LETTER

Native and alien flower visitors differ in partner fidelity and network integration

Kristian Trøjelsgaard,[1] 　ⓘ Ruben Heleno[2] and Anna Traveset[3]

[1]*Department of Chemistry and Bioscience, Aalborg University, Fredrik Bajers Vej 7H, Aalborg East 9220, Denmark*

[2]*Centre for Functional Ecology, Department of Life Sciences University of Coimbra Coimbra, Portugal*

[3]*Global Change Research Group Instituto Mediterráneo de Estudios Avanzados, CSIC-UIB Esporles, Mallorca, Spain*

Correspondence: E-mail: k.troejelsgaard@gmail.com

Abstract

Globalisation persistently fuels the establishment of non-native species outside their natural ranges. While alien plants have been intensively studied, little is known about alien flower visitors, and especially, how they integrate into natural communities. Here, we focus on mutualistic networks from five Galápagos islands to quantify whether alien and native flower visitors differ consistently in their pairwise interactions. We find that (1) alien flower visitors have more interaction partners and larger species strengths (i.e. plants are more connected to alien insects), (2) native insects tend to have higher partner fidelity as they deviate more from random partner utilisation, and iii) the difference between native and alien flower visitors in network integration intensifies with island degradation. Thus, native and alien flower visitors are not interchangeable, and alien establishment might have yet unforeseen consequences for the pairwise dynamics between plants and flower visitors on the Galápagos – especially on the heavily disturbed islands.

Keywords

biotic homogenisation, ecological network, exotic, interaction partner, mutualism, oceanic island, plant, pollinator, species roles.

INTRODUCTION

Natural ecosystems are increasingly threatened by biotic homogenisation driven by the expansion of some 'winning species' and the concomitant extinction of 'loser species' – a situation fuelled by the introduction of species outside their native ranges (McKinney & Lockwood 1999; Gossner *et al.* 2016). One key question arising under such scenario is to what extent these alien species can match the ecological roles currently upheld by the indigenous biota. Species roles are to a large extent governed by the way they engage in complex interaction networks with co-occurring species (e.g. Baker *et al.* 2015). Accordingly, ecological network analysis have proved a most valuable tool to explore the links between species roles and community structure (Bascompte & Jordano 2014), and for evaluating the impact of different types of disturbances (Hagen *et al.* 2012), including biological invasions (Tylianakis *et al.* 2008). Recent studies suggest that species do not interact with a random assemblage of all potential partners, and that species roles can be spatio-temporally conserved (e.g. Baker *et al.* 2015; Carstensen *et al.* 2018). One explanation is that phenological and morphological matches between co-occurring species constrain the pool of potential interactions (Olesen *et al.* 2011; Rosas-Guerrero *et al.* 2014). If invading alien species differ from indigenous ones in their interaction patterns (due to differences in e.g. phenology, morphology or behaviour), then they may not be able to match the roles of the native species. Here, we use an extensive sampling of plant–pollinator networks across the Galápagos Islands to quantify whether native and alien flower visiting insects differ in their establishment of pairwise interactions.

Animal pollination is critical for many plant species and can affect plant population and community dynamics (Kearns *et al.* 1998). Thus, if native and alien pollinators systematically differ in the interactions they establish, invaded and uninvaded communities may follow different evolutionary trajectories (Aizen *et al.* 2008; Tylianakis & Morris 2017). Despite a long-standing interest in understanding the changes imposed by alien species on pollination interactions (Olesen *et al.* 2002; Lopezaraiza-Mikel *et al.* 2007), firm generalisations have been hard to achieve (Tylianakis & Morris 2017; Timóteo *et al.* 2018). This difficulty is likely rooted in the intrinsic idiosyncrasies of natural communities (Padrón *et al.* 2009) as well as the species (Bartomeus *et al.* 2008), but also due to a shortage of multispecies comparisons from identical communities. Indeed, many studies have focused on one or a few dominant invasive species (e.g. Lopezaraiza-Mikel *et al.* 2007; Bartomeus *et al.* 2008; Padrón *et al.* 2009; Albrecht *et al.* 2014), whereas the combined effects of multiple non-invasive aliens have received comparatively little attention (but see Aizen *et al.* 2008). While dominant invasive species can outcompete natives, non-invasive aliens may alter the interaction patterns of the recipient communities through, for example, behavioural interference, resource depletion, usurpation of pollinators, or altered resource availability (Dupont *et al.* 2004; Ghazoul 2004; Clavero & García-Berthou 2005; Stout & Morales 2009). Although somewhat harder to document, these subtle changes may also harm the native biota, and might function as an early warning signal of community degradation.

While most studies have focused on the effects of alien plants or honey bees, the effects of multiple non-invasive alien flower visitors on pollination networks have been largely ignored (Timóteo *et al.* 2018). We therefore implemented a network approach to assess if the interactions established by alien flower visitors consistently differ from those of the

native species, and ultimately whether these two groups are integrated differently. The surveyed habitats on the Galápagos are ideal for exploring this because they contain multiple alien flower visitors but relatively few alien plant species. Specifically, we hypothesised that: (1) due to their 'likely' more generalised behaviour, alien flower visitors will interact with more plant species and take up more central roles in the communities; (2) that native species, due to their longer residence times (likely increasing the potential for co-adaption), exhibit higher partner fidelity across the archipelago; and (3) that alien and native flower visitors contribute differently to network structure. For example, if alien flower visitors are more centrally positioned they would be expected to contribute more to nestedness, and if they are more generalised they would likely reduce overall network specialisation.

We find that alien flower visitors interact with more plant species, they have higher species strengths, and they display lower partner fidelity than natives. Moreover, we find that alien and native flower visitors are integrated differently into the communities, and further show that the difference in integration between alien and native species increases with island degradation.

METHODS

Study sites and sampling protocol

Flower visitor observations were performed during February 2010 and 2011 in the arid zone at five major islands within the Galápagos archipelago viz. San Cristobal (0°53′26.35 S, 89°36′36.76 W), Santa Cruz (0°45′22.70 S, 90°19′42.97 W), Santiago (0°12′39.41 S, 90°49′58.15 W), Pinta (0°32′42.61 N, 90°44′20.65 W) and Fernandina (0°18′21.35 S, 91°39′06.75 W) (as described in Traveset et al. 2013). Every flowering plant species detected within 1 km of the embarkment area was surveyed in 15 min observation periods. The sequence of observation was randomised among plant species to minimise any diurnal effects. The plant species varied in their floral-display (from 100 flowers per individual for some trees, to less than 10 for some herbs), but in each survey we maximised the number of flowers observed. The number of plant species varied from island to island (Table 1), but because we used a plant focused sampling protocol, the time spent per plant remained about the same across the islands. Each plant species was surveyed 8 h on average (depending on its presence across the islands, and whether it flowered each year), totalling 518 h of observations (446 h of diurnal observations; 72 h of nocturnal observation). During each floral census, the total number of insects touching the reproductive parts of the flowers were scored, and in order to avoid misidentification, a total of 710 specimens (especially smaller insects difficult to identify in the field) were collected for taxonomic identification (deposited at the Charles Darwin Research Station). If identification to species level was unachievable, specimens were instead classified according to morphotypes within the genus or family. Floral abundance of each flowering plant species was determined by counting the number of flowers along a 500 m transect on each island and year. Although the number of plant species was fairly stable between years, more

pollinators and interactions were observed in 2011 (see Appendix S1 in Supporting Information). To provide a robust quantitative interaction network for each island, we pooled interaction data from 2010 and 2011. All networks were organised as interaction matrices, and the matrix element a_{ji} was the flower visitation rate (FVR) between plant species j and animal species i, given as: FVR = [Total number of flowers visited/(Total flowers observed × Total census duration)] × Total number of flowers estimated for the area. All FVR values were multiplied by 1000, to avoid very low values for some species pairs.

Species were categorised as 'native', 'alien' or 'unknown' based on the updated Insect Checklists of Galapagos (http://www.darwinfoundation.org/datazone/checklists/). All species labelled as 'native', 'endemic', or 'questionable native' were grouped as 'native', while all species introduced by humans were labelled as 'alien' (Table 1). Thus, aliens are here solely defined according to their origin. Some flower visitors could only be identified to genus level, and unless the entire genus could be categorised as either 'native' or 'alien' these species were designated as having an 'unknown' origin (Table 1).

Species–level indices

For all native and alien flower visitors we quantified their generalisation through (1) degree (number of interaction partners), and (2) d', a quantitative specialisation measure, which ranges from 0 (low specialisation) to 1 (high specialisation) (Blüthgen et al. 2006). Furthermore, we also quantified species strength, an overall measure of the importance (based on the number of visits) of each flower visitors for the entire plant community (Bascompte et al. 2006), and closeness centrality, which measures their overall topological distance to other species (Martín González et al. 2010). The difference between native and alien species in these species–level indices was analysed using Linear Mixed Effects Models (LMEM). Because multiple entries from the same species (or island) cannot be treated as independent values we included species identity and island as random factors. We used the package GLMMTMB v.0.2.0 (Brooks et al. 2017) in R v.3.3.3 (R Core Team 2017). Models were evaluated by inspecting the residuals for normality and homoscedasticity (Zuur et al. 2009).

Quantifying partner fidelity of native and alien flower visitors

Partner fidelity was determined for all flower visitors occurring on ≥2 islands, by comparing the empirical partner similarity across all islands, with the expected similarity if the flower visitor interacted with a random set of the available plant species at a given island. Thus, partner fidelity becomes a matter of consistency in partner utilisation, rather than a question of having many or few partners. The procedure was as follows: (1) for an animal i occurring on ≥2 islands we calculated every empirical partner similarity among all pairwise island combinations at which i occurred. Similarity was determined with the Morisita-Horn index, which is an abundance-based similarity index (i.e. it relies on both the identity of the partners and the frequencies with which they interact) that is insensitive to both incomplete and unbalanced sampling

Table 1 Number of species classified as being either native, alien, or having an unknown origin. Numbers in parenthesis are the percentage in each category in relation to the total number of plants or animal species in each interaction network

Island	Plant species			Flower visitor species			
	Total	Native	Alien	Total	Native	Alien	Unknown
San Cristobal	21	20 (100%)	0 (0%)	93	38 (41%)	31 (33%)	24 (26%)
Santa Cruz	23	22 (96%)	1 (4%)	76	32 (42%)	22 (29%)	22 (29%)
Santiago	24	22 (92%)	2 (8%)	69	36 (52%)	17 (25%)	16 (23%)
Pinta	21	21 (100%)	0 (0%)	76	41 (54%)	15 (20%)	20 (26%)
Fernandina	18	18 (100%)	0 (0%)	60	27 (45%)	13 (22%)	20 (33%)

(Chao *et al.* 2006). (2) We then identified how many interaction partners i had at a particular island and allocated an equal number of random partners by selecting among the available plants at that island. We subsequently assigned interaction frequencies with a bootstrapping procedure by subsampling the randomly selected plant species (with replacement), with a probability proportional to their floral abundance in the transects. Subsampling continued until the sum of all pairwise interactions of the focal flower visitor (i.e. the marginal total) was reached. Therefore, both the empirical number of partners and the marginal total was maintained during the randomisation. After performing this procedure across all islands at which i occurred, we recalculated every random pairwise partner similarity. This process was repeated 5000 times and we determined how much i's empirical partner similarities (MH_{Emp}) deviated from the random expectation by calculating z-scores, given as $(MH_{Emp} - MH_{Rand})/SD_{Rand}$, where MH_{Rand} and SD_{Rand} are the mean Morisita-Horn value and standard deviation from the 5000 randomisations respectively. Positive values indicate that in a given comparison the animal interacts with a non-random selection of the available partners (high partner fidelity), while negative values suggest that the animal is largely opportunistic (low partner fidelity). Morisita–Horn values were calculated with VEGAN *v.*2.4-3 (Oksanen *et al.* 2017) in R.

The z-scores were analysed with a LMEM (using GLMMTMB *v.*0.2.0 in R), where we included both 'origin' and the 'empirical Morisita–Horn values' as explanatory variables. The former because we wanted to quantify whether alien and native insects differ in their partner fidelity, and the latter because we wanted to ensure that any difference between native and alien flower visitors was not just a consequence of one of the groups simply having larger empirical Morisita–Horn values. Species identity and island pair (the identity of the two islands giving rise to a given partner similarity value) were included as random factors. We used a Gaussian error distribution, and the model was evaluated by inspecting the residuals for normality and homoscedasticity (Zuur *et al.* 2009).

Quantifying the integration level

If alien and native flower visitors are integrated similarly into the communities, then the community response to the removal of either natives or aliens should be similar for the two groups. Because network size is known to influence network structure (e.g. Jordano 1987; Trøjelsgaard & Olesen 2013; Cirtwill *et al.* 2015), we mitigated the impact of altered network sizes by removing the same number of native and alien species from a given community. The number of aliens was consistently lower than that of natives (Table 1), and the former therefore became the common target-point on all islands. For each island-network we therefore randomly and sequentially removed either all alien flower visitors, or an equal number of native species, resulting in alien-free or native-reduced networks respectively. The removal simulations were repeated 200 times for both alien and native flower visitors, and for each individual removal we quantified the topological changes by calculating three macroscopic network descriptors (see below). In total, we calculated each network descriptor for 39,200 networks. We did not incorporate potential rewiring among the remaining species (see e.g. Kaiser-Bunbury *et al.* 2010; Costa *et al.* 2018), as our goal was not to predict community resilience to primary extinctions, but instead to quantify whether alien and native flower visitors are integrated differently.

Network measures

We identified three macroscopic descriptors (sensu Trøjelsgaard & Olesen 2016) that focus on different aspects, that represent binary and quantitative measures, and that collectively provide a broad assessment of how the network structure respond to the removal of alien and native species. These were as follows: (1) interaction richness (I), i.e. the total number of unique interactions; (2) Weighted nestedness ($WNODF$), measuring to what extent specialist species interact with a subset of the species with which the generalist interact (Almeida-Neto & Ulrich 2011); and (3) network specialisation (H_2'), a quantitative metric that ranges from 0 (highly generalised, i.e. maximum niche overlap) to 1 (highly specialised, i.e. maximum niche divergence) (Blüthgen *et al.* 2006). $WNODF$ and H_2' were calculated with the package BIPARTITE *v.*2.08 (Dormann *et al.* 2008) in R. Because nestedness can be influenced by matrix fill and size, we calculated standardised nestedness values. Therefore, we made 100 random matrices at every removal step n (using 'shuffle.web' in BIPARTITE *v.*2.08, which maintains size and connectance), for both the native and alien removal sequences at each island, and for all 200 iterations (resulting in 3.92×10^6 randomised networks). For each removal step we report the standardised nestedness value as: $WNODF_{z-\text{score}} = \left(WNODF_n^{Emp} - WNODF_n^{Rand}\right)/SD_n^{Rand}$, where $WNODF_n^{Emp}$ is the empirical weighted nestedness value at removal step n, and $WNODF_n^{Rand}$ and SD_n^{Rand} are the mean and standard deviation of the weighted nestedness values from 100 random matrices at removal step n.

Difference between native and alien removals

To quantify whether alien and native flower visitors were integrated differently, we calculated the difference in the three network descriptors between the alien and the native removal for each removal step n, and all iterations (200 for each island). The differences were denoted as ΔI, $\Delta WNODF_{z\text{-score}}$, and $\Delta H'_2$, and for all metrics the computation were $\Delta Metric_n = M_n^{Alien} - M_n^{Native}$, where M_n is the metric value at removal step n for either the alien or the native removal. Importantly, if there is a systematic trend in the Δ-values, it suggests that these two groups are integrated differently into the communities. Conversely, if the difference remains close to zero it does not matter whether we remove native or alien species because the network metric is affected equally, hereby indicating that natives and aliens are integrated similarly and take up similar positions within the network.

The output from the removal simulations was explored using three different analytical approaches. First, we investigated whether the Δ-values changed consistently in relation to the ratio of species removed using the Kendall's tau coefficient – a non-parametric measure based on rank correlation that runs from -1 (strong negative association) to $+1$ (strong positive association) (Davis & Chen 2007). If any association exists it indicates that native and alien removal affect the network structure differently.

Second, we compare the final endpoint values from the alien and native removals (using the final averages from the 200 iterations) with a paired Wilcoxon test (see Brosi *et al.* 2017), in order to assess whether the removal simulations produced similar responses across the five islands.

Third, because the historical anthropogenic impact (and therefore also potential alien impact) varies widely across the archipelago, we explored whether any island specific patterns could be explained by such differences. Therefore, we used linear regressions to examine whether the final Δ-values (i.e. final average differences from the 200 iterations) were related to island degradation (as quantified by Watson *et al.* 2010). For San Cristobal, Santa Cruz and Santiago, the percentage of each island that has been modified amounts to 17, 14 and 0.1% respectively (Watson *et al.* 2010). The level of degradation has not been evaluated for Pinta and Fernandina, but neither has been inhabited (contrary to the three other islands) and therefore have a completely negligible human impact (certainly smaller than on Santiago, i.e. 0.1%), and we therefore assumed 0% degradation on these two islands.

RESULTS

Species–level indices

The total number of flower visitors within each island-network ranged from 60 (Fernandina) to 93 (San Cristobal), and the proportion of alien flower visitors ranged from 20% (Pinta) to 31% (San Cristobal) (Table 1). Each island had more native than alien flower visitors, although the ratio was close to one on San Cristobal. An average of 27.4% (± 0.04 SD) of all the animals in each network could not be assigned unambiguously as either native of alien (Table 1). Across all five islands, there

were 60 plant species in total, and only three (5%) were labelled as aliens; two on Santiago (*Cleome viscosa*, *Tamarindus indica*) and one on Santa Cruz (*Mormordica charantia*). The remaining 57 species (95%) were categorised as natives. Thus, alien flower visitors constitute a much larger fraction of the alien species pool in the current system.

Linear Mixed Effects Models imply that native flower visitors on the Galápagos have significantly fewer interaction partners ($P = 0.019$) and significantly lower species strengths ($P = 0.004$) than alien flower visitors, while specialisation (d') ($P = 0.579$) and closeness centrality ($P = 0.103$) did not differ significantly between the two groups (Table 2 and Fig. 1). The difference in species strength was not significant when including degree as an explanatory variable ($P = 0.106$), suggesting that this difference was largely driven by the difference in degree between the two groups (Table 2).

Partner fidelity

The deviation from random partner utilisation was expressed through z-scores, and when analysing these with a LMEM (with species identity and island pair as random factors), we found that native flower visitors have significantly larger z-scores compared to alien flower visitors (Coef. = 0.271, SE = 0.082, $z = 3.32$, $P < 0.001$), and that the z-scores increased significantly with the empirical Morisita–Horn values (Coef. = 6.17, SE = 0.153, $z = 40.3$, $P < 0.001$) (Fig. 2). The inclusion of the empirical Morisita–Horn values ensured that the difference in z-scores between natives and aliens was not simply a consequence of native flower visitors having larger empirical Morisita–Horn values. Thus, for a given level of empirical similarity, native flower visitors tend to deviate more from random partner utilisation.

Quantifying the integration level

Removing species inevitably results in the loss of interactions, so the number of interactions was expected to decrease during

Table 2 Coefficients from linear mixed effects models when exploring the difference between native and alien pollinators (Origin) in terms of number of interaction partners (degree), specialisation (d'), species strength (Strength), and centrality within the networks (Closeness centrality). Because degree differed significantly between native and alien pollinators we ran models with and without degree as an explanatory variable when examining the effect of origin on the other response variables. In all models 'species identity' and 'island' were included as random factors. Negative coefficients for the variable 'Origin' means that native pollinators have smaller values

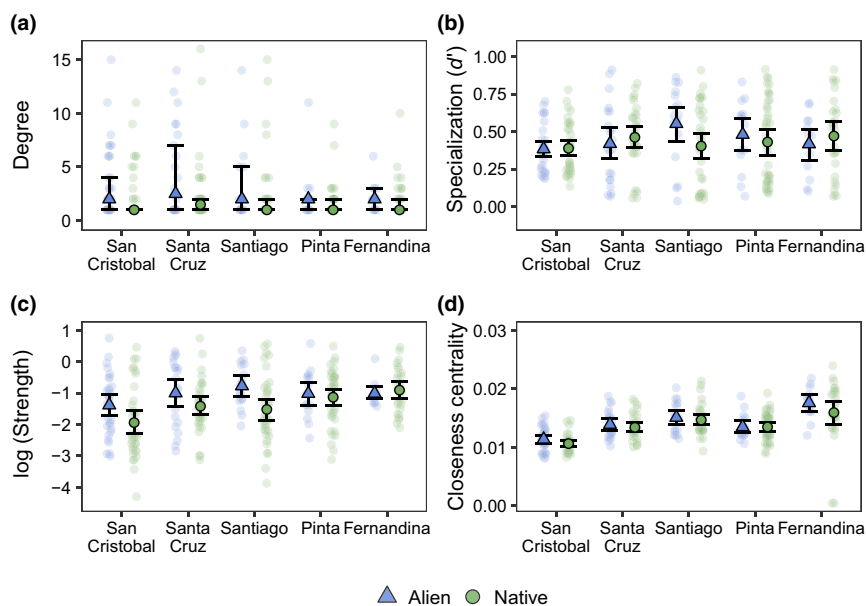| Response variable	Explanatory variable(s)		Distribution
	Origin	Origin + Log$_{10}$(Degree)	
Degree	**−0.327***		Poisson
d'	−0.066	−0.119 − 0.382*	Beta
Log$_{10}$(Strength)	**−0.374****	−0.128 + 2.056***	Gaussian
Closeness centrality	−0.061	−0.014 + 0.416***	Beta

*$P < 0.05$
**$P < 0.01$
***$P < 0.001$.

Figure 1 Comparison of native and alien flower visitors in terms of (a) degree, (b) quantitative specialisation (d'), (c) species strength, and (d) closeness centrality. Error bars delimit bootstrap confidence intervals of either the median (a), or the mean (b, c and d). Enlarged points represent the median (a) or the mean (b, c and d)
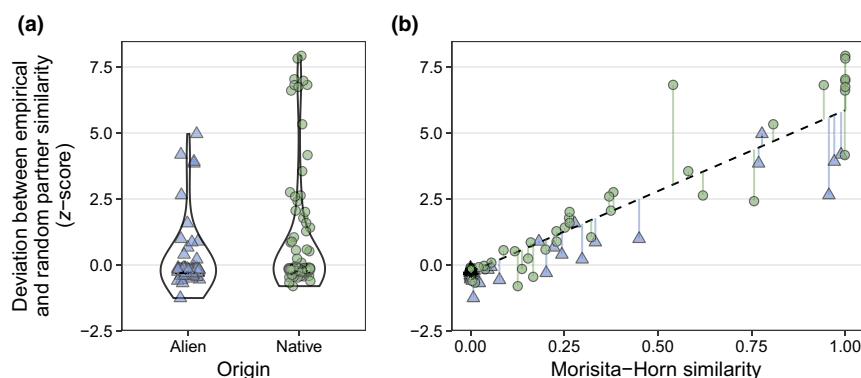

Figure 2 Deviation from random partner utilisation (measured with z-scores) as a function of (a) Origin and (b) the empirical partner similarity (measured with the Morisita-Horn index). In (b) violin plots emphasise the distribution of the z-scores within the alien and native flower visitors. Alien and native flower visitors are in both panels represented by blue triangles and green circles, respectively. Linear mixed effects model suggests that even when accounting for the empirical similarity values, native flower visitors had significantly larger z-scores ($P < 0.001$), i.e. on average they deviated more from random partner utilisation than alien flower visitors.

the elimination process. However, on San Cristobal, Santa Cruz, Santiago and Pinta, this decrease was more pronounced for the alien removal than for the native removal (Fig. 3a), resulting in significant negative associations between ΔI-values and the ratio of species removed (San Cristobal: Kendall's $\tau = -0.571$, $P < 0.001$; Santa Cruz: $\tau = -0.529$, $P < 0.001$; Santiago: $\tau = -0.202$, $P < 0.001$; Pinta: $\tau = -0.277$, $P < 0.001$) (see also Table S2 and Fig. 3b). Therefore, the patterns on these four islands suggest that alien flower visitors, on average, have more interactions than the natives. On Fernandina, the difference between alien and native removal resulted in a positive, but very weak, association between the ΔI-values and the ratio of species removed ($\tau = 0.054$, $P < 0.001$) (Table S2 and Fig. 3).

On nearly all the islands, the removal of species (both native and alien) lowered $WNODF_{z\text{-score}}$. However, on the more invaded islands the alien removal lowered $WNODF_{z\text{-score}}$ more than the native removal, leading to significant negative associations between $\Delta WNODF_{z\text{-score}}$ and the proportion of species removed (San Cristobal: $\tau = -0.355$, $P < 0.001$; Santa Cruz: $\tau = -0.213$, $P < 0.001$) (Table S2 and Fig. 3b). On the less disturbed islands, the pattern was opposite, leading to positive associations between $\Delta WNODF_{z\text{-score}}$ and the proportion of species removed (Santiago: $\tau = 0.111$, $P < 0.001$; Pinta: $\tau = 0.325$, $P < 0.001$; Fernandina: $\tau = 0.343$, $P < 0.001$) (Fig. 3b).

On San Cristobal ($\tau = 0.653$, $p < 0.001$), Fernandina ($\tau = 0.113$, $p < 0.001$), and Pinta ($\tau = 0.169$, $p < 0.001$) we
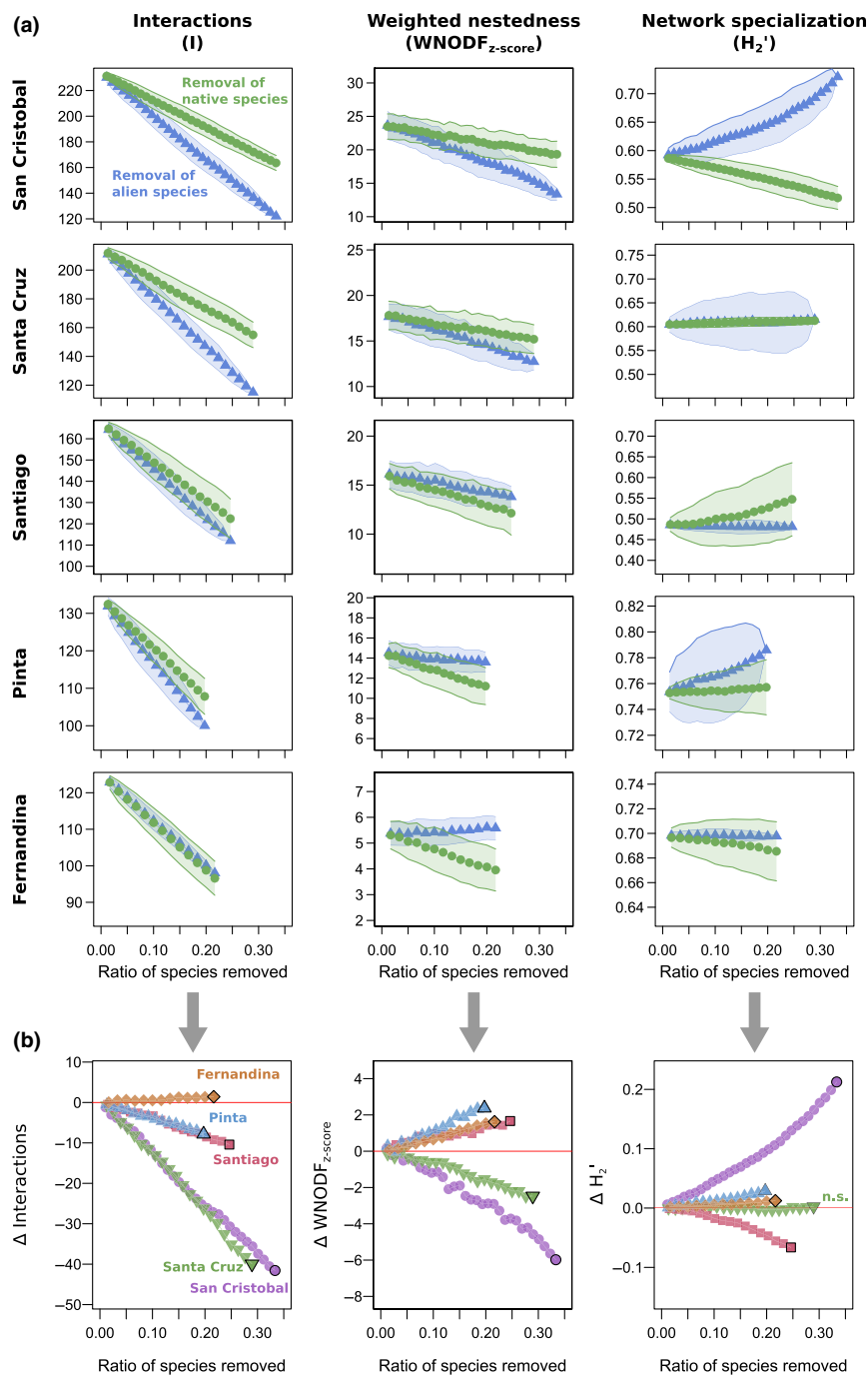
Figure 3 Panels in (a) demonstrate how total number of interactions, weighted nestedness ($WNODF_{z\text{-score}}$) and network specialisation (H_2') are affected when either alien (blue triangles) or native flower visitors (green circles) are sequentially removed from the five island networks. In all cases, points are averages and lines represent ± 1 SD from the 200 simulations. Summary panels in (b) visualise the differences (Δ-values) between the native and alien removal scenarios on each island, Fernandina = orange diamonds, Pinta = blue upward-triangles, Santiago = red squares, Santa Cruz = green downward-triangles, San Cristobal = purple circles. Variability around the average differences in b) has been omitted to increase clarity. In both (a) and (b) the x-axis represents the percentage of flower visitors removed during each simulation (see also materials and methods). All associations (except the one marked with n.s.) between the Δ-values and the percentage of species removed were significant at $P < 0.001$ (see Table S2), indicating that the networks are affected differently by the native and alien removals. The highlighted points in (b) are the final endpoint values used in Fig 4.

found a significant positive association between $\Delta H_2'$ and the proportion of species removed, which suggests that removal of native flower visitors, in general and when compared to the alien removal, leads to more generalised networks. On

Santiago ($\tau = -0.184$, $P < 0.001$), the pattern was opposite, as the native removal led to a more specialised network, and on Santa Cruz ($\tau = 0.006$, $P > 0.05$) there was no difference between the two groups (Table S2 and Fig. 3b).

Most of the Δ-values (all except one) were significantly associated with the proportion of species removed (Table S2), suggesting that macroscopic network descriptors responded differently to native and alien removal. Paired Wilcoxon tests revealed that for none of the network descriptors did the removal of native and alien insects lead to consistent responses across the islands (all $P > 0.1$; Fig. S3). We subsequently made linear regressions between the final endpoint Δ-values (see Fig. 3b) and the percentage of the islands that have been anthropogenically modified. The relationship was strong and significant for ΔI ($R^2 = 0.92$, $F = 49.8$, $P = 0.006$) and $\Delta WNODF_{z\text{-score}}$ ($R^2 = 0.92$, $F = 48.5$, $P = 0.006$), while the correlation was positive but not significant for $\Delta H_2'$ ($R^2 = 0.31$, $F = 2.8$, $P = 0.20$) (Fig. 4). Thus, two out of the three network descriptors suggest that the difference between native and alien integration increases on the more disturbed islands.

DISCUSSION

Here, we utilised a set of spatially replicated interaction networks across the Galápagos Islands to elucidate whether native and alien flower visitors differ in their community integration. We found that alien flower visitors interact with more plant species, that alien insects tend to be topologically more important for the plants than natives (larger species strength) (Fig. 1), and that native flower visitors have higher partner fidelity (Fig. 2). Furthermore, removal simulations showed significant differences in the way that key network descriptors respond to the removal of native and alien flower visitors, indicating that these two groups are indeed integrated differently (Fig 3). Importantly, the magnitude and direction of this difference varied across the archipelago, and when using an independent measure of island degradation we found significant correlations between the actual differences and the percentage of each island that has been anthropogenically modified. This tentatively suggests that the combined impact of alien flower visitors, measured by their influence on the network structure, intensifies on the more disturbed islands.

Species–level indices

In a pollination context, work on alien species has traditionally focused on a single or a few dominant invasive alien plants (Lopezaraiza-Mikel *et al.* 2007; Bartomeus *et al.* 2008; Vilà *et al.* 2009; Ferrero *et al.* 2013; Albrecht *et al.* 2014) (but see Olesen *et al.* 2002; Aizen *et al.* 2008), and among the flower visitors, *Apis mellifera* has undoubtedly received most attention (Goulson 2003). However, these widespread and abundant species – often with invasive behaviour – represent only a minority of all alien species. Non-invasive alien species can also impact recipient communities, although such effects have received little attention and produced few generalisations so far (Timóteo *et al.* 2018). If the many non-invasive alien species differ consistently from the native species in for example their interaction patterns it might impose unforeseen consequences in the long run. Using a multi-species approach, we found that alien flower visitors on the Galápagos tend to be more generalist, hereby corroborating findings from plant focused (Bartomeus *et al.* 2008; Albrecht *et al.* 2014; Maruyama *et al.* 2016) and single pollinator focused studies (Santos *et al.* 2012). However it stands in contrast to the fairly specialised alien pollinators on Ile aux Aigrettes and Azores (Olesen *et al.* 2002). In some network studies pollinators have been found to have a high dependency on alien plants (Bartomeus *et al.* 2008; Stouffer *et al.* 2014; Maruyama *et al.* 2016), and this is here extended to alien flower visitors because the plant species on the Galápagos had a tendency to be more connected to the alien than the native flower visitors (i.e. aliens had higher species strength). The ultimate consequences of such patterns are difficult to predict, but it seems likely that this profound integration of alien flower visitors may have a marked influence on the plant species. Eventually, these differences might influence vegetation dynamics (Kearns *et al.* 1998) and alter the plant communities on the Galapagos, for example by favouring generalist plant species. More detailed investigations of e.g. the pollen transport network (Tur *et al.* 2014), and the effectiveness of these flower visitors as pollinators, would help identifying any ecological and evolutionary implications. Contrary to expectations, we
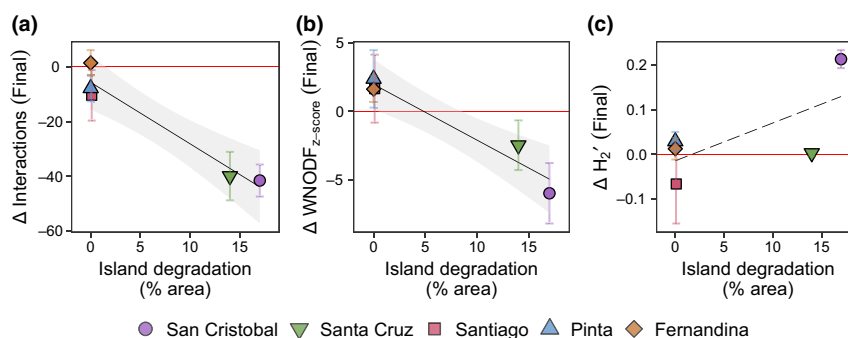

Figure 4 The final average difference in total number of interactions (a), standardised weighted nestedness (b) and network specialisation (c) between the native and alien removal simulations (i.e. the highlighted points in Fig. 3b) as a function of island degradation (measured as the percentage of each island that had been anthropogenically modified; quantified in Watson *et al.* (2010)). Using linear regressions the correlations were strong and significant for $\Delta Interactions$ ($R^2 = 0.92$, $P = 0.006$) and $\Delta WNODF_{z\text{-score}}$ ($R^2 = 0.92$, $P = 0.006$), but not significant for $\Delta H_2'$ ($R^2 = 0.31$, $P = 0.20$). Error bars around each point represent the spread (± 1 SD) in the final average difference from the 200 simulations.

did not find significant differences between native and alien flower visitors in terms of quantitative specialisation and closeness centrality.

Partner fidelity

Partner fidelity, as defined here, is not simply a matter of interacting with many or few species, but rather it is a matter of consistency in partner utilisation (MacLeod *et al.* 2016). According to our expectation, we found that native flower visitors showed higher partner fidelity as they deviated more from random partner utilisation than alien flower visitors. Our measure of fidelity is based on across-island comparisons (similar to Trøjelsgaard *et al.* 2015; Carstensen *et al.* 2018), and the results therefore suggest that alien flower visitors use a broader assemblage of the available plant species when viewed at the scale of the archipelago. If such behaviour can be transferred to the community level it might have implication for plant reproduction. For example, heterospecific pollen transfer is to a large extent governed by the fidelity and generalisation level of the pollinators (Morales & Traveset 2008). Indeed, low floral fidelity among pollinators may increase the transfer of pollen between plant species, and ultimately translate into lower seed set (Brosi & Briggs 2013). Thus, the lower fidelity of alien flower visitors on the Galápagos may eventually have consequences for plant reproduction, although the severity of this effect, if any, is currently unknown. Furthermore, it should be mentioned that species with an overall low partner fidelity could actually by comprised of individuals with high fidelity over the timescale important for pollination (Tur *et al.* 2014; Brosi 2016), and the exploration of the drivers of individual fidelity remain an interesting research area.

Unveiling whether this lower fidelity is a product of their shorter residence time, or whether it is an inherent characteristic of alien species would require further scrutiny. For example, it has been shown that, the network role of alien species in their native ranges tends to be a good predictor of their role in alien ranges (Emer *et al.* 2016). Accordingly, estimating the partner fidelity of alien species in both their native and alien ranges would offer novel understanding of whether this is an inherent characteristic or something they eventually acquire in their alien range.

Network integration

Two things are noteworthy regarding the integration of alien flower visitors on the Galápagos. First, most macroscopic network descriptors were affected differently by the alien and native removals (Fig. 3), which suggests that alien and native insects do not integrate similarly. Therefore, the ecological roles currently upheld by the natives will probably not experience a 1 : 1 replacement should they be outcompeted by the aliens. Second, and importantly, the magnitude and direction of the responses varied across the islands. As noted by Aizen *et al.* (2008), alien species may range in impact from mostly harmless commensals in the early stages of invasion to monopolising and functionally important species at later stages. Similarly, longer residence time increase the likelihood

that naturalised species become invasive (Trueman *et al.* 2010), and Heleno *et al.* (2013) found a time-lag in the impact of fruit-producing alien plants upon seed-dispersal networks. Together, this suggests that the integration of alien flower visitors on more recently invaded islands may differ from the integration on islands that have been invaded for a longer period.

Here, we used the proportion of each island that has been modified (Watson *et al.* 2010), as a measure of the combined anthropogenic pressure (i.e. time since human arrival, human population size, cultivation etc.), and for two out of three network descriptors we find that the difference between native and alien integration is strongly and significantly related to island degradation. This emphasises that the current homogenisation of the world's biota might have nonlinear impacts on the functioning of recipient communities, as the difference between native and alien species likely intensifies with the level of degradation. With the current data it is not possible to evaluate whether this is related to longer residence time, larger alien populations, or whether the alien flower visitors simply have moved up the invasion ladder (Blackburn *et al.* 2014). In order to evaluate the generality of these patterns it would be fruitful to include e.g. Floreana and Isabella in future studies, as both have a long history of human influence (Trueman *et al.* 2010).

CONCLUSION

While there has been a solid focus on understanding the impact of aggressive invasive species, non-invasive aliens have received comparatively little attention. By using spatially replicated networks across the Galápagos, and by focusing on multiple alien species the current study emphasises that non-invasive aliens should not be neglected when attempting to preserve pristine communities. Successful management strategies requires detailed information about the ecological role and integration of alien species (Valdovinos *et al.* 2009; Ferrero *et al.* 2013), and the approaches outlined here, e.g. estimation of partner fidelity and the artificial removal of species to quantify the combined impact, offer a step towards understanding such roles at the community level. Moreover, the current data support the proposition of early management actions (Simberloff *et al.* 2013), because the differences between native and aliens species intensified on islands with a longer human history.

AUTHORSHIP

KT and AT conceived the ideas. KT analysed the data and wrote the first draft. RH and AT collected the data and contributed substantially to the writing.

DATA AVAILABILITY STATEMENT

The Plant–Flower visitor networks used in this publication are available at Figshare (https://doi.org/10.6084/m9.figshare.8081567.v1).

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