Albrecht *et al.* 2013; also called *vulnerability*), a weighted average number of frugivores per plant; *niche overlap*, a measure of the similarity in interaction patterns between the species of the group; *extinction slope*, inverse measure of the strength of the secondary extinction among the species in one group (e.g. plants) followed by the simulated extermination of species in the other group (birds); *robustness* (ranging 0–1), ability of the species in one group (e.g. plants) to survive after the extermination of species in the other group (birds). All metrics were calculated with the package BIPARTITE 2.01 (Dormann *et al.* 2009) in R 2.14.0 (R Development Core Team 2012).

EFFECT OF FRUGIVORY BY EXOTICS ON NETWORK STRUCTURE

Our goal was to evaluate changes in the structure of local interaction networks along a gradient of relative frugivory by exotic species. For that, we estimated the proportion of interactions accounted for by exotic birds as the proportion of fruits consumed by exotic species (blackbird, song thrush and starling) from all fruits consumed in a given site. We used this parameter as a predictor of each network metric in a series of linear regressions. We also fit nonlinear trends of the response of network structure to frugivory by exotics (exponential decay, exponential rise, power and quadratic fits), after visual inspection of x,y scatterplots (Quinn & Keough 2002). For each relationship between frugivory by exotics and a given network metric, we chose a nonlinear model as a best fit if, being significant at $\alpha = 0{\cdot}05$, it also provided a lower value of AICc (Akaike Information Criterion with sample size correction; Quinn & Keough 2002).

To control the potential effect of outlier points on the occurrence of spurious relationships between frugivory by exotics and network metrics, we estimated Cook's distance (D) of each sampling point for all linear fits. The significance of linear fits was checked again after the removal of those points with Cook's D > 1.

Results

GENERAL OVERVIEW

We found 42 plant species (six exotic) bearing fleshy fruits or arilated seeds, and 13 potentially frugivorous bird species (three exotic) across all sites (Table S2, Supporting Information). Fruit absolute abundance ranged from 9592 to 79 143 fruits per sampling round per site, whereas bird absolute abundance ranged from 86 to 659 birds per 10 h per site (Table S3, Supporting Information). The absolute abundances of both native and exotic frugivores were positively related to the absolute total abundance of frugivorous birds across sites (Poisson GLM, quasi-likelihood, log link, $F_{1,7} \geq 17{\cdot}33$, $P < 0{\cdot}01$, for both variables). The local relative abundance of exotic frugivores across sites averaged 0·276 (±0·037SE, range 0·090–0·495), and was independent of the absolute total abundance of frugivorous birds (binomial GLM, quasi-likelihood, logit link, $F_{1,7} = 0{\cdot}06$, $P = 0{\cdot}822$). The absolute total abundance of frugivorous birds, as well as that of both native and exotic frugivores, were positively related to the absolute total abundance of fruits per site (Poisson GLM, quasi-likelihood, log link, $F_{1,7} \geq 6{\cdot}06$, $P < 0{\cdot}05$, for both variables).

Fruit consumption observations revealed 102 different plant–frugivore matches (links) between 31 plant and 12 bird species (Table S4, Supporting Information). We recorded 887 events of frugivory, including 4655 consumed fruits. Native birds (mostly waxeye, tui *Prosthemadera novaeseelandiae* Gmelin, kereru and bellbird *Anthornis melanura* Sparrman) accounted for 78·11% of fruits consumed, whereas exotic birds (mostly blackbird) accounted for 21·88% (Fig. 1a). The fruits of exotic plants represented 5·75% of these consumptions, from

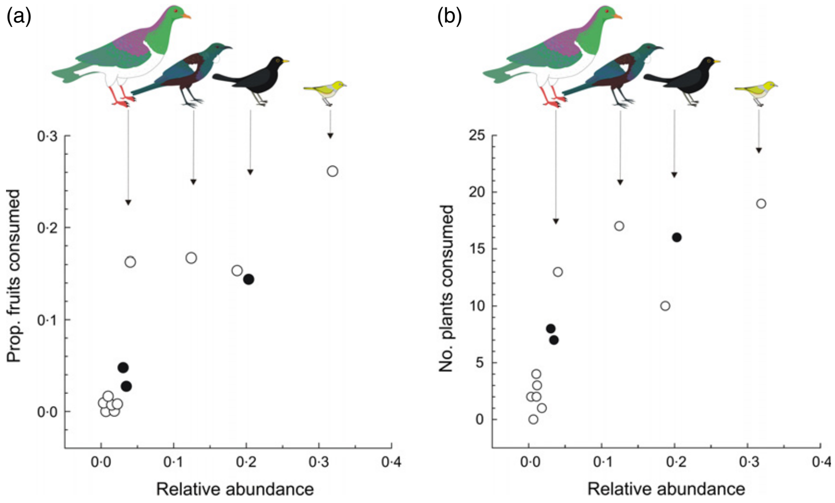

Fig. 1. Effects of the relative abundance of different bird species (white dots: native; black dots: exotic) on the proportion of fruits (a) and the number of plants (b) consumed by each species ($N = 12$). Kereru, tui, blackbird and waxeye are shown (left to right) to represent a gradient of bird size (approximate scale; artwork by Daniel Martínez).

Table 1. Effects of the relative abundance and the body size of different bird species on their frugivore role (proportion of fruits and number of plant species consumed). The interaction term (relative abundance × body size) was included into the Generalized Linear Model only when significant ($P < 0·05$)

Proportion of fruits consumed

Parameter	Estimate (± SE)	*t* ratio	*P*	Dev.[a]	Res. d.f.	Res. Dev.	*P* (> *F*)
Intercept	−2·87 ± 0·22	−12·84	<0·0001				
Relative abundance	1·03 ± 0·17	6·06	0·0002	3408·4	10	2226·8	0·0003
Body size	0·55 ± 0·15	3·78	0·0043	1268·5	9	958·4	0·006

Number of plants consumed

Parameter	Estimate (± SE)	*z*	*P*	Dev.[b]	Res. d.f.	Res. Dev.	*P* (> Chi)
Intercept	2·02 ± 0·12	6·11	<0·0001				
Relative abundance (RA)	0·93 ± 0·18	4·93	<0·0001	30·58	10	26·26	<0·0001
Body size (BS)	0·62 ± 0·17	3·53	0·0004	9·95	9	16·31	0·0016
RA x BS	0·75 ± 0·35	2·10	0·036	4·17	8	12·14	0·0410

[a] Null deviance 5635·3 (11 d.f.).
[b] Null deviance 56·89 (11 d.f.).

which native and exotic birds accounted for, respectively, 4·85 and 0·90%. The proportion of fruit consumed by exotic birds per site ranged from 0·08 (Blue Duck Reserve) to 0·57 (Wright Hills Reserve).

EFFECT OF SPECIES RELATIVE ABUNDANCE AND BODY SIZE ON FRUGIVORY

The proportion of fruits consumed per bird species increased proportionally with bird species relative abundance, indicating that more abundant species had a stronger role in the frugivore guild (Table 1; Fig. 1a). Bird body size also had a positive and independent, but weaker than relative abundance, effect on the proportion of fruits consumed (Table 1; Fig. 1a). The number of plant species consumed per bird species also increased significantly with bird relative abundance and, to a lesser extent, with bird body size (Table 1; Fig. 1b). We observed also a positive interaction between relative abundance and body size, derived from the fact that moderately abundant and mid-to-large native species, like tui and kereru, covered almost as many fruit species as the dominant, but smallest, waxeye (Fig. 1b). Exotic species followed the general patterns described above, and showed a frugivore role proportional to their relative abundance and body size. In particular, blackbird accounted for medium-to-high values in both the proportion of fruits and the number of plants consumed, as expected from its medium-to-high relative abundance and intermediate size (Fig. 1).

FRUIT CONSUMPTION PREFERENCES

The analysis of fruit consumption showed that, on average, many paired interactions between plants and frugivores were nearly proportional to the respective local relative abundances of fruits and birds. The average preference ($\log \gamma_{ij}$) value was 0·09 (± 0·23SE, median = −0·50, $N = 441$ interactions). Exotic and native birds showed no significant differences in their average preference value (Welch ANOVA, $F_{1,425{\cdot}35} = 2{\cdot}62$, $P = 0{\cdot}110$, Fig. 2). Nevertheless, exotic birds showed significantly smaller variability in preferences than native species (Barlett's test for unequal variances, $F = 65{\cdot}24$, $P < 0{\cdot}0001$), indicating that selective fruit consumption was less frequent in exotic than in native birds (Fig. 2).

EFFECTS OF FRUGIVORY BY EXOTICS IN PLANT–FRUGIVORE NETWORK STRUCTURE

Local plant–frugivore networks involved 12–23 species and accounted for 156–1641 interactions (Table S4, Supporting Information). Among birds, only waxeye and blackbird were present in all networks. Network metrics varied across sites, and most were independent of both the network size and the number of interactions (Table S5, Supporting Information). Network size and the number of interactions were uncorrelated to sampling effort (the number of observation rounds per site; Pearson's correlation, $\rho < 0{\cdot}31$, $P > 0{\cdot}40$, $N = 9$, for all correlations). The number of interactions of local networks was positively correlated with the absolute abundance of fruits per site (Pearson's correlation, $\rho = 0{\cdot}73$, $P < 0{\cdot}05$, $N = 9$).

Network size, the number of interactions and the average number of interactions per species were independent of the proportion of interactions accounted for by exotic birds (Table S5, Supporting Information). Intriguingly, we found significant, and mostly nonlinear, variation in many network metrics along the gradient of frugivory by exotic birds (Table S6, Supporting Information). The degree of specialization (H_2'), for example, decayed exponentially when the proportion of interactions accounted for by exotic birds increased (Exponential decay fit, $R^2 = 0{\cdot}88$, $F_{1,7} = 64{\cdot}47$, $P < 0{\cdot}0001$, Fig. 3). This was mostly because exotic birds widened the frugivore guild of many plant species, whereas native birds tended to generate more specialized interactions from the plant's perspective (Fig. 3). Both the diversity of interactions and the number of links per species increased asymptotically with the proportion of interactions accounted for by exotic birds (Exponential rise fit, $R^2 > 0{\cdot}50$, $F_{1,7} > 7{\cdot}0$, $P < 0{\cdot}05$, in both response variables, Fig. 4a,b). Networks with stronger frugivory by exotic birds were also more nested, as judged by WNODF (Exponential rise fit, $R^2 = 0{\cdot}77$, $F_{1,7} = 27{\cdot}49$, $P < 0{\cdot}01$, Fig. 4c). Frugivory by exotics also affected plant-level network metrics, increasing the average number of frugivores per plant species (redundancy: Exponential rise fit, $R^2 = 0{\cdot}54$, $F_{1,7} = 10{\cdot}26$, $P < 0{\cdot}05$, Fig. 4d), as well as the response of plants to the simulated extinction of frugivores (extinction slope; Linear fit, $R^2 = 0{\cdot}59$, $F_{1,7} = 12{\cdot}73$, $P < 0{\cdot}01$, Fig. 4e; robustness; Power fit, $R^2 = 0{\cdot}42$, $F_{1,7} = 6{\cdot}69$, $P < 0{\cdot}05$, Fig. 4f). All the linear relationships between these network metrics and the proportion of interactions accounted for by exotic birds were also significant after controlling the effect of outlier points (Table S7, Supporting Information). The other estimated network metrics were originally independent of the proportion of interactions by exotic birds (bird niche overlap, bird extinction slope and bird robustness) or rendered independent after control of outliers (connectance, plant niche overlap, generality; Tables S6 and S7, Supporting Information).

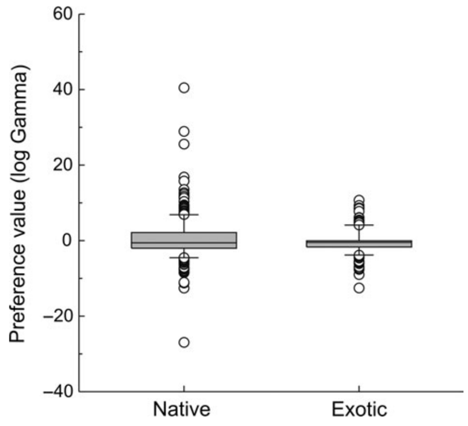

Fig. 2. Box-plots representing the distribution of values of preference (log Gamma) in fruit consumption from different interactions (fruit and bird species pairs), for both native and exotic frugivores.

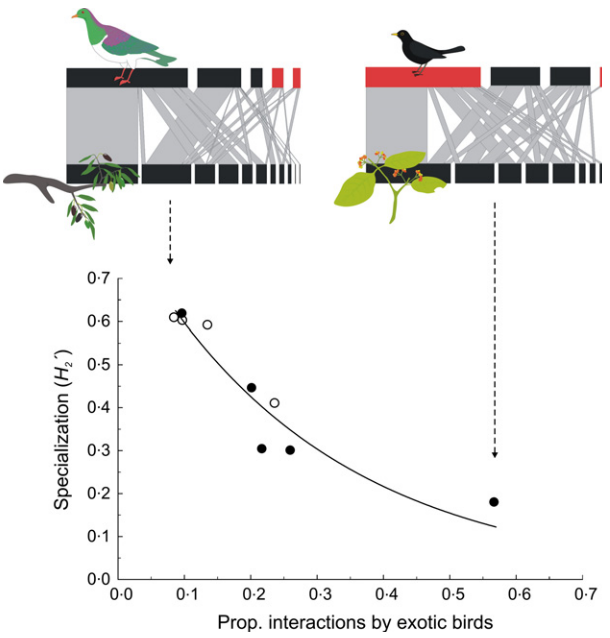

Fig. 3. Effect of the proportion of interactions accounted for by exotic birds (proportion of fruits consumed by exotics from all fruits consumed) on the degree of specialization in local fruit–frugivore networks (white dots: South Island; black dots: North Island; $N = 9$). Two networks of extreme values are shown, representing the proportion of fruits of different plant species (lower row) consumed by different bird species (upper row, exotic birds in red), and the proportion of each plant species consumed by each bird (grey links). The strongest link is illustrated (left: Blue Duck Reserve, kereru and *Beilschmiedia tawa*; right: Wright Hills Reserve, blackbird and *Coprosma grandifolia*; artwork by Daniel Martínez).

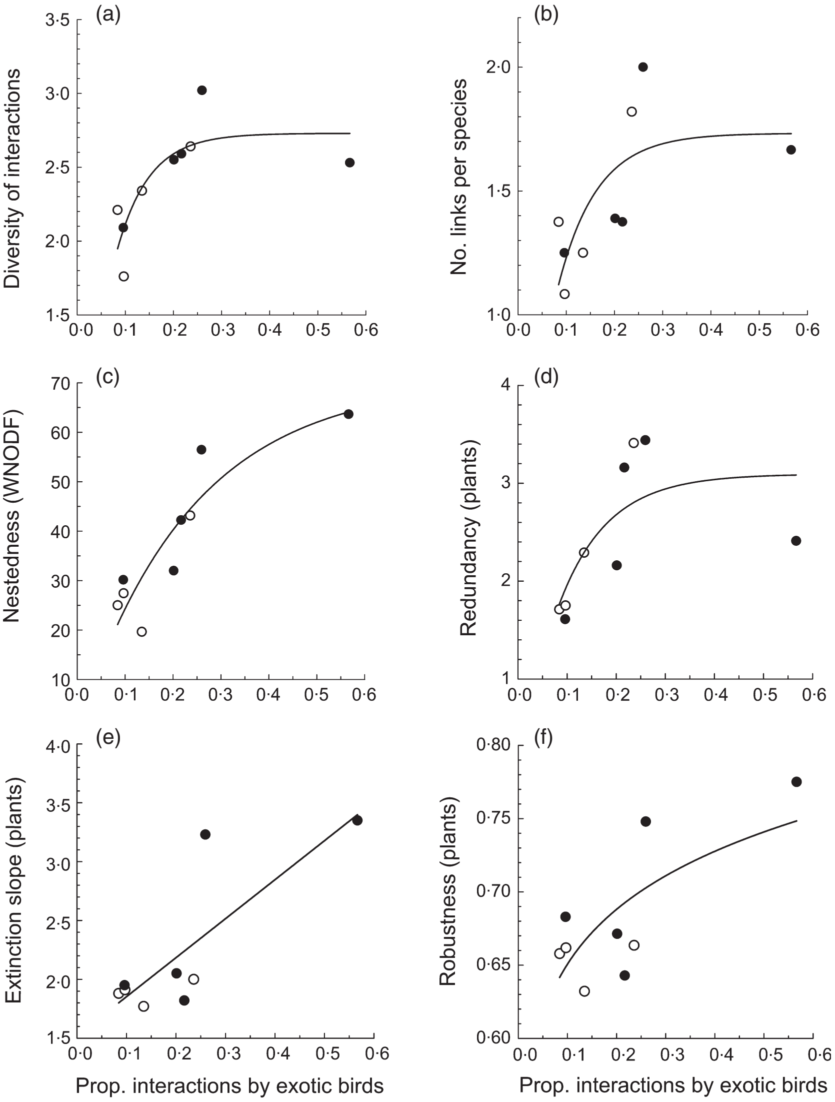

Fig. 4. Effect the proportion of interactions accounted for by exotic birds (proportion of fruits consumed by exotics from all fruits consumed) on fruit–frugivore network and plant-level metrics (white dots: South Island; black dots: North Island): diversity of interactions (a), number of links per species (b), network nestedness (c), redundancy of plants (d), extinction slope of plants (e) and robustness of plants (f).

Discussion

In this work, we set up a large-scale study across different New Zealand forests to evaluate the role of European birds in plant–frugivore assemblages. We show that these exotic species were widespread, and even locally dominant, frugivores of native plants, in contrast to what has been suggested by previous research (Kelly *et al.* 2006). More importantly, our results suggest that exotic animals alter the global structure of plant-seed disperser assemblages. Exotic birds contributed particularly to, and even increased, the generalization of New Zealand seed dispersal mutualisms. Low levels of specialization seem to be the norm in plant-seed disperser assemblages (Blüthgen *et al.* 2007; Schleuning *et al.* 2012; Albrecht *et al.* 2013), nominally because generalization should benefit plants since having a broader spectrum of dispersers would increase the probability of seeds reaching sites suitable for recruitment (Schupp, Jordano & Gómez 2010). In the following sections, we will disentangle the effect of exotic birds on generalization from three complementary sources: specific frugivory patterns, fruit preferences and network topology. We will finally discuss the potential consequences of exotic birds for the stability and resilience of seed dispersal function.

ROLE OF EXOTIC BIRDS IN NEW ZEALAND PLANT–FRUGIVORE ASSEMBLAGES

The role of exotic birds in the structure of plant–frugivore assemblages may be explained from the mechanisms driving interactions between birds and plants. In this sense, a high generalization is expected when interaction patterns emerge from neutral processes (i.e. interactions mostly reflect the probabilities driven by the abundances of animals and plants) rather than from trait matching (Vázquez, Chacoff & Cagnolo 2009). In our case, the importance of bird species as frugivores, in terms of both proportion of fruits and number of plant species consumed, depended more on their abundance than on their body size. For this reason, the globally dominant waxeye contributed the most to frugivory patterns, despite the fact that its small body size precluded interaction with some large-fruited plants (Kelly *et al.* 2006). On the other hand, a larger body size – through a wider gape width – enabled other native species to consume more plant species than expected from their abundance. This was the case for kereru and tui, both of which consumed even large fruits like those of tawa and miro (*Prumnopitys ferruginea* (G. Benn. ex D. Don) de Laub.)(see also Kelly *et al.* 2006, 2010). Exotic birds fit well into a general pattern of frugivory driven predominantly by abundance: blackbird, one of the most common birds in New Zealand (Innes *et al.* 2010), had a role similar to the most important native frugivores. The intermediate size of the European species should also contribute to this role, by giving them the ability to consume at least the smaller fruits of some large-fruited species (Kelly *et al.* 2010).

Our analysis of fruit consumption preferences corroborates the relative role of abundance-driven processes vs. trait matching as determinants of plant–frugivore interactions. We found that most of the observed interactions could be explained by random encounters of fruits by birds with no phenotypic constraints to consume them (see also Burns 2013). Anyway, we also found evidence of fruit over-consumption and rejection (Fig. 2). These preferences could be explained by, complementarily, size constraints (larger fruited species avoided by smaller birds; Kelly *et al.* 2010) and fruit selection (with large birds searching selectively for largest fruits, e.g. kereru feeding on tawa and miro; Table S4, Supporting Information; but see Burns 2013), but also potentially to some phenological mismatch undetected by the sampling procedure. In any case, the present analysis suggests that exotic birds made the New Zealand frugivore guild less selective (they reduced the variability in preferences) and, therefore, the whole plant–frugivore assemblage more generalized.

Our network approach enabled us to explicitly relate the global structure of plant–frugivore assemblages to exotic integration. The differences in network structure found across study sites were not an artefact of differences in sampling effort, network sizes or numbers of interactions, the last features probably shaped by, respectively, the size of local species pools and the tracking response of birds to local fruit availabilities. Previous research has shown plant–frugivore networks to be highly sensitive to habitat-mediated changes in the frugivore guild (e.g. Schleuning *et al.* 2011; Albrecht *et al.* 2013; but see Plein *et al.* 2013). Our results go beyond these findings, as they demonstrate that the compositional gradients imposed by exotic animals affected the architecture of plant-seed disperser assemblages. In contrast, a previous study focused on exotic plants in the Galápagos suggested a weak effect of invaders on the structure of plant-seed disperser networks (Heleno *et al.* 2013; but see Heleno, Ramos & Memmott 2013; Spotswood, Meyer & Bartolome 2012). Thus, in accordance with plant–pollinator systems (Traveset & Richardson 2006), seed dispersal networks seem more prone to be affected by exotic integration of animals rather than plants.

Exotic birds rendered the New Zealand plant–frugivore networks less specialized, more diverse and more nested. The changes in specialization and interaction diversity derived more from increases in the average number of frugivores per plant than from changes in bird generalization, as judged by, respectively, redundancy and generality. In other words, exotic birds created more generalized plant–frugivore assemblages largely by providing complementary seed dispersal to many native plants (e.g. blackbirds fed on all plant species present in Wright Hills Reserve; Fig. 3, Table S4, Supporting Information). The increase in nestedness seems mostly related to generalist exotics becoming the only consumers of rare plants (e.g. *Aristotelia serrata* Oliv. in Wright Hills Reserve; *Ripogonum scandens* J. R. Forst. & G. Forst. in Zealandia; Table S4, Supporting Information), but also to some rare exotics interacting with super-generalist plants (e.g. song thrush and starling with *Coprosma grandifolia* Hook. f. in Northern Town Belt and Wright Hills Reserve respectively; Table S4, Supporting Information). Finally, the nonlinear trends between network metrics and frugivory by exotics shown here suggest that the process of integration in the plant–frugivore assemblages was initially quick before later reaching saturation. Further study, enlarging the gradient towards higher values of frugivory by exotics, would be required to confirm the prevalence of the nonlinear trends found here, but also to demonstrate whether saturation results from numerical constraints (the number of animal and plant species to be included in interaction networks) or, alternatively, emerges from deterministic processes (e.g. competition between frugivores).

CONSEQUENCES OF EXOTIC FRUGIVORES FOR SEED DISPERSAL MUTUALISM

Fruit consumption represents the quantitative contribution of frugivorous animals to seed dispersal, but seed treatment and the spatial patterns of seed deposition ultimately drive frugivore effectiveness (Schupp, Jordano & Gómez 2010). Although we lack explicit information on frugivore quality, previous findings suggest some functional similarities between native and exotic birds. First, all exotic birds studied here may be considered as legitimate seed dispersers, as they swallow the fruit and defecate/regurgitate intact seeds (Kelly *et al.* 2010). Second, the germination of seeds of many species studied here seems to be scarcely affected by bird's gut treatment, and independent of bird origin (Kelly *et al.* 2010). Third, like in native species (e.g. kereru; Wotton & Kelly 2012), a strong spatial heterogeneity is also expected in the seed rain of exotics (e.g. thrushes), as judged by movement patterns in their native ranges (e.g. Morales *et al.* 2013).

Considering their potential seed dispersal service, our results indicate that exotic frugivores have positive, rather than negative (i.e. invasive), effects in New Zealand forests.

On the one hand, the exotic birds here were not drivers of invasion of alien plants, which occurred in a low proportion in the sampled assemblages and were, in fact, mostly dispersed by native birds. Similarly, exotic frugivores are not considered to cause native decimation by over-competition (Diamond & Veitch 1981). On the other hand, our results suggest that, by increasing generalism, exotic birds would enhance the opportunities of effective seed dispersal of many native plants. Finally, the relationships between frugivory by exotics and both nestedness and resistance to secondary extinction suggest a positive effect of exotics in the stability of plant–frugivore assemblages (Thébault & Fontaine 2010; Tylianakis *et al.* 2010).

Concluding remarks

Using a community-wide approach based on plant–animal interactions, our study suggests that exotic animals (i.e. frugivorous birds) may exert an insurance effect for a given ecosystem function (i.e. seed dispersal of native woody plants). Exotic birds may relieve native ones where they have been lost, maintaining the chance of fruit removal for a diverse array of plant species. By diversifying the coterie of dispersal vectors available to co-occurring native plants, they could actually generate a 'portfolio' effect that would stabilize the average function of seed dispersal (Tilman 1999). Such a stabilizing effect may be especially crucial in the context of the increased anthropogenic disturbances that are leading native plants to dispersal bottlenecks and establishment collapse (Wotton & Kelly 2011). We finally suggest that it would be valuable to assess these patterns in other insular plant-seed disperser assemblages across the world, given that they now host strongly impoverished frugivore guilds (Schleuning *et al.* 2013), and suffer similar anthropogenic impacts (Kaiser-Bunbury, Traveset & Hansen 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Geographical details of the study sites

Table S2. Studied plant and bird species

Table S3. Abundance of fruits and birds at each study site

Table S4. Fruit consumption observations at each study site

Table S5. Correlations between network metrics, abundance and frugivory by exotic birds

Table S6. Linear and nonlinear fits between network metrics and frugivory by exotic birds

Table S7. Outlier analysis on fits between network metrics and frugivory by exotic birds