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Pollination networks from natural and anthropogenic-novel communities show high structural similarity

Sérgio Timóteo[1] · Catherine J. O'Connor[1,2] · Francisco A. López-Núñez[1] · José M. Costa[1] · António C. Gouveia[1,3] · Ruben H. Heleno[1]

Abstract

The Anthropocene is marked by an unprecedented homogenisation of the world's biota, confronting species that never co-occurred during their evolutionary histories. Interactions established in these novel communities may affect ecosystem functioning; however, most research has focused on the impacts of a minority of aggressive invasive species, while changes inflicted by a less conspicuous majority of non-invasive alien species on community structure are still poorly understood. This information is critical to guide conservation strategies, and instrumental to advance ecological theory, particularly to understand how non-native species integrate in recipient communities and affect the interactions of native species. We evaluated how the structure of 50 published pollination networks changes with the proportion of alien plant species and found that network structure is largely unaffected. Although some communities were heavily invaded, the proportion of alien plant species was relatively low (mean = 10%; max. = 38%). We further characterized the pollination network in a botanic garden with a plant community dominated by non-invasive alien species (85%). We show that the structure of this novel community is also not markedly different from native-dominated communities. Plant–pollinator interactions revealed no obvious differences regarding plant origin (native vs. alien) or the native bioregion of the introduced plants. This overall similarity between native and alien plants is likely driven by the contrasting patterns of invasive plants (promoting generalism), and non-invasive aliens, suggested here to promote specialization.

Keywords Biological homogenisation · Biological invasions · Botanic garden · Alien plants · Novel communities

Introduction

The intensification of international trade has resulted in an unprecedented reshuffling of species across national and continental borders with the concomitant homogenisation

✉ Sérgio Timóteo
stimoteo@gmail.com

[1] Department of Life Sciences, Centre for Functional Ecology (CFE-UC), University of Coimbra, Coimbra, Portugal

[2] Cardiff School of Biosciences, Cardiff University, Cardiff, UK

[3] Botanic Garden of the University of Coimbra, Coimbra, Portugal

of the world's biota (McKinney and Lockwood 1999; Olden et al. 2006; Devictor et al. 2010). Accordingly, the progressive taxonomic, genetic, and functional similarity of communities in response to the rapid translocation of species among previously isolated bioregions is currently a central concern in conservation (Olden et al. 2006; Smart et al. 2006; Barnosky et al. 2012). Plants, in particular, are often introduced into non-native ranges—alien species, either intentionally for their agricultural or ornamental value, or accidentally (Potts et al. 2010). Many of these species can overcome the biotic and abiotic barriers that limit their survival and reproduction in their recipient communities, and some can rapidly spread in the new ranges to become invasive, i.e. "winners" (sensu McKinney and Lockwood 1999), outcompeting many native species ("losers") (Vilà et al. 2009; Richardson 2010). Community-level studies showed that this replacement might lead to a reduction in plant species richness that can ripple through food-webs, causing further simplification of entire communities (e.g. Heleno et al. 2009; López-Núñez

et al. 2017), threatening community stability and ecosystem services (Richardson et al. 2000a; Traveset and Richardson 2006). Many of these changes have been recently highlighted by implementing a network/food web approach to explore the interplay between community composition, structure, and functioning (e.g. Heleno et al. 2014; Tylianakis and Morris 2017). Overall, the invasion of plant–animal mutualistic networks seems to increase the level of generalism of interaction networks as these become dominated by generalist alien species (Aizen et al. 2008; Tylianakis and Morris 2017). Importantly, however, most of these studies are largely restricted to the impacts of only one or a few dominant invasive species, such as *Impatiens glandulifera* in the UK (Lopezaraiza-Mikel et al. 2007), *Carpobrotus affine* and *Opuntia stricta* in Spain (Bartomeus et al. 2008), *Opuntia* spp. in the Canaries and Balearics (Padrón et al. 2009), and others (e.g. Aizen et al. 2008; Vilà et al. 2009; Albrecht et al. 2014). Even if some of these studies monitored highly invaded sites, the focus was on the impacts of one or a few aggressive invasive species (e.g. Stouffer et al. 2014; Albrecht et al. 2014; Kaiser-Bunbury et al. 2017). However, it is estimated that only 11% of the alien plant species in Europe are invasive, which fits the informal tens-rule by which only one in 10 introduced species becomes invasive (Williamson 1993; Vilà et al. 2010). While understandable, the emphasis put on documenting the impacts of invasive species is in sharp contrast with the relative small proportion of all alien species that actually have a documented invasive behaviour (Williamson 1993; Vander Zanden 2005; Vilà et al. 2010), thus generating a bias towards invasive species in the literature. For example, in the studies of Traveset et al. (2013), and Memmott and Waser (2002), which look at the impact of alien plants, only 5% and 12% of the plant species on invaded communities are actually introduced to the Galapagos and the United States, respectively. These studies are indeed highly informative regarding the impacts of invasive alien plant species (e.g. Albrecht et al. 2014). However, they tend to neglect the potential impacts of a vast majority of non-invasive alien species that slowly naturalize in the wild without significant spread (Richardson et al. 2000b; Olden et al. 2006). Consequently, these studies might not fully capture the effects of biotic homogenisation resulting from direct or indirect human disturbance (e.g. Lurgi et al. 2012). Understanding the interaction patterns that characterize novel communities, i.e. those formed by species that do not share a common evolutionary history (Hobbs et al. 2006), is essential to evaluate community resilience and the capacity of these communities to continue to delivery key ecosystem services (Razanajatovo et al. 2015; Hui et al. 2016; Le Roux et al. 2017). In this context, botanical gardens represent an invaluable experimental ground for comparative and community-wide studies as they host a wide range of species from different origins, growing under the same climatic and ecological conditions (Primack and Miller-Rushing 2009; Razanajatovo et al. 2015, 2018).

Here, we first evaluate if the proportion of alien plant species present in 50 quantitative pollination networks available in the literature result in any consistent change on network structure. Changes in community structure resulting from the incorporation of alien species may result in the redistribution of links among species (Aizen et al. 2008; Grass et al. 2013). We hypothesise that the integration of alien plant species will tend to increase network connectivity as alien plant species tend to produce many large and conspicuous flowers –with abundant nectar and pollen rewards (Chittka and Schürkens 2001; Morales and Aizen 2006; van Kleunen et al. 2018), thus attracting a large assembly of pollinators (Aizen et al. 2008; Albrecht et al. 2014). Second, we reconstruct the pollination network of the highly anthropogenic setting of a botanical garden in Portugal to explore if the structure of this novel community significantly differs from the structure of spontaneous communities dominated by native plant species. Finally, we aimed to investigate whether native and alien plant species in this novel community consistently differ in the interaction patterns established with the pollinator fauna, and if plant species native from different global biogeographic regions (hereafter bioregions) diverge in their visitation patterns. We expect that alien species will tend to be visited by a greater number of pollinators and a higher specialization of native species,and that Holarctic plants will differ in the interaction patterns from the those observed for species from the remaining bioregions.

Methods

Is community structure affected by the incorporation of alien plant species?

To evaluate how the structure of pollination networks is affected by alien species we calculated eight network-level descriptors for 50 quantitative plant-pollinator networks available in the ecological literature (Table 1, and Supplementary references). As independent estimates of plant species abundance are rarely available we used the proportion of alien plant species in the network as a proxy of alien plant integration (Traveset et al. 2016). Alternative measures could include the proportion of insect visits to alien plant species (% of the matrix marginal sums of alien plants), although such a metric would be largely constrained by species visitation patterns and, therefore, a result of network structure (Dormann et al. 2017). Thus, the proportion of alien species provides in our view a more independent benchmark to explore the consequences of all alien plants regardless of their local abundance and visitation patterns.

Table 1 Study location, pollination network size and number of alien plant species from the literature (full references in the ESM)

Study location	Network size (plant sp. × animal sp.)	Number of alien plant species (%)	References
Berchtesgaden NP, Germany	121×410	0 (0.0)	Benadi et al. (2013)
Nahuel Huapi NP, Argentina	41×90	2 (14.3)	Vázquez and Simberloff (2002)
Kosciusko NP, Australia	41×83	2 (4.9)	Inouye and Pyke (1988)
Avon Gorge, UK	64×174	7 (10.9)	Carvalheiro et al. (2008)
Bristol, UK	25×79	0 (0.0)	Memmott (1999)
Bristol, UK	23×147	1 (4.3)	Lopezaraiza-Mikel et al. (2007)
Duke forest, North Carolina, USA	13×47	0 (0.0)	Motten (1986)
Cap de Creus NP, Spain	32×81	7 (20.4)	Bartomeus et al. (2008)
University of Wurzburg, Germany	56×257	4 (7.1)	Junker et al. (2013)
Hestehaven, Denmark	28×82	8 (28.6)	Olesen (unpublished data)
Norwood farm, UK	47×241	9 (19.1)	Pocock et al. (2012)
Ottawa, Canada	13×24	0 (0.0)	Small (1982)
Nahuel Huapi NP, Argentina	27×111	10 (35.8)	Aizen et al. (2008)
Western Sahara	12×82	1 (8.3)	Trøjelsgaard et al. (2015)
Cairngorms NP, UK	28×162	1 (3.6)	Devoto et al. (2012)
Latnjajaure, Abiskoosta, Sweden	23×118	0 (0.0)	Elberling and Olesen (1999)
Hickling, Norfolk, UK	17×61	0 (0.0)	Dicks et al. (2002)
Shelfanger, Norfolk, UK	16x 36	0 (0.0)	Dicks et al. (2002)
Ilê aux Aigrettes, Mauritius	14×13	5 (8.6)	Olesen et al. (2002)
Lake Hazen, Ellesmere Is., Canada	29×81	0 (0.0)	Hocking (1968)
Lake Hazen, Ellesmere Is., Canada	30×114	0 (0.0)	Kevan (1970) (PhD thesis)
Black River Gorge NP, Mauritius	58×100	5 (8.6)	Kaiser-Bunbury et al. (2009)
Flores Is., Azores	10×12	3 (30.0)	Olesen et al. (2002)
Las Conchas, Graciosa, Canary Is.	25×61	0 (0.0)	Castro-Urgal and Traveset (2014)
Caletón Blanco, Lanzarote, Canary Is.	18×60	1 (5.6)	Castro-Urgal and Traveset (2014)
Son Bosc, Mallorca, Balearics	67×123	2 (3.0)	Castro-Urgal and Traveset (2014)
Cala Mesquida, Mallorca, Balearics	42×118	0 (0.0)	Castro-Urgal and Traveset (2014)
Puig Major, Mallorca, Balearics	54×183	0 (0.0)	Tur (2015) (PhD thesis)
Nakaikemi, Tsuruga, Japan	64×187	3 (4.7)	Kato and Miura (1996)
Mt Kushigata, Japan	90×356	1 (1.1)	Kato et al. (1993)
Mt Yufu, Kyusyu, Japan	99×294	4 (4.0)	Yamazaki and Kato (2003)
Melville Is., Canada	11×18	0 (0.0)	Mosquin and Martin (1967)
Fernandina Is., Galapagos, Ecuador	18×60	0 (0.0)	Traveset et al. (2013)
Pinta Is., Galapagos, Ecuador	21×76	0 (0.0)	Traveset et al. (2013)
Santiago Is., Galapagos, Ecuador	24×69	2 (8.3)	Traveset et al. (2013)
San Cristobal Is., Galapagos, Ecuador	21×93	3 (14.3)	Traveset et al. (2013)
Santa Cruz Is., Galapagos, Ecuador	23×76	1 (4.3)	Traveset et al. (2013)
Kyoto City, Japan	113×314	43 (38.1)	Kakutani et al. (1990)
Uummannaq Is., Greenland	17×26	1 (2.6)	Lundgren and Olesen (2005)
Amami-Ohsima Is., Ryukyu, Japan	110×609	4 (3.6)	Kato (2000)
Jamaica, Carabbean	12×43	2 (6.9)	Ingversen (2006) (MSc thesis)
Dominica, Caribbean	31×43	1 (3.2)	Ingversen (2006) (MSc thesis)
Gran Canaria, Canary Is.	12×73	0 (0.0)	Trøjelsgaard et al. (2015)
La Gomera, Canary Is.	15×73	0 (0.0)	Trøjelsgaard et al. (2015)
Fuerteventura, Canary Is.	9×74	0 (0.0)	Trøjelsgaard et al. (2015)
Teno, Tenerife, Canary Is.	19×89	0 (0.0)	Trøjelsgaard et al. (2015)
Fasnia, Tenerife, Canary Is.	16×92	0 (0.0)	Trøjelsgaard et al. (2015)
Fårö, Baltic Is., Sweden	34×88	2 (5.9)	Johansson (2012)
Gotska Sandon, Baltic Is., Sweden	44×160	2 (4.5)	Wallin (2011) (MSc thesis)

Table 1 (continued)

Study location	Network size (plant sp. × animal sp.)	Number of alien plant species (%)	References
Hierro, Canary Is.	11 × 62	0 (0.0)	Trøjelsgaard et al. (2015)
Coimbra, Portugal	132 × 176		This study

Because interaction frequency has been quantified differently across studies (e.g. number of visits, visitation rate), all matrices were standardized by dividing its interaction weights by the lowest non-zero interaction weight in the matrix and rounded it to nearest integer. This transformation converts interactions in each matrix to multiples of the lowest link weight. The following descriptors were evaluated: (1) mean number of links per species; (2) weighted connectance, the link density divided by the total number of species present in the network (Tylianakis et al. 2007); (3) weighted nestedness (WINE—Weighted Interaction Nestedness Estimator), measuring the extent to which the interactions are hierarchically arranged around a core of generalist interactions (Galeano et al. 2009); (4) network specialisation (H_2'), a discriminative measure of network selectiveness (Blüthgen et al. 2006); (5) pollinator robustness, the extent to which the pollinator community is resilient to the random loss of plant species; and (6) plant robustness, the extent to which the plant community is resilient to the random loss of pollinators (Memmott et al. 2004).

Because several network-level descriptors are not independent from network size and sampling effort (Fründ et al. 2016), we compared community structure by means of null model-corrected network descriptors, which allow for comparisons across networks based on the relative departure of the observed structure from that predicted by a null model expectation based on random interactions (Thebault and Fontaine 2010; Schleuning et al. 2012; Costa et al. 2015). This was done by calculating the difference between each network descriptor and those from 1000 randomized networks obtained with Patefield's null model (Patefield 1981), which reshuffles interactions while constraining species richness and the number of interactions per species (Dormann et al. 2008), and dividing it by the mean of the randomized networks.

To assess the effect of the proportion of alien species on the number of links per species and weighted connectance we used a Generalized Linear Models (GLM) with Gamma and Gaussian errors, respectively, with the R function *glm()*. To account for the presence of extreme values and heteroscedasticity when exploring the effects on nestedness, network specialization, insect robustness, and plant robustness we used a robust generalized linear model with Gamma errors. Robust regressions have the advantage of down-weighting the influence of outliers and being more robust to heterogeneous variance than standard regressions, allowing the effect of variables and their direction not to be affected by a few highly influential points (Cantoni and Ronchetti 2001, 2006). This procedure was implemented with the function *glmrob()* from the R package robustbase 0.92-8 (Rousseeuw et al. 2017). All response variables were transformed to meet the assumptions of the respective models and achieve a better fit (see Table 2 for details).

Table 2 Effects of the proportion of alien species on network structure descriptors explored by GLMs and robust GLMs

	Links per species	Weighted connectance	Weighted nestedness	Network specialization	Pollinator robustness	Plant robustness
Transformation	$-y$		$-(y-1)$	$\log(y)$	$-y$	$-y$
Model	GLM	LM	Robust GLM	Robust GLM	Robust GLM	Robust GLM
Error family	Gamma		Gamma	Gamma	Gamma	Gamma
Link function	Identity		Inverse	Inverse	Inverse	Inverse
Intercept	48.509	53.051	0.037	0.151	0.110	0.066
(SE)	(3.360)	(2.389)	(0.004)	(0.004)	(0.012)	(0.009)
p	<2e−16***	<2e−16***	<2e−16***	<2e−16***	<2e−16***	2e−13***
% Aliens	0.299	0.065	−0.0001	−0.0001	−0.001	−0.0004
(SE)	(0.309)	(0.194)	(0.0003)	(0.0003)	(0.001)	(0.001)
p	0.338	0.737	0.817	0.821	0.564	0.527

All descriptors were corrected against a null model based on the Patefield's algorithm. *P* values were derived with a *t* test for links per species and weighted connectance, and with a *z* score test for the remaining descriptors. *$p < 0.1$; **$p < 0.05$; ***$p < 0.01$

How does a novel community differ from spontaneous communities dominated by native plant species?

To assess the structural differences between a highly anthropogenic novel community and those dominated by native plant species, we reconstructed the plant-pollinator network of the Botanic Garden of the University of Coimbra, central Portugal (40°12′N, 8°25′W, ESM Fig. S1). The garden is primarily host to species of medical interest and ornamental alien flora, many of which originated from former Portuguese colonies around the world, including Angola and Mozambique (Africa), Brazil (South America), and across Asia, with selected representative species from all the main branches of the plant phylogenetic tree distributed in flower beds, and active maintenance is kept to the minimum necessary. The site has a Mediterranean climate influence with mild-humid winters and hot-dry summers.

We recorded flower-visitation interactions by conducting timed censuses to focal flowers (Castro-Urgal et al. 2012), between 9:00 h and 19:30 h during favourable weather conditions from 28-Oct-2016 to 20-May-2017. We conducted at least 15 min of observations on each plant species twice per week during their complete flowering season, recording all contacts of flying animals with the reproductive organs of open flowers. Although pollination effectiveness was not experimentally confirmed, we only recorded visitors that directly contacted with the stigmas or the anthers, and hereafter we refer to them as pollinators for simplicity. Overall, we accumulated 255 h of visitation census, which is within the range of the sampling effort of the networks retrieved from the literature (mean = 142 h; min. = 18 h; max. = 300 h); the observation time of each plant species being proportional to its abundance and to the duration of its flowering period, so that rare interactions are not oversampled. Initially voucher specimens of all pollinating insects were collected and identified by expert taxonomists to lowest possible taxonomic level. To minimize the disturbance of the local pollinator fauna, on subsequent visits by visually similar insects, these were captured, photographed, and immediately released on site, being latter identified based on the voucher specimens. Flower abundance was estimated by weekly floral surveys, counting all open flowers of each species along three linear transects of 200 m × 10 m. We considered flower units as separate entities if the distance between them required the pollinator to fly from one unit to the other (e.g. Carvalheiro et al. 2008).

All pairwise interactions between plants and pollinators were organised into an interaction matrix, where each pairwise interaction was quantified in terms of flower visitation rate, i.e. number of visits/number of open flowers/time, which allows a realistic representation of the community structure (Castro-Urgal et al. 2012). The same network standardization and null model corrected network descriptors used in the previous section were applied to the Botanic Garden network. Network descriptors from this network were then compared to those from the literature and significant differences were inferred whenever a descriptor of the novel networks lay outside the 95th percentile range of the corresponding descriptor on the reference networks.

Do native and alien plant species differ in their pollinator visitation patterns?

To look for differences in interactions established by different plant groups, we characterized all plant species according to their origin, i.e. native or alien to Portugal, and according to their native bioregion (Cox 2001). Bioregions define areas with unifying geographic features and marked by broad similarities in their flora and fauna (e.g. de Buffon 1761; von Humboldt 1816; Cox 2001). Plant species were assigned to a bioregion based on the online databases Global Biodiversity Information Facility (GBIF 2017) and World Checklist of Selected Plant Families (WCSP 2017). For each of these plant species, we then calculated three widely used descriptors of species-level interaction patterns: (1) plant degree (or linkage level), the number of pollinator species visiting each plant; (2) plant species strength, a measure of plant species' importance for the overall pollinator community; and (3) plant specialization index (d'), describing the level of plant selectiveness for pollinators as departing from an expected visitation frequency based exclusively on species abundances (Blüthgen et al. 2006). The effect of plant origin and bioregion on species-level descriptors was explored with independent (GLM) with negative binomial, Gamma and Gaussian errors, respectively, using the function *glm()* available from software R 3.3.3 (R Development Core Team 2017). To meet the assumption of normality and homoscedasticity, specialisation d' was square root transformed. Pairwise differences were assessed using Tukey tests, with R's multcomp package (Hothorn et al. 2008).

All species- and network-level descriptors were calculated with the R package bipartite 2.08 (Dormann et al. 2009; Dormann 2011).

Results

Is community structure affected by the incorporation of alien plant species?

The number of plant species in the 50 networks retrieved from the literature varied between 22 and 719 (mean = 158), and the proportion of alien plant species between 0% (i.e. all plants being native) and 38% (mean = 7%, median = 12%; (Table 1). Contrary to our expectations, we found no

significant effect of the proportion of alien plant species on any network descriptor (p > 0.34 for all descriptors; Fig. 1, Table 2).

How does a novel community differ from spontaneous communities dominated by native plant species?

Overall, we recorded 17,206 visits between 176 pollinators species and 132 plant species in the novel community of the botanical garden (Fig. 2). Most plants (85%) were identified to the species level, and the remainder (15%) to the genus level: 46% of the pollinators were identified to the species level, and the remainder were grouped into

morphospecies within the lowest possible taxonomical level: genus (30%), family (17%), or order (7%) (ESM Fig. S2). We recorded 9 orders of insects and a single bird species (blue tit, *Cyanistes caeruleus*), visiting flowers for pollen or nectar.

Most of the censused plant species were alien (85%, 112 species), and most of them were intentionally planted and cultivated in the garden for several decades, and the remaining 20 plant species (15%) were native. Nevertheless, the structure of the pollination network in this novel community is very similar to that of spontaneous communities reported in the literature, with all metrics falling within the 95th percentile range of the published networks (Fig. 1).
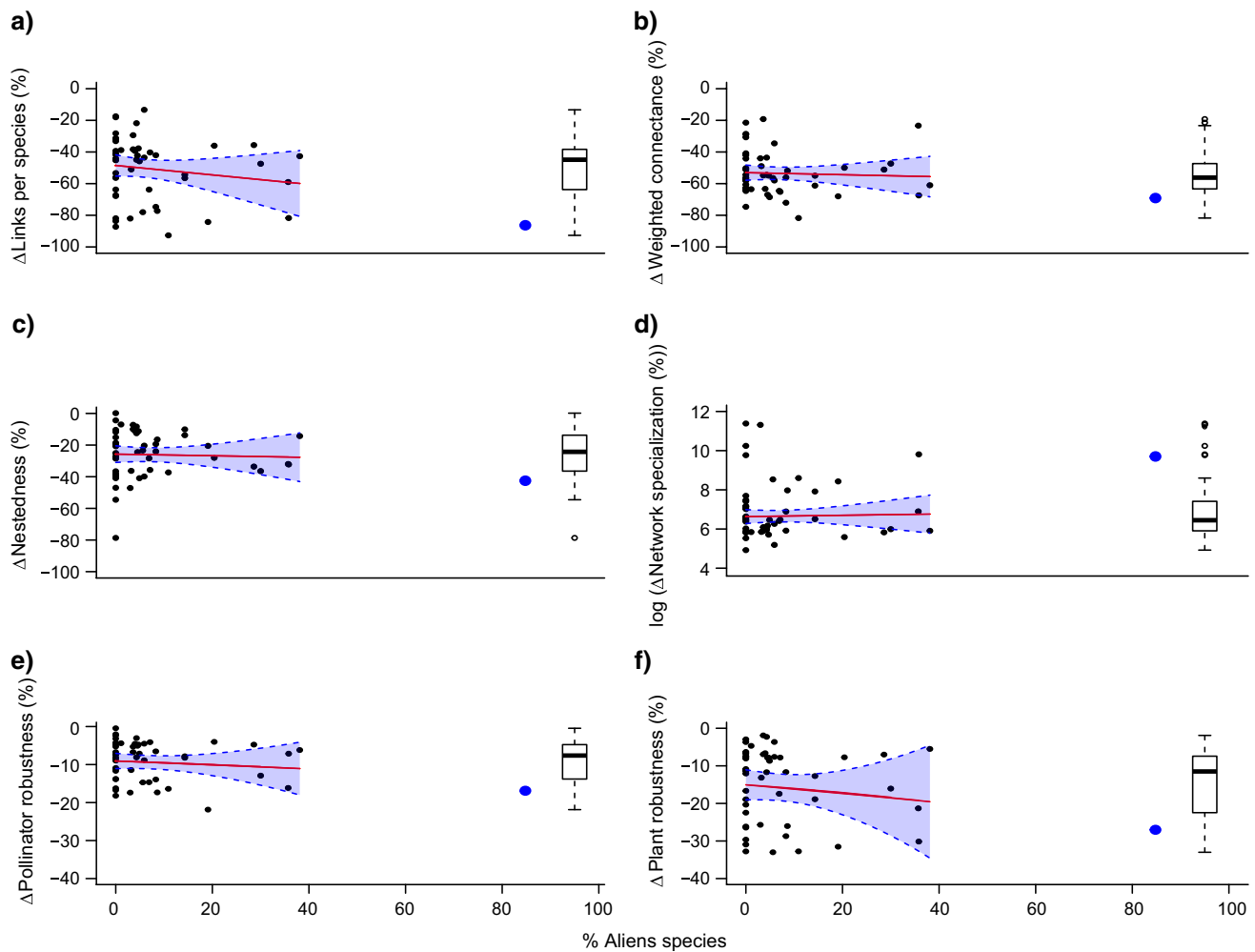

Fig. 1 Effect of the proportion of alien plant species on six network structure descriptors. Changes on each descriptor are considered in relation to the deviance of null model expectations to account for different network sizes (see "Methods"). Communities retrieved from the scientific literature are depicted in black, and the highly anthropogenic novel community of the Botanic Garden of the University of Coimbra—Portugal, in blue. The red line indicates the back-transformed fitted values of the regression and the shaded area represents the 95% confidence interval of the regression. The boxplots on the right represent the distribution of the values of each descriptor for the 50 published networks, regardless of their level of invasion. Colour version of this figure is available online
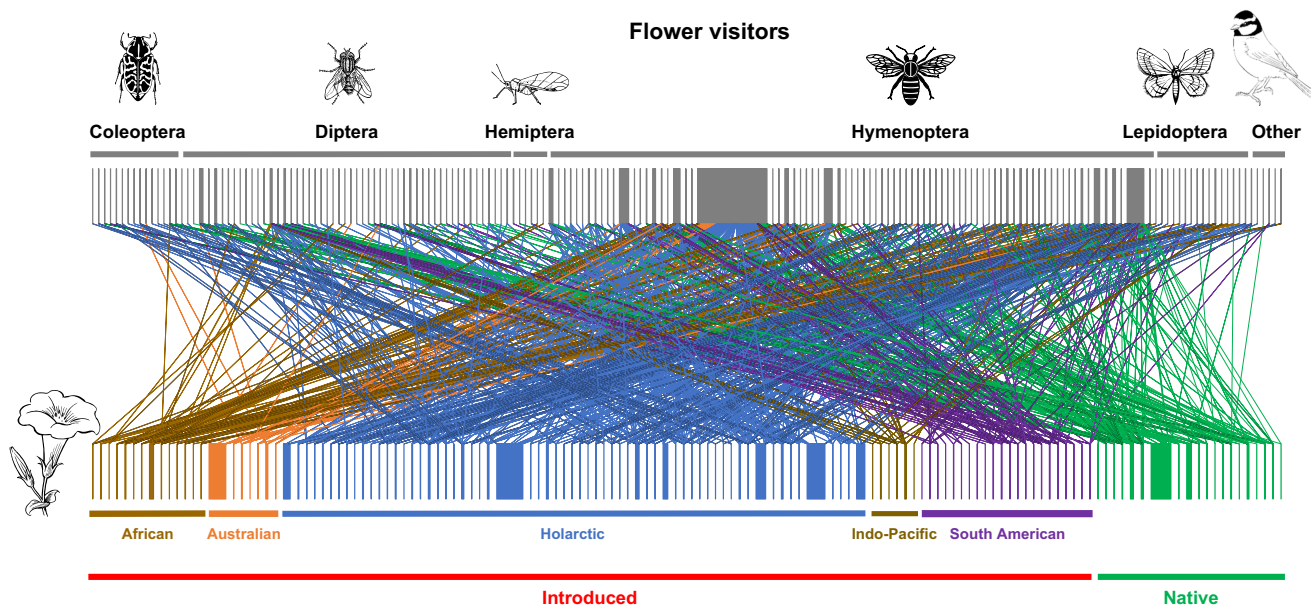
Fig. 2 Quantitative plant visitation network of the Botanic Garden of the University of Coimbra, Portugal. The network represents the interactions between 176 pollinators and 132 plant species and the width of each interaction is proportional to the number of visits/ flower/minute. Network based on 255 h of direct observations to flowers between November 2016 and May 2017. Species identities provided in ESM Fig. S2. Colour version of this figure is available online

Do native and alien plant species differ in their pattern of interaction with pollinators?

The alien species present in the botanical garden are native to the Holarctic (48%, 63 species), South America (17%, 22 species), Africa (10%, 14 species), Australia (5%, 7 species), and the Indo-Pacific (5%, 6 species). The main pollinators were Hymenoptera, with respect to both species richness (45%) and interaction frequency (87%), followed by Diptera (31% and 11%, respectively). *Apis mellifera* was the most frequently recorded pollinator species with 6142 visits recorded (36% of the total) and was also the most generalist, visiting the flowers of 67 plant species (50% of all plants in the network; Fig. 1). On average, each pollinator species visited 4.6 plant species (Min = 1; Max = 67), which in turn received, on average, visits from 6.1 pollinator species (Min = 1; Max = 29). We found no significant differences (all Tukey test, $p > 0.18$) between alien and native plant species regarding the richness of pollinators (Fig. 3a; GLM: $\chi^2 = 1.37$, $df = 1$; $p = 0.24$), specialisation d' (Fig. 3c; LM: $\chi^2 = 0.11$, $df = 1$; $p = 0.07$), or plant species strength (Fig. 3e; GLM: $\chi^2 = 0.72$, $df = 1$; $p = 0.55$). Similarly, we found no consistent differences (all Tukey test, $p > 0.11$) between the interaction patterns established by plants from different bioregions regarding their number of pollinators (Fig. 3b; GLM: $\chi^2 = 11.30$, $df = 4$; $p = 0.02$), specialisation d' (Fig. 3d; LM: $\chi^2 = 0.05$, $df = 4$; $p = 0.82$), or species strength (Fig. 3f; GLM: $\chi^2 = 15.27$, $df = 4$; $p = 0.07$).

Discussion

Despite the large body of knowledge documenting the negative effects of invasive alien species on biodiversity and on community structure, there is still very little information regarding the effects on non-invasive alien plants, which form the largest component of species naturalized outside their native ranges worldwide. Contrary to our hypothesis, we did not detect any consistent effect of the proportion of alien plant species on the structure of published pollination networks. Additionally, we did not detect any major deviation between the trends found for the structure of previously published networks dominated by native plants (< 38% alien species) and a highly anthropogenic novel community from the Botanic Garden of the University of Coimbra, which to the best of our knowledge, corresponds to the largest proportion of alien plant species reported for any pollination network to date (85%). Instead, the structure of this novel community network lies completely within the observed structure of native-dominated networks. Thus, the novel community was not more connected than the reference networks as initially expected, and no consistence trends were found for most descriptors, namely connectance, links per species, nestedness, and network robustness. If anything, the data could suggest a slight trend for higher network specialization; however, having data from only one novel network precludes any generalization on this matter. Contrary to our expectations, pollinators exhibited no evident preferences
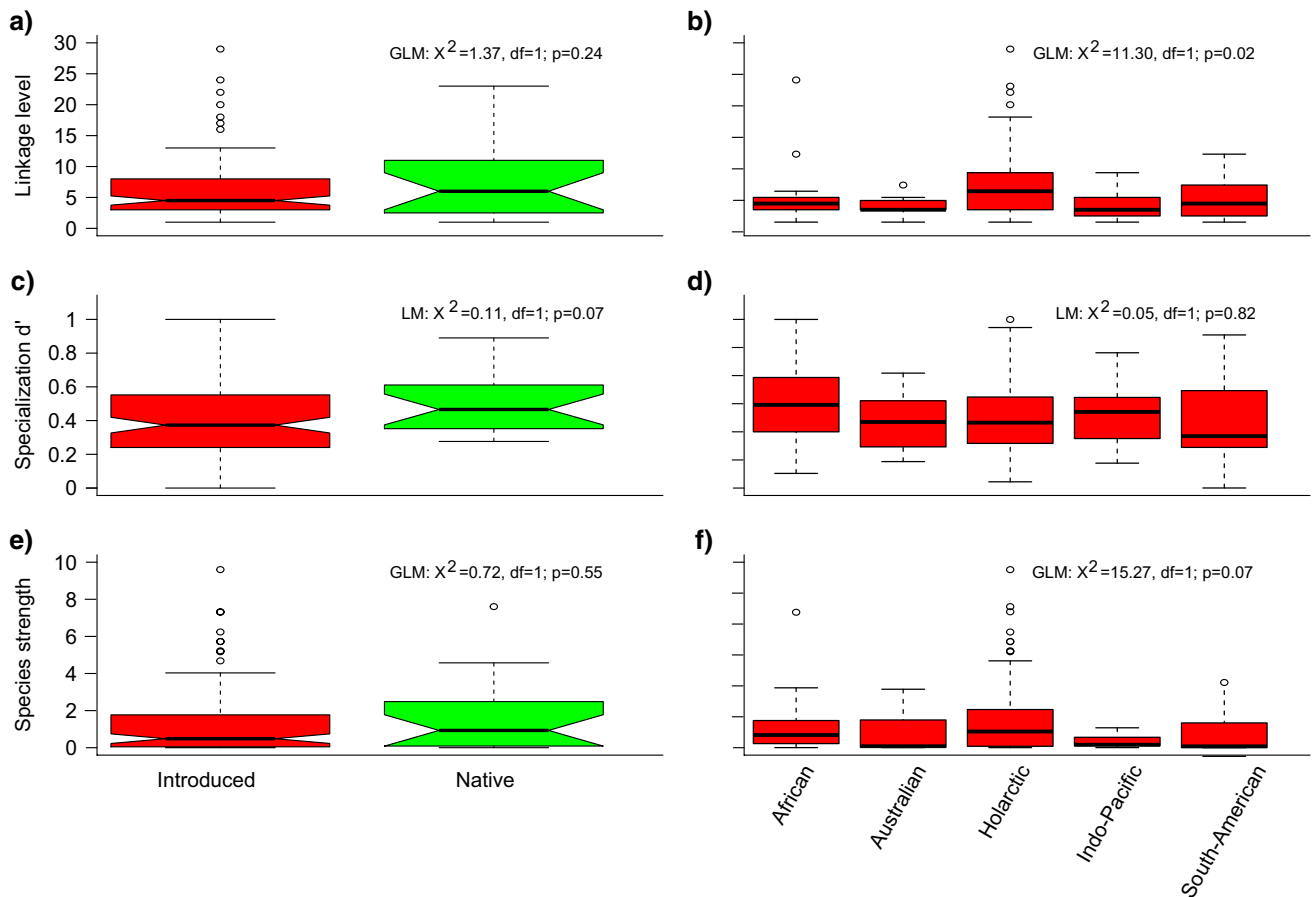
Fig. 3 Differences on interaction patterns established by plants and their pollinators, according to **a**, **c**, **e** plant origin and **b**, **d**, **f** plant bioregion. Pairwise differences were assessed using Tukey tests, and the χ^2 tests report the deviance of the final model against that of a null model. Colour version of this figure is available online

towards native or alien plants, neither in terms of diversity (plant linkage level), "selectiveness" (d'), nor on the importance of native and alien plant species for the whole pollinator fauna. Furthermore, we did not detect differences between the interactions established with plants from different native bioregions.

Negative impacts resulting from biological invasions on native biodiversity are now undisputable, frequently triggering secondary extinctions and disrupting important ecosystem functions (Traveset and Richardson 2006; Kaiser-Bunbury et al. 2011; Rumeu et al. 2017; López-Núñez et al. 2017). However, no definite trend for the effect of alien species on the structural properties of networks is unequivocally shown (e.g. Tylianakis and Morris 2017). When considering the proportion of alien plant species across networks we did not find any consistent changes on the network structure of the native-dominated communities (Fig. 3). This might be due to a large idiosyncrasy in the community-level changes, as these obviously depend on the identity of the species and their abundance in the recipient community (Albrecht et al.

2014). Notwithstanding, even when considering a highly anthropogenic novel community formed by 85% of alien plant species (more than tenfold the average proportion of alien species in the published networks and twice its maximum), a remarkable similarity still exists compared to what would be expected based on the trajectory of the known communities (Fig. 1). The apparent trend for a slightly higher overall specialization in our novel community might be counter-intuitive as most alien plants are frequently associated with high generalism (Aizen et al. 2008; Albrecht et al. 2014). This divergence can be driven by a traditionally stronger focus on alien species with a clear invasive behaviour (e.g. Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2008; Heleno et al. 2009). However, it can also result from opposing effects of invasive plants, generally assumed to promote generalism, and non-invasive alien plants, which might promote network specialization. Actually, only five out of 139 plant species (3.6%) in this novel community have a known history of invading natural communities, namely Japanese Honeysuckle (*Lonicera japonica*), Calla lily

(*Zantedeschia aethiopica*), West-Indian Lantana (*Lantana camara*), Bigleaf hydrangea (*Hydrangea macrophylla*), and Bermuda buttercup (*Oxalis pes-caprae*), and only the latter has shown invasive behaviour in Portugal mainland as an early-successional invader of disturbed grounds (Marchante et al. 2014). Logically, the successful integration of alien plants in their recipient communities is dictated by the specific traits that mediate their capacity to compete for pollinators, naturalize, and eventually spread (Razanajatovo et al. 2015; Hui et al. 2016). This distinction between invasive and non-invasive alien plants thus marks a very important difference between this study and the dominant literature on the impact of biological invasions. The virtual lack of invasive species in the botanical garden of the University of Coimbra prevents from formally contrasting the visitation patterns of invasive and non-invasive aliens; however, this should be taken into account in future studies.

In the current scenario of accelerating biotic homogenization, most introduced species are not invasive and it is vital to know to what extent they can act as functional surrogates of native vegetation, to fully understand the long-term effects of homogenisation (Olden et al. 2006). Here we failed to detect structural differences in pollination networks as a result of the incorporation of alien plant species, even when the community was almost exclusively formed by alien plants. Clearly, it is too early for generalizations, and future studies of highly artificial communities (such as those from urban environments) will be highly valuable to validate these trends. Similarly, it remains to be tested if these novel interactions are as effective as native ones in promoting pollen deposition and effective pollination (Morton and Rafferty 2017). There is an increasing and well-justified interest in understanding the functioning of highly disturbed ecosystems, leading to new research fronts such as urban ecology and taxon substitutions (Hansen et al. 2010). We are, therefore, largely optimistic that the implementation of network studies and the use of botanical gardens as experimental grounds for the effects novel biological contexts will continue to shed light into some of the central theorems of ecology, including community assembly rules, and informing conservation efforts in an increasingly homogenized world.

Compliance with ethical standards

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Pollination networks from natural, and anthropogenic-novel communities show high structural similarity

Sérgio Timóteo[1], Catherine J. O'Connor, Francisco A. López-Núñez, José M. Costa, António C. Gouveia, Ruben H. Heleno

[1]Corresponding author:

Sérgio Timóteo; Centre for Functional Ecology (CFE-UC), Department of Life Sciences, University of Coimbra, Portugal; stimoteo@gmail.com
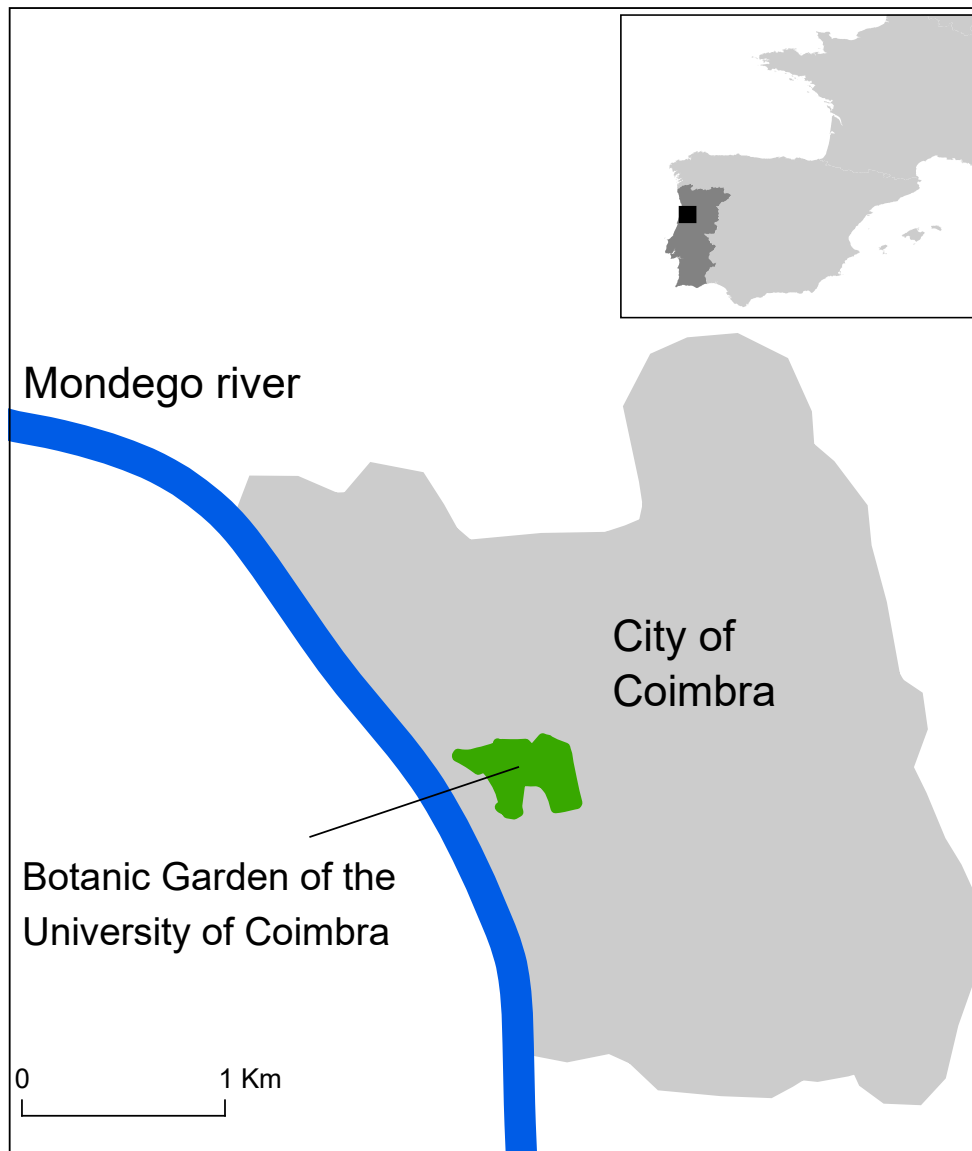
Fig. S1 Location of the Botanic Garden of the University of Coimbra, within the regional and local urban context.

Fig. S2 Quantitative plant visitation network of the Botanical Garden of the University of Coimbra, Portugal, including the identification of plants and flower visitors. The network represents the interactions between 176 pollinators and 132 plant species and the width of each interaction is proportional to the number of visits/flower/minute. Network based on a total effort of 255 hours of direct observations to flowers between November 2016 and May 2017.

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