How exotic plants integrate into pollination networks

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Summary

1. There is increasing world-wide concern about the impact of the introduction of exotic species on ecological communities. Since many exotic plants depend on native pollinators to successfully establish, it is of paramount importance that we understand precisely how exotic species integrate into existing plant–pollinator communities.

2. In this manuscript, we have studied a global data base of empirical pollination networks to determine whether community, network, species or interaction characteristics can help identify invaded communities.

3. We found that a limited number of community and network properties showed significant differences across the empirical data sets – namely networks with exotic plants present are characterized by greater total, plant and pollinator richness, as well as higher values of relative nestedness.

4. We also observed significant differences in terms of the pollinators that interact with the exotic plants. In particular, we found that specialist pollinators that are also weak contributors to community nestedness are far more likely to interact with exotic plants than would be expected by chance alone.

5. Synthesis. By virtue of their interactions, it appears that exotic plants may provide a key service to a community’s specialist pollinators as well as fill otherwise vacant ‘coevolutionary niches’.

Key-words: coevolution, competition, extinction, generalists, indirect facilitation, invasion ecology, mutualistic networks, nestedness, plant–animal interactions, specialization

Introduction

There is increasing world-wide concern about the impact of introductions of exotic species on ecological communities (Rejmánek & Richardson 1996; Sax & Gaines 2008). In particular, the successful introduction of exotic species can create effects that cascade through existing communities, for example by creating novel communities that are more resistant to restoration efforts (Aizen, Morales & Morales 2008; Tylianakis 2008; Valdivinos et al. 2009; Traveset et al. 2013). Given the breadth of their impacts (Vilà et al. 2011), it is of paramount importance that we develop stronger theories with which to better predict the risk of future invasions (Rejmánek & Richardson 1996).

A key first barrier that any exotic species must overcome prior to establishment is competition with endemic species for existing resources (Levine et al. 2003; Ricciardi & Atkinson 2004; Powell, Chase & Knight 2011). Indeed, since many community properties, such as total species richness, are considered to be reasonable proxies for the amount of competition in a community (Levine 2000; Naem et al. 2000; Strauss, Webb & Salamin 2006; Hayes & Barry 2008; Cadotte, Hamilton & Murray 2009), it is widely expected that they provide key indicators of invasibility. Many exotic species also depend on native pollinators to successfully establish (Memmott & Waser 2002; Aizen, Morales & Morales 2008; Bartomeus, Vilà & Santamaría 2008), and pollinators may be a key resource over which plants compete (Levin & Anderson 1970; Mosquin 1971; Moeller 2004; Bastolla et al. 2009; Jakobsson, Padrón & Traveset 2009; Mitchell et al. 2009).

More generally, the mutualistic interactions that occur between plants and pollinators are known to play a critical role in overall biodiversity maintenance (Bond 1994; Bascompte & Jordano 2007; Bastolla et al. 2009). As a result, it has also been suggested that the overarching structure of plant–pollinator mutualistic networks might also play a role in determining the invasibility of a community (Bartomeus, Vilà & Santamaría 2008; Padrón et al. 2009; Traveset et al. 2013). There are multiple hypotheses for how the structure of mutualistic networks can facilitate species coexistence (Bascompte, Jordano & Olesen 2006; Bascompte & Jordano 2007; Bascompte 2009). At the whole community level, it appears that both network connectance – the number of possible interactions that are actually observed in a community – and nestedness – a measure of whether these interactions are organized such that specialists interact with proper subsets of the species with whom generalists interact – are strongly related to community stability and persistence (Bastolla et al. 2009).

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Networks study and explore a global data set of empirical pollination interactions. Nevertheless, our primary objective was to develop a methodology that also controls for potential bias in the community composition: plant richness $A$, pollinator richness $P$, total species richness $S = A + P$, the ratio $R = A/P$ of pollinator to plant species.

**Materials and methods**

**EMPIRICAL POLLINATION NETWORKS**

Here we analyse a data set comprised of 59 plant–pollinator mutualistic networks from a wide range of locations around the globe and with diverse species assemblages (Web of Life, available at http://www.web-of-life.es; Fig. 1 and Table S1 in Supporting Information).

The interaction structures of each of the empirical networks are based on observed patterns of visitation of flowering plants by their insect pollinators. Of the 59 networks, 39 are qualitative networks where each interaction solely indicates presence or absence and 20 are quantitative networks in which each interaction has a ‘weight’ that corresponds to the observed frequency of visits (Jordano 1987).

**IDENTIFICATION OF EXOTIC SPECIES**

In order to identify the exotic plant species across each of the empirical networks, we cross-referenced each species’ name and network location (i.e. country) with its classification in both the Global Invasive Species Database (GISD; http://www.issg.org/database/welcome/) and the Global Invasive Species Information Network database (GISIN; http://www.gisin.org). In the GISD, species are classified as ‘Native’ or ‘Alien’; in the GISIN, the equivalent classifications are ‘Indigenous’ or ‘Exotic’. We considered all species as exotic if they were so classified in either (or both) of the two data bases. Lastly, note that records in GISIN classify species as different degrees of ‘Harmful’ as an indication of the species’ impact in the community: ‘Yes’, ‘Potentially’ and ‘No’. Under this classification, invasive species should return ‘Harmful = Yes’; therefore, to capture as many species as possible within our data set, we consider here all non-native species regardless of their ‘Harmful’ classification. It is also for this reason that we refer to these species as exotic as opposed to invasive, recognizing that the definition of what precisely constitutes invasive is open to interpretation (Colautti & MacIsaac 2004).

Unfortunately, not all plants in the data set were identified at the species level. To err on the side of caution, these plants were never considered as exotic since it was technically impossible to determine their exact status. Furthermore, not all known exotic or invasive species can be found in these data bases (e.g. one of the focal species of Bartomeus, Vilà & Santamaria 2008). Nevertheless, matching all plants across the same data bases provides the most accurate and reproducible methodology that also controls for potential bias in the final results.

**COMPARISON OF COMMUNITY-LEVEL PROPERTIES**

In order to determine whether communities with exotic plants differed in any characteristic manner, we calculated five properties related to community composition: plant richness $P$, pollinator richness $A$, total species richness $S = A + P$, the ratio $R = A/P$ of pollinator to plant species present.

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Fig. 1. Map of the empirical pollination networks studied here. Green circles indicate the location of pollination networks that did not have exotic plants present while white circles indicate pollination networks with exotic species present.
richness and the phylogenetic diversity of the plant community (as quantified by the average distance from all plants to their most recent common ancestor). We decided to focus on these five properties because each provides a proximate measure of community saturation and/or niche (or resource) availability, both of which have been argued to influence the ability of exotic species to establish in a novel community (Levine 2000; Strauss, Webb & Salamin 2006; Hayes & Barry 2008; Cadotte, Hamilton & Murray 2009). All community-level properties were calculated using a Kruskal–Wallis rank sum test.

Given an observed plant–pollinator interaction network, the first four properties are straightforward to determine. To calculate the last property, we first constructed each community’s phylogenetic tree using the **phylogenetic ‘mega-tree’** (version R20120829) which defines relationships between higher plants (Webb, Ackerly & Kembel 2008). We then dated nodes across this tree according to Wikström, Savolainen & Chase (2001) and used the branch length adjustment algorithm BLADJ (Webb, Ackerly & Kembel 2008) to estimate the age of all remaining, undated nodes. Though this procedure implies that ages within our phylogenies should be treated as approximations (Beaulieu et al. 2007), previous analysis indicates marked improvements of phylogenetic analyses when even a limited number of nodes are properly dated (Webb 2000).

**COMPARISON OF NETWORK-LEVEL PROPERTIES**

In order to determine whether networks with exotic plants differed in any characteristic manner, we calculated five properties related to the plant–pollinator network structure: overall network connectance \( C = L/(PA) \), average number of interactions per plant \( C_P = LI/P \), average number of interactions per pollinator \( C_i = LI/A \), nestedness \( N \) and relative nestedness \( N^* \). Here, \( L \) is the total number of mutualistic interactions observed in the community. We measured nestedness \( N \) using the metric NODF since it accounts for potential bias introduced by network size and topology compared with alternative measures (Almeida-Neto et al. 2008), and we measured relative nestedness – the degree to which nestedness compares to the amount expected at random – following Bascompte et al. (2003). Though network attributes, such as connectance, may not always be perfect indicators of community status (Heleno, Devoto & Pocock 2012), each of the five properties selected here has previously been shown to be associated with increased community stability (Allesina & Tang 2012), persistence (Saavedra et al. 2011; Saavedra & Stouffer 2013) and a community’s overall ability to support higher levels of biodiversity (Bastolla et al. 2009). All network-level comparisons were made using a Kruskal–Wallis rank sum test.

**COMPARISON OF SPECIES-LEVEL PROPERTIES**

In order to determine whether the exotic plants themselves differed in any characteristic manner, we calculated three properties with which to compare them to other plant species within the same network. For each plant species \( i \), this included its rank \( d_i \) of phylogenetic ‘uniqueness’, the rank \( k_i \) of its degree and the rank \( c_i \) of its nestedness contribution (Saavedra et al. 2011). Here, we define the phylogenetic uniqueness of species \( i \) as the average phylogenetic distance between it and all other plants in its community. We quantified each species’ nestedness contribution as the degree to which the observed nestedness of the network changes when randomizing just the interactions of the focal species (Saavedra et al. 2011). As with our analysis of relative nestedness, we randomized individual species’ interactions according to Bascompte et al. (2003). We chose to study phylogenetic relatedness because it underpins key theories regarding community saturation and invasibility (Strauss, Webb & Salamin 2006; Fridley 2010). In addition, multiple theoretical studies indicate that having many connections and/or having a low nestedness contribution can reduce a species’ vulnerability to extinction (Saavedra et al. 2011; Allesina 2012; Saavedra & Stouffer 2013).

All ranks were normalized within each network to vary between 0 and 1 such that a value of 0 corresponded to the smallest value in the network (e.g. the most phylogenetically typical) and a value of 1 corresponded to the largest value in the network (e.g. the most phylogenetically distinct). Because of the relationship between species abundance and network properties (Vázquez et al. 2007), species with low-rank degree can also be thought of as rare species. We chose to analyse ranks of all of these properties because the distributions of the raw values of each can show considerable variation across empirical networks (Jordan, Bascompte & Olesen 2003; Rezende et al. 2007; Saavedra et al. 2011). All species-level comparisons were made using a Kruskal–Wallis rank sum test.

**COMPARISON OF INTERACTION-LEVEL PROPERTIES**

To determine whether pollinators’ interactions with exotic plants showed any characteristic differences from those with native plants, we calculated three interaction-level properties. For every observed interaction between a plant \( i \) and a pollinator \( j \), we calculated the dependence \( D^P_{ij} \) of the plant on the pollinator (i.e., the proportion of pollinator visits to \( i \) that come from pollinator \( j \)) and the corresponding dependence \( D^P_{ji} \) of the pollinator on the plant (Vázquez, Morris & Jordano 2005; Bascompte, Jordano & Olesen 2006). It has previously been argued that some variation in species’ dependences can arise because of inherent differences in species abundance (Vázquez et al. 2007). Therefore, we also calculated each interactions’ ‘preference’ \( V_{ij} \) which quantifies the degree to which the interaction deviates from a random-encounter (or mass-action) model (Staniczenko, Kopp & Allesina 2013). Here, a value of \( V_{ij} \) > 1 indicates that the interaction is preferred – in that it occurs more often than expected at random – whereas \( V_{ij} < 1 \) indicates that the interaction is less preferred.

Note that the calculation of dependences and interaction preferences requires prior information about relative interaction weights. Therefore, all interaction-level comparisons were restricted to the quantitative empirical networks in our data set. To statistically compare species’ dependences, we used a binomial regression (Quinn & Keough 2002) with proportional visitation as the dependent variable and the plant species’ classification (as native or exotic) as the independent variable; this regression was performed separately for plants and for pollinators. We compared interaction preferences using a simple linear regression with log-preferences as the independent variable and the plant species’ classification as the independent variable.

**COMPARISON OF POLLINATOR PROPERTIES**

We lastly explored whether there were characteristic differences in terms of the pollinators that interacted with exotic plants. In particular, we quantified (i) whether more generalist pollinators showed a tendency to interact with exotic plants and (ii) whether pollinators that are stronger contributors to nestedness tended to interact with the exotic plants. In addition, we wanted to assess whether any relationship in the empirical data is not only statistically significant but also significantly different from what we would expect at random. The appropriateness of this distinction can most easily be understood when considering the case of specialist vs. generalist pollinators: though
generalists may indeed show a tendency in our data to interact with exotic plants (Memmott & Waser 2002), generalist pollinators must be more likely to interact with any given plant tautologically. Therefore, it is critically important to determine whether any observed relationship is truly relevant ecologically and above and beyond what would be expected solely by chance.

To perform the above-described comparison, we compared the empirically observed tendencies to the same tendencies for 100 networks whose interactions have been randomized. We randomized the empirical networks using the swap method that shuffles interactions between species while simultaneously preserving each species’ total number of interactions (Fortuna et al. 2010). By randomizing the networks in this way, we also explicitly maintain each network’s overall probability of connecting to an exotic plant, implying that the only noteworthy differences across randomizations should be the identities of the pollinators that interact with the exotic plants.

Lastly, to statistically quantify how the probability that a pollinator is connected to an exotic plant varied depending on the pollinator’s degree or contribution to nestedness, we used a mixed-effects logistic regression (Zuur et al. 2009) that takes the form:

\[
\text{logit}(p) = (\alpha + \alpha^*) + (\beta + \beta^*) k + (\gamma + \gamma^*) c + (\delta + \delta^*) n + \epsilon
\]

Here, the dependent variable \( p \) is the probability of interacting with an exotic plant, and the independent variables include each pollinator’s ranked degree \( k \), ranked nestedness contribution \( c \), a statistical interaction between the two and a random effect \( n \) for network identity that accounts for underlying variation between networks in the overall tendency for pollinators to interact with exotic plants. The coefficient \( \alpha \) defines the model intercept, \( \epsilon \) is the model residual, \( \beta \) quantifies the effect of species’ degree, \( \gamma \) the effect of nestedness contribution and \( \delta \) the strength of the interaction effect. Lastly, the coefficients \( \alpha^* \), \( \beta^* \), \( \gamma^* \) and \( \delta^* \) quantify the differences between the empirical and randomized data.

**Results**

**IDENTIFICATION OF EXOTIC PLANT SPECIES**

Within the set of 2230 flowering plants present across all networks in our data set (of which 1746 were taxonomically unique), we conclusively identified a total of 48 exotic plant species (of which 29 were taxonomically unique) (Table 1). These plants were present within 25 of the 59 networks; graphically, these 25 networks also came from six of the seven major continents (Fig. 1). Thirteen of the 25 networks featured a single exotic species, seven included two exotic species, one included three exotic plants, three included four exotic plants, and the remaining network had six exotic plants (Table S1).

| Exotic species            | Location where exotic | Number of networks |
|---------------------------|-----------------------|--------------------|
| Aegopodium podagraria     | Denmark               | 2                  |
| Ageratum conyzoides       | Galapagos Islands (Ecuador) | 1               |
| Bidens pilosa             | Galapagos Islands (Ecuador) | 1               |
| Bidens pilosa             | Japan                 | 1                  |
| Calystegia sepium         | Denmark               | 2                  |
| Campanula rotundifolia    | Denmark               | 2                  |
| Cirsium arvense           | New Zealand           | 1                  |
| Cirsium arvense           | United Kingdom        | 2                  |
| Cytisus scoparius         | New Zealand           | 1                  |
| Daucus carota             | Denmark               | 2                  |
| Daucus carota             | United Kingdom        | 1                  |
| Eupatorium cannabinum     | Denmark               | 2                  |
| Hieracium pilosella       | New Zealand           | 1                  |
| Leucuaena leucocephala    | Mauritius             | 1                  |
| Leucanthemum vulgare      | Azores (Portugal)     | 1                  |
| Linaria vulgaris          | United States         | 1                  |
| Lotus corniculatus        | Azores (Portugal)     | 1                  |
| Opuntia stricta           | Spain                 | 1                  |
| Oxlis corniculata         | Japan                 | 2                  |
| Oxlis pes-caprae          | Canary Islands (Spain) | 1               |
| Oxlis pes-caprae          | Greece                | 1                  |
| Passiflora foetida        | Galapagos Islands (Ecuador) | 2               |
| Prunus serotina           | Denmark               | 1                  |
| Psidium guajava           | Galapagos Islands (Ecuador) | 1               |
| Scaveola frutescens       | Japan                 | 1                  |
| Senecio lautus            | Mauritius             | 1                  |
| Solidago sempervirens     | Azores (Portugal)     | 1                  |
| Tanacetum vulgare         | Denmark               | 2                  |
| Trifolium pratense        | Denmark               | 1                  |
| Trifolium repens          | Denmark               | 3                  |
| Trifolium repens          | Japan                 | 3                  |
| Trifolium repens          | New Zealand           | 1                  |
| Verbascum thapsus         | New Zealand           | 1                  |
| Vicia sativa              | United Kingdom        | 1                  |

and pollinator richness ($\chi^2 = 6.48$, \( P = 0.011 \)); in each of these three instances, communities with exotic plants exhibited tended to exhibit greater richness across the board. In contrast, we observed no significant differences for the ratio of pollinator to plant diversity ($\chi^2 = 0.90$, $P = 0.612$) nor phylogenetic diversity of the plant community ($\chi^2 = 1.22$, $P = 0.269$).

Despite any hypothesis to the contrary (Levine et al. 2003), there was no indication within the data that the networks with more exotic plants also had greater endemic plant richness ($P = 0.188$). Furthermore, the relative proportion of exotic to native plants in a community was a decreasing function of total species richness ($P = 0.018$), plant richness ($P = 0.003$) and pollinator richness ($P = 0.028$). Overall, these community-level results indicate that more speciose communities are generally more likely to contain exotic plants whereas less speciose communities tend to support a greater proportion of exotic plants.
At the network level, we found no significant differences in terms of network connectance ($\chi^2 = 2.77, P = 0.096$), the average number of interactions per plant ($\chi^2 = 2.70, P = 0.192$), the average number of interactions per pollinator ($\chi^2 = 1.62, P = 0.203$) or nestedness ($\chi^2 = 1.62, P = 0.203$). On the other hand, we did observe that communities with exotic plants had significantly different relative nestedness ($\chi^2 = 7.97, P = 0.005$) in that they tended to exhibit higher values of relative nestedness.

In slight contrast to what we observed at the community and network levels, we found no evidence that exotic plants themselves exhibited characteristic differences when compared to other plants in their community. Specifically, our analyses indicated that exotic plants were statistically indistinguishable from native plants in terms of their ranks of phylogenetic uniqueness ($\chi^2 = 2.34, P = 0.126$), degree ($\chi^2 = 0.154, P = 0.694$) and nestedness contribution ($\chi^2 = 1.52, P = 0.218$). Moreover, these conclusions did not change when testing for differences between the absolute species-specific values as opposed to within-network ranks ($P = 0.761$, $P = 0.332$ and $P = 0.404$, respectively).

**INTERACTION-LEVEL DIFFERENCES**

In contrast to what we observed at the community, network and species levels, our subsequent analysis indicated statistically significant differences at the interaction level (Fig. 3). When examining species’ dependences, we found that pollinator species had significantly higher dependences on exotic plants than on native plants ($z = 20.21, P < 10^{-7}$). For exotic plants, we observed the opposite trend, such that exotic plants had, on average, significantly lower dependences than their native counterparts ($z = -6.60, P < 10^{-7}$). These differences in species’ dependences would appear to indicate that interactions between pollinators and exotic plants are fundamentally different. However, when extending our test of this hypothesis by examining interaction preferences, we found no additional statistical support; that is, interactions between pollinators and exotic plants showed no tendency to occur more or less often than would be expected by random chance ($z = 1.31, P = 0.187$).

**POLLINATOR-LEVEL DIFFERENCES**

Our mixed-effects logistic regression of the empirical networks gave indications of multiple significant predictors of the probability that a pollinator interacts with an exotic plant (Table 2 and Fig. 4). Both a pollinator’s degree and nestedness contribution appear to play a significant role, and there is also a significant, positive interaction between these two pollinator attributes.

Focusing first on pollinator degree, we find that the larger it is the more likely it is that the pollinator interacts with an exotic plant. This result itself may be rather unsurprising as it is akin to a confirmation of what it means to be a generalist. The significant interaction, however, implies that the ‘generalist behaviour’ of generalist pollinators becomes stronger as we move from the smallest nestedness contributor in a community to the largest (and despite the fact that degree and nestedness contribution are only weakly correlated). Moving to pollinator nestedness contribution, we find that there is a significant negative relationship between contribution and the probability that the most specialist pollinators interact with exotic plants. However, this relationship becomes significant and positive for more generalist pollinators such that, the larger the pollinator’s nestedness contribution, the higher the
probability it interacts with an exotic plant. Generalizing across all of the empirical networks, the most likely pollinator to interact with an exotic plant is one that is both highly generalist and a strong contributor to nestedness.

Notably, we also observed comparable relationships between the probability of interacting with an exotic plant and a pollinator’s degree and its nestedness contribution across the ensemble of randomized networks (Table 2). Similar to what we observed in the empirical data, the relationship with degree was significant and positive, and the strength of this relationship increased with increasing nestedness contribution of the pollinator. Likewise, the relationship with nestedness contribution in the randomized networks shifted from significantly negative for poorly connected pollinators to significantly positive for the most connected pollinators; overall, however, these patterns for nestedness contribution were generally weaker in the randomized networks than in the empirical networks.

Since we observed significant relationships in both the empirical and randomized networks, we also directly compared the two to gain additional insight regarding which pollinators in a community are most likely to interact with an exotic plant (Fig. 4). Intriguingly, this comparison indicated that the pattern in the empirical webs was significantly different from that in the randomized webs. In particular, weak contributors to nestedness in the empirical networks are more likely to interact with exotic species than similar species in the randomized networks. On the other hand, strong contributors to nestedness in the empirical networks are less likely to interact with exotic species than comparable species in the randomized networks. In addition, there is a significant interaction between degree and nestedness contribution such that poorly connected pollinators that are also weak contributors to nestedness are significantly more likely to interact with exotic plants in the empirical networks than would be expected by random chance alone.

**Discussion**

Across our globally distributed data set of pollination networks, we found multiple threads of evidence to support the suggestion that community properties provided a significant predictor of communities with non-native plant species (Rejmánek & Richardson 1996; Naeem et al. 2000; Kennedy et al. 2002; Fridley 2010). Somewhat paradoxically, we found that both plant richness and pollinator richness were positively associated with the presence of exotic plants, despite the fact that the two are thought to influence plant–plant competition in opposite ways (Levine 2000; Levine et al. 2003; Mitchell et al. 2009; Powell, Chase & Knight 2011). On the other hand, we found no indication that the exotic plants themselves were different than their native counterparts (e.g. in terms of their generalism or phylogenetic uniqueness).

Previous research on pollination networks has also indicated a strong link between network structure and species’ coexistence (Bascompte, Jordano & Olesen 2006; Thébault & Fontaine 2010; Saavedra & Stouffer 2009) as well as tends to
to maximize individual species’ abundances (Suweis et al. 2013).

Here, we also identified clear differences with regard to how exotic plants’ interactions were distributed across the pollinator community. On one hand, exotic plants exhibited significantly lower dependences on their pollinators than did native species; conversely, pollinators showed significantly higher dependences on exotic plants. The underlying asymmetry of this relationship is broadly consistent with earlier research that concluded that mutualistic relationships tend to be asymmetric in nature (Bascompte, Jordano & Olesen 2006; Aizen, Morales & Morales 2008), whether the result of coevolution within mutualistic communities (Thompson 1994) or because of variation in species’ relative abundances (Vázquez et al. 2007). The exotic nature of the flowering plants studied here, however, would appear to rule out the former hypothesis while future tests of the latter would require additional abundance data that are based on independent observations as opposed to the interaction matrix (Staniczenko, Kopp & Allesina 2013; García et al. 2014).

Above all else, the most consistent pattern we observed was in the network attributes of pollinator species that interact with exotic plants. When compared to the random expectation, the data indicated in particular that there was a significant tendency for exotic plants to interact with specialist pollinators that are also weak contributors to nestedness. This pattern is particularly intriguing since theoretical research has suggested that specialists should be the most vulnerable to extinction (Allesina 2012) but that being a weak contributor to nestedness can counterbalance this effect (Saavedra et al. 2011). Viewed from this perspective, it is possible that the establishment of exotic plants is, in fact, beneficial for these otherwise highly vulnerable specialist pollinators. As future studies begin to compile better resolved data regarding the long-term dynamics of mutualistic communities (Burkle, Marlin & Knight 2013), we expect there to be more conclusive evidence regarding the positive impacts of non-native plants.

Within this present study, we have focused on the question of whether network structure facilitates or prevents establishment of exotic plant species, or whether exotic plants exhibit characteristic differences when compared to their native counterparts. In doing so, we have adopted an explicitly macroecological perspective (Trojelsgaard & Olesen 2013) while setting aside the related question of whether and how non-native plants modify the resulting network structure of the pre-existing community (Moragues & Traveset 2005; Aizen, Morales & Morales 2008; Bartomeus, Vilà & Santamaria 2008; Jakobsson, Padrón & Traveset 2009). Unfortunately, this latter question is best addressed by studying paired networks (Albrecht et al. 2014) across an equally large geographic extent and is therefore beyond the possibilities provided by our present data set. Methodologically, we also recognize that the testing of some of our hypotheses could have been hampered by aspects of the data set (Moran 2003); examples include the proportion of networks with exotic species to those without, an imbalance of native to exotic spe-
cies, or a lack of abundance data with which to distinguish between 'superabundant' invasive plants and exotic plants as a whole. The breadth of interrelated patterns we have uncovered here, however, suggests multiple promising avenues for more detailed or mechanistic studies in the future.

Thinking more broadly, all plant species are constantly adopting new strategies with which to respond to competition for pollination (Moeller 2004; Mitchell et al. 2009). Along these lines, it has previously been shown that natural selection 'within a network context' (Fontaine 2013) should favour a reduction of effort towards interactions that negatively influence plants' short- and long-term fitness (Thompson 1994; Zhang, Hui & Terblanche 2011; Suweis et al. 2013). Consequently, sufficiently strong competition should hypothetically lead to coevolutionary selection and adaptation away from interactions with pollinators who themselves are most vulnerable to extinction (Slobodkin 1964) – specialists (Allesina 2012) and strong contributors to nestedness (Saavedra et al. 2011). It is therefore an enticing possibility that the patterns we have observed for exotic plants appear because these species fill otherwise vacant 'coevolutionary niches' that are the natural result of the internal dynamic of mutualistic networks.

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Data accessibility

All data studied here are publicly available via the Web of Life Database (http://www.web-of-life.es), GISD – the Global Invasive Species Database (http://www.isg.org/database/welcome/) and GISIN – the Global Invasive Species Information Network (http://www.gisin.org).

References

Aizen, M.A., Morales, C.L. & Morales, J.M. (2008) Invasive mutualists erode native pollination webs. PLoS Biology, 6, 31e.

Albrecht, M., Padrón, B., Bartomeus, I. & Traveset, A. (2014) Consequences of plant invasions on compartmentalization and species roles in plant-pollinator networks. Proceedings of the Royal Society of London, Series B: Biological Sciences, 281, 20140773.

Allesina, S. (2012) Ecology: the more the merrier. Nature, 487, 175–176.

Allesina, S. & Tang, S. (2012) Stability criteria for complex ecosystems. Nature, 483, 205–208.

Almeida-Neto, M., Guimarães, P., Guimarães, P.R.J, Loyola, R.D. & Urich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117, 1227–1239.

Bartomeus, I., Vilà, M. & Santamaría, L. (2008) Contrasting effects of invasive plants in plant-pollinator networks. Oecologia, 155, 761–770.

Bascompte, J. (2009) Disentangling the web of life. Science, 325, 416–419.

Bascompte, J. & Jordano, P. (2007) Plant-animal mutualistic networks: the architecture of biodiversity. Annual Review of Ecology Evolution and Systematics, 38, 567–593.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the USA, 100, 9383–9387.

Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science, 312, 431–433.

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Loque, B. & Bascompte, J. (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature, 458, 1018–1020.

Beaulieu, J.M., Moles, A.T., Leitch, I.J., Bennett, M.D., Dickie, J.B. & Knight, C.A. (2007) Correlated evolution of genome size and seed mass. New Phytologist, 173, 422–437.

Bond, W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 344, 83–90.

Burkle, L.A., Martin, J.C. & Knight, T.M. (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science, 339, 1611–1615.

Cadotte, M.W., Hamilton, M.A. & Murray, B.R. (2009) Phylogenetic relatedness and plant invader success across two spatial scales. Diversity and Distributions, 15, 481–488.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define invasive species. Diversity and Distributions, 10, 135–141.

Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? Trends in Ecology & Evolution, 14, 135–139.

Elton, C.S. (1958) Ecology of Invasions by Animals and Plants. Chapman & Hall, London, UK.

Fontaine, C. (2013) Ecology: Abundant equals nested. Nature, 500, 411–412.

Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R. & Bascompte, J. (2010) Nestedness versus modularity in ecological networks: two sides of the same coin? Journal of Animal Ecology, 79, 811–817.

Fridley, J.D. (2010) Biodiversity as a bulwark against invasion: Conceptual threads since Elton. Fifty Years of Invasion Ecology, pp. 121–130. Wiley-Blackwell, Oxford, UK.

García, D., Martínez, D., Stouffer, D.B. & Tylianakis, J.M. (2014) Exotic birds increase generalization and compensate for native bird decline in plant-frugivore assemblages. Journal of Animal Ecology, doi: 10.1111/j.1365-2652.2013.1237.

Hayes, K.R. & Barry, S.C. (2008) Are there any consistent predictors of invasion success? Biological Invasions, 10, 483–506.

Heleno, R., Devoto, M. & Pocock, M. (2012) Connectance of species interaction networks and conservation value: is it any good to be well connected? Ecological Indicators, 14, 7–10.

Jakobsson, A., Padrón, B. & Traveset, A. (2009) Competition for pollinators between invasive and native plants: effects of spatial scale of investigation. Ecology, 16, 138–141.

James, A., Pitchford, J.W. & Plank, M.J. (2012) Disentangling nestedness from models of ecological complexity. Nature, 487, 227–230.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. The American Naturalist, 129, 657–677.

Jordano, P., Bascompte, J. & Olesen, J.M. (2003) Invariant properties in coevolutionary networks of plant-animal interactions. Ecology Letters, 6, 69–81.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M., Tilman, D. & Reich, P. (2002) Biodiversity as a barrier to ecological invasion. Nature, 417, 636–638.

Kruger, F.J., Breitенbach, G.J., MacDonald, I.W. & Richardson, D.M. (1989) The characteristics of invaded Mediterranean-climate regions. Biological Invasions: A Global Perspective (ed. J.A.P. Drake), pp. 181–213. John Wiley & Sons Ltd., New York.

Levin, D.A. & Anderson, W.W. (1970) Competition for pollinators between simultaneously flowering species. The American Naturalist, 104, 455–467.

Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. Science, 288, 852–854.

Levine, J.M. & D’Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasiveness. Ecology, 80, 15–26.

Levine, J.M., Vila, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London, Series B: Biological Sciences, 270, 775–781.

Memmott, J. & Waser, N.M. (2002) Integration of alien plants into a native flower-pollinator visitation web. Proceedings of the Royal Society of London, Series B: Biological Sciences, 269, 2395–2399.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009) New frontiers in competition for pollination. Annals of Botany, 103, 1403–1413.
