Running title: Compartmentalization in invaded plant–pollinator networks

Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks

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Summary

Compartmentalization – the organization of ecological interaction networks into subsets of species that do not interact with other subsets (true compartments) or interact more frequently among themselves than with other species (modules) – has been identified as a key property for the functioning, stability and evolution of ecological communities. Invasions by entomophilous invasive plants may profoundly alter the way interaction networks are compartmentalized. We analyzed a comprehensive dataset of 40 paired plant–pollinator networks (invaded vs. uninvaded) to test this hypothesis. We show that invasive plants have higher generalization levels with respect to their pollinators than natives. The consequences for network topology are that rather than displacing native species from the network, plant invaders attracting pollinators into invaded modules tend to play new important topological roles (i.e. network hubs, module hubs and connectors) and cause role shifts in native species, creating larger modules that are more connected among each other. While the number of true compartments was lower in invaded compared to uninvaded networks, the effect of invasion on modularity was contingent on the study system. Interestingly, the generalization level of the invasive plants partially explains this pattern, with more generalized invaders contributing to a lower modularity. Our findings indicate that the altered interaction structure of invaded networks makes them more robust against simulated random secondary species extinctions, but more vulnerable when the typically highly connected invasive plants go extinct first. The consequences and pathways by which biological invasions alter the interaction structure of plant–pollinator communities highlighted in this study may have important dynamical and functional implications, for example, by influencing multi-species reciprocal selection regimes and co-evolutionary processes.

Key words

Biological invasions of mutualistic interaction networks, , exotic species, nestedness, pollination, robustness, specialization

Introduction

Despite the crucial role that species interaction networks play for the maintenance of biodiversity [1] and the functioning and stability of ecosystems [2,3] we still know very little about the consequences of different components of global change on its structure and dynamics [4,5].

A recurrent property in the organisation of complex biological systems ranging from metabolic [6] to species interaction networks [7-9] is compartmentalization. Compartmentalization of ecological networks refers to the existence of subsets of more closely interacting species with relatively few or no interactions to other subsets [8,10]. In food webs, a long history of research has described such subsets, usually termed compartments [e.g. 2,7] or modules [e.g. 8,9]. Recently, it has been shown that also mutualistic networks, such as pollination [8,11-13] or seed dispersal networks [9], exhibit some level of compartmentalization.

Compartmentalization has been predicted to stabilize trophic networks [2] and references therein,14], which has recently been corroborated for the persistence [2] and resilience [15] of antagonistic interaction networks, while the persistence of mutualistic networks may in contrast decrease with increasing compartmentalization [15]. Moreover, modules have been suggested as potentially important units of evolution and co-evolution [8,11], and they may have important functional implications for ecosystems [3]. Finally, modularity is also related to other important network properties such as nestedness and connectance [16], which have been proposed to have strong dynamical implications for the coexistence [16], stability [15] and functioning [3] of ecological communities. Consequently, anthropogenic impacts on these properties of species interaction networks may have profound consequences for ecological and evolutionary dynamics and ecosystem functioning..

Biological invasions by alien species may strongly affect species interactions, such as those among plants and their pollinators, both directly and indirectly [17]. Pollination interactions are essential for the reproductive success of many plant species and of crucial importance for the maintenance of the diversity and functioning of most terrestrial ecosystems [18]. Most plant and pollinator species exhibit a higher degree of opportunism and thus generalization in their interactions with mutualistic partner species than previously thought [18], facilitating the integration of alien species into native plant–pollinator interaction networks [19-25]. Pollinators use, but appear not to prefer, alien plant species over natives [26]. However, when these alien plants become invasive (*sensu* 27) and have highly attractive flowers present in high abundances in the community, they may have profound effects on pollinators and their interactions with native plants [28]. Hence, the impact of invasions on network topology may critically depend on the generalization level of the invaders [22]. Super-generalist invaders [*sensu* 29] may cause a fusion of previously separate compartments or modules, as predicted by Olesen *et al.* [8], resulting in fewer – but larger – modules (i.e. more species forming a module). However, overall module number may not be altered, but the boundaries among modules may be “blurred”, resulting in more connected modules and thus more cohesive interaction networks. Alternatively, if the invasive species monopolize generalist native partner species from the core of nested networks [22], the invader could lead to a fragmentation of the network into more but smaller modules. Invaders might also form new modules either by usurping species from existing modules, thereby reducing module size, or by attracting pollinators (not previously present) into the invaded communities, thereby increasing network size (i.e. the total number of interacting species). This may not only affect the number of modules and modularity, but also related important structural and dynamical network properties, such as pollinator-plant ratio, nestedness, connectance and network robustness [e.g. 8,30].

A further important, yet largely unexplored question is how invasion may impact upon the individual topological roles native species play in the network. Species specific contributions to module formation offer a perfect framework to answer this question. Even if the modular structure of the interaction networks should be robust against the invasion of alien species, invaders are likely to displace native species from topologically important roles. Such role shifts of species may differ between plant and pollinators, possibly resulting in predictable changes in the proportion of plants and pollinators occupying different roles in the network, with potentially profound implications for species persistence, network functioning and reciprocal selection regimes.

Here, we investigate consequences and underlying mechanisms of plant invasions on the compartmentalization of plant–pollinator networks and the associated topological roles of the species forming these networks. To this end, we analysed 40 networks including a range of different alien invader species, native communities and geographical regions. We specifically addressed the following questions: (1) how does plant invasion affect network structure (i.e. nestedness, connectance and pollinator-plant ratio), and in particular the level of compartmentalization, and the number and size of compartments and modules and (2) is this modulated by the behaviour (e.g. generalization level) of the invader species in the community? or (3) are these effects driven by increased size of invaded networks, (4) do invasive plants exhibit different topological roles compared to natives and how does plant invasion alter the composition of topological roles played by native plant and pollinator species with respect to network compartmentalization? and, finally, (5) does plant invasion alter the robustness of these networks against secondary species extinctions under different scenarios of species loss?

Material and Methods

Database

We analyzed 40 plant–pollinator networks representing 20 independent pairs of networks from seven study systems, each pair consisting of a network invaded by at least one invasive plant species [*sensu* 27] (hereafter "invaded") and a network without any alien plants present, or, in four network pairs [see 20], with only alien, non-invasive plants present in the network ("uninvaded") (Electronic Supplementary Information 1a). The dataset includes our own and published data that fulfilled the following criteria: (1) network data are collected following a paired (invaded vs. uninvaded) approach sampled at different locations within the same region that represent identical habitat types and similar native plant communities; (2) sampling method, period and effort is identical within a network pair. The main characteristics of the analysed plant–pollinator systems are described in Electronic Supplementary Information 1a; for detailed description of field sampling procedures see publications listed there.

All plant and pollinator species included in the analysed networks are identified at the species or morpho-species level. Interaction frequency was quantified in all networks as visitation rate, i.e. the total number of visits per sampling time. Flower-visiting animals were regarded as pollinators, if they were observed contacting the reproductive parts of the flower.

Network analysis

A traditional measure of compartmentalization is the number of "true" compartments [*sensu* 31], defined as the number of subsets in the network with no link to any other subset (i.e. Jordan blocks in the mathematical nomenclature). Although this metric is sensitive to sampling thoroughness, our paired networks have equal sampling effort making relative comparisons meaningful. Furthermore, it has been widely used to analyse compartmentalization in food webs as a "coarse" measure of compartmentalization [e.g. 32]. Following [32] and [33] we use the simpler term "compartment" instead of true compartment hereafter. Compartment number was calculated using the *network level* function of the *bipartite* package [34] implemented in R [35].

Subsets of highly linked nodes that have much weaker links to other subsets of nodes in the network were defined as "topological modules" (*sensu* [36]; hereafter referred to as "modules"). To determine the level of modularity and the number and composition of modules in the plant–pollinator networks we used the software NETCARTO based on the functional cartography method [6]. Modules are identified by maximising a measure of modularity M using simulated annealing (SA), a stochastic optimization technique based on presence–absence data. M increases with increasing link density within modules and decreasing connectedness between different modules. The results of this algorithm are robust, yielding almost identical partitions in different runs [6,11]. The software identifies modules with an accuracy of 90% [10], and is among the most accurate module-detecting algorithms available to date [10,36]. The algorithm defines modules as subsets of both plants and pollinators that are highly connected to each other, rather than separate subsets of plants and subsets of pollinators as a function of their shared interactions, and thus modules have a clear biological meaning [8,13]. The SA-algorithm also assigns each species to a topological role in a network based on the within-module degree z_i (the standardized number of links a species i is connected with others in its own module) and the among-module connectivity c_i (measuring how connected a species i is to all modules) [6,8]. A network hub is not only highly linked to species of its own but also species of other modules, making it important for the connectivity of among species in both its own module and the entire network [8]. A module hub plays an important role in its own module, increasing its coherence. A connector species is important for among-module connectivity, and consequently network coherence, but plays an inferior role within its own module. Peripheral species have all or most of their relative few interactions within their own module, playing a topologically inferior role in the network [8].

For further details of the functional cartography method see Electronic Supplementary Information 1b.

In order to examine the role of the generalization level of the invader species driving changes in network compartmentalization we calculated standardized species degree (*SD*, i.e. the number of interaction partners of a species relative to the maximum possible) as a standardized measure of species generalisation in bipartite ecological networks [37]. For these analyses, five pairs of networks – those studied by [20] and [24] – invaded by several alien plant species, for which an unambiguous assignment to either alien invasive or alien non-invasive was not possible, were excluded .

Due to its proposed important dynamical implications and relatedness to compartmentalization [16] we also analysed the degree of nestedness in the compiled plant–pollinator networks. Bipartite ecological networks are nested if little connected species tend to interact with a proper subset of interaction partners of highly connected species (e.g. [16,30]). Nestedness was calculaed as *BINMATNEST* temperature using the *R* package *bipartite* [38]; results of other nestedness metrics such as *NODF* were qualitatively identical.

To assess the robustness of networks to secondary species extinctions we used the robustness index *R* proposed by [39]. The index is a quantitative modification of the concept of secondary extinction curves (or attack tolerance curve (ATC) [39]) introduced by [40] to assess the tolerance of bipartite mutualistic interaction network to secondary extinctions. The ATC curve is based on the fact that if a given proportion of one mutualistic guild (e.g. plants or pollinators) is eliminated from the network (“attacked”), a certain proportion of species of the partner guild become extinct [39]. The index *R* calculates the area below the ATC curves. $R \to 1$ corresponds to a curve that decreases very slowly until the point at which almost all species are eliminated, while $R \to 0$ corresponds to curve that abruptly declines already after eliminating a single species. In addition to simply cumulatively removing species in a random order from the network [e.g. 41], we tailored the extinction order for the analysis of compartmentalized networks to allow us to account for the topological role of a species with respect to compartmentalization. Thus, either peripheral species were removed first, followed by connectors, module hubs and finally network hubs, or species were removed in the opposite order, starting with network hubs. Secondary extinction was modelled separately for plants and pollinators, using 500 simulations for the calculation of *R*. It is clear that the modelled species eliminations not necessarily represent real extinctions events in nature, because not all plant species require animal pollination for population persistence, and because plant and pollinator mutualists may "switch" interaction partners to a certain degree following the loss of one or a few species (re-wiring [42,43] and adaptive foraging [44]). Nevertheless, comparisons of such species removal simulations, especially when accounting for the topological role in the removal order of species, can provide relative estimates of the tolerance of mutualistic communities with respect to network functioning [41].

Statistical analysis

To address research questions (1) and (5) linear mixed effect models using the *lme*-function of the *nlme* package [45] in *R* were fitted to test the effect of invasion status (invaded vs. uninvaded) on the following response variables: number of compartments (log-transformed), modularity (*M*, logit-transformed [46]), number of modules, nestedness (log-transformed), connectance (logit-transformed), pollinator-plant ratio (log-transformed) and robustness (*R*). Invasion status was treated as fixed effect and site nested within study system as random effects. Further, we analysed the effect of invasion status on module size (i.e. the number of species per module) and among-module interactions (i.e. the number of links of all species of a module that are to species of other modules) (both log-transformed) at the module level. For these models, network identity (nested within site and study system) was also included as a random effect in the model. The presence of invasive plant species was determined for each module, and this variable (module with or without invasive plant species) and its interaction with invasion status were included as fixed effects in the model. To examine which factors accounted for the effect of invasion on module size, we further analysed the number of plant species per module and the number of pollinator species per module separately. To test research question (3), i.e. whether the effects of invasion were mediated by changes in network size, we used the same models described above but included network size (before invasion status in the sequentially fitted model) as covariate. Thus, we tested whether the variation explained by invasion status (in the model without the co-variate network size) is actually explained by network size and whether invasion status still explains a significant part of the residual variation (not explained by the co-variate network size). To analyse the effects of invader generalization on the response variables (research question (2)), invaded networks where modelled with *SD* of the invader as fixed effect and the same random effects as described above.

To assess how plant invasion promoted shifts in the proportion of species with a particular topological role (network hubs, module hubs, connectors or peripherals) (research question (4)), separate generalized linear mixed-effects models (GLMM) for each role with binomial error distribution and logit link function, were fitted using the *lmer*-function implemented in the *R*-package *lme4* [47] with invasion status as fixed factor and site nested within study system as random effects. To further explore the consequences of invasion on the topological role shifts of individual species, we report species shifts for the subset of all plant and pollinator species occurring in both the uninvaded and the invaded network of each site pair. In order to test whether the probability of role shifts differed between plants and pollinators, a GLMM with a binomial error (change or no change of role) and trophic level (plant or pollinator) as fixed effects, and site nested within study as random effects was fitted. None of the GLMM was overdispersed. Inference was based on likelihood ratio tests [48]. For all analyses, model fit was assessed by plotting the residuals against the predicted values. Means ± 1 standard error are reported.

Results

Impacts of invasion on network compartmentalization

Network size increased in invaded compared to uninvaded networks ($F_{1,19} = 6.22$, $P = 0.022$), and this was caused by an increase in the number of pollinator species from 29.8 ± 5.1 to 39.1 ± 5.9 ($F_{1,19} = 7.52$, $P = 0.013$) – but not in the number of plant species (invaded: 12.9 ± 2.5, uninvaded: 11.6 ± 3.3; $F_{1,19} = 1.58$, $P = 0.224$). The latter result was expected because the sampling was designed to compare sites with similar plant communities. Consequently, pollinator-plant ratio was slightly, but statistically not significantly increased in invaded networks (3.5 ± 0.4 vs. 3.1 ± 0.4; $F_{1,19} = 2.58$, $P = 0.125$). Both connectance and nestedness were strongly positively correlated ($r = 0.79$) and negatively related to network size (connectance: $F_{1,18} = 47.00$, $P < 0.001$; nestedness: $F_{1,18} = 87.17$, $P < 0.001$), which accounted for a tendency towards decrease in connectance (0.22 ± 0.01 to 0.19 ± 0.02; $F_{1,19} = 3.74$, $P = 0.068$) and nestedness (25.7 ± 2.4 to 21.7 ± 1.6; $F_{1,19} = 3.57$, $P = 0.074$), which disappeared after accounting for network size (connectance: $F_{1,18} = 0.43$, $P = 0.521$, nestedness: $F_{1,18} = 0.06$, $P = 0.806$). Neither connectance nor nestedness were significantly affected by invader generalization ($P > 0.140$).

The number of compartments in invaded networks tended to be lower than in uninvaded ones (invaded: 1.35 ± 0.13, uninvaded: 1.70 ± 0.18; $F_{1,19} = 4.17$, $P = 0.053$, also after accounting for the increased size of the invaded networks ($F_{1,18} = 3.05$, $P = 0.098$). Invader generalization had no detectable effect on compartment number of invaded networks ($F_{1,9} = 0.03$, $P = 0.857$).

Neither modularity (M; $F_{1,18} = 0.12$, $P = 0.738$) nor the number of modules (uninvaded: 5.0 ± 0.3, invaded: 5.1 ± 0.3; $F_{1,18} = 0.15$, $P = 0.703$) were significantly altered following plant invasion. However, the direction and magnitude of invasion effects were contingent on the system studied: M was significantly reduced in three out of seven study systems, whilst it increased in only one system (Fig. 1; invasion × study system: $F_{6,13} = 3.45$, $P = 0.029$). This variation among study systems was at least partly driven by invader generalization: modularity ($F_{1,9} = 12.96$, $P = 0.006$), but not average number modules ($F_{1,9} = 0.25$, $P = 0.628$), decreased with the level of generalization of the invader species (Fig. 2,3). M was not significantly correlated with nestedness ($r = 0.16$) or connectance ($r = -0.03$) ($P > 0.337$).

Modules of invaded networks consisted of more species (10.4 ± 0.7) than uninvaded ones (8.4 ± 0.8) ($F_{1,18} = 7.68$, $P = 0.014$; Fig. 3). This increase in module size was mainly due to a higher number of pollinator species within a module (7.8 ± 0.6 vs. 6.0 ± 0.6; $F_{1,18} = 7.20$, $P = 0.015$), while the number of plant species per module did not significantly change (invaded networks: 2.6 ± 0.3; uninvaded: 2.3 ± 0.3). Modules containing invasive plant species (12.4 ± 1.3) were larger compared to modules without invasive plant species (8.6 ± 0.6) (Fig. 3; $F_{1,158} = 7.13$, $P = 0.008$). Indeed, module size of modules without invasive plant species did not significantly differ between invaded (9.0 ± 0.8) and uninvaded (8.4 ± 0.8) networks (Fig. 3). Furthermore, plants and pollinators of invaded networks interacted more with pollinators and plants, respectively, belonging to other – not their own – modules ($F_{1,19} = 9.32$, $P = 0.007$). This connectivity among modules was still higher in invaded compared to uninvaded networks ($F_{1,18} = 4.78$, $P = 0.042$) after accounting for variation explained by network size, but was not significantly influenced by invader generalization ($F_{1,9} = 0.74$, $P = 0.413$).

Effects of invasion on species roles

Invasive plants were more generalized ($SD = 0.40 \pm 0.03$) with respect to their flower visitors than native plants ($SD = 0.19 \pm 0.01$). In 33% of networks invaded by a single plant species the invader played a new important topological role as a network hub, module hub or connector that was not occupied in the uninvaded network. Indeed, the invader acted as a network hub in 20% of these invaded networks, as a module hub in 33.3%, as a connector in 20% and only in 26.7% as a peripheral species. By contrast, 80.0% of native plant species were peripherals. The average proportions of topologically important species ("generalists" *sensu* [11]: network hubs, module hubs and connector species) were slightly, but statistically not significantly (all $P > 0.1$), higher on average in invaded compared to uninvaded networks (Fig. 4). However, invaded networks were more likely to contain a module hub (85%, $\chi^2_1 = 4.24$, $P = 0.040$), usually the invader species, or a connector (100%, $\chi^2_1 = 4.07$, $P = 0.044$) than uninvaded networks (65% with module hub, 75% with connector), but not a network hub (25% compared to 15% in uninvaded networks, $\chi^2_1 = 1.87$, $P = 0.175$).

Of the 469 native plant and pollinator species present in both the uninvaded and the invaded network within a site pair, 111 species (23.7%) showed a role shift following invasion, with plants showing more shifts (31.9%) than pollinators (19.2%) ($\chi^2_1 = 7.65$, $P = 0.006$). Most role shifts of native plant species were from important roles to peripherals (53.1%), while 28.6% were from peripherals to important roles. In contrast, slightly more role shifts of pollinator species were from peripheral to important roles (54.2%), while 45.8% of shifts were from important to peripheral.

Impacts of invasion on network robustness

Invaded networks were more robust against the removal of either pollinators ($R = 0.751 \pm 0.025$) or plants ($R = 0.629 \pm 0.022$) than uninvaded networks (pollinators removed: $R = 0.678 \pm 0.025$, $F_{1,19} = 6.11$, $P = 0.023$; plants removed: $R = 0.562 \pm 0.027$, $F_{1,19} = 5.02$, $P = 0.037$) when peripheral species were removed first and network hubs last. After accounting for variation in network size, there was still a trend for a higher robustness of invaded networks (pollinators removed: $F_{1,18} = 4.14$, $P = 0.057$; plants removed: $F_{1,18} = 3.15$, $P = 0.093$). Similar effects of plant invasion were found when species were removed randomly (plants removed: $F_{1,19} = 8.25$, $P = 0.010$; pollinators removed: $F_{1,19} = 11.94$, $P = 0.003$). In contrast, when network hubs were removed first and peripheral species last, the effect of invasion on robustness against the removal of pollinator (*R* invaded: 0.666 ± 0.023, *R* uninvaded: 0.656 ± 0.021) or plant species (*R* invaded: 0.402 ± 0.20, *R* uninvaded: 0.388 ± 0.030) was no longer significant (all $P \geq 0.5$).

Discussion

Entomophilous invasive plants are usually characterized by showy flowers and high abundances in the communities. We show here that these characteristics tend to confer them higher generalization levels than natives. The consequences for network topology are that invasions by such highly generalized plants decrease compartmentalization and increase connectivity among modules. However, rather than displacing native species from the network, plant invaders tend to play new important topological roles creating larger modules that are more connected among each other. We discuss several structural and dynamical consequences of how plant invasions alter the way these networks are compartmentalized and identify some of the underlying mechanisms.

Consequences of invasions on network structure

As predicted, plant invasion resulted in a decline in the number of true compartments, increased connectivity among modules and tended to reduce modularity, but only in the plant-pollination networks invaded by highly generalized alien plants. Indeed, invader generalization showed to be a key predictor of changes in modularity confirms our hypothesis based on existing evidence for a positive relationship of interaction specialization and network compartmentalization mostly from trophic interaction networks [33,49].

As a consequence, modules of invaded networks were larger and more connected among each other. The main mechanistic process behind these changes on network structure was that the alien plant invaders attracted new pollinator species into the invaded plant communities resulting in an increase in network size due to a higher number of pollinator – but not plant – species, which in turn was associated with a tendency towards lower connectance and nestedness [21, but see 12,23]. This increase was largely restricted to the modules containing these highly generalized plant invaders, increasing the size of these modules but without significantly altering the size of other modules without alien plant invaders. These findings highlight that alien plant invaders not simply usurp pollinator species from native plant species [17] but also new pollinator species are attracted into the invaded communities. A similar process has been predicted for enhanced pollinator population sizes through increased resource availability offered by abundantly flowering alien plant invaders [26]. With the number of species also the absolute number of interactions between plants and pollinators increased in invaded compared to uninvaded networks, both within and among modules Consequently, plant invasion did not cause a fusion of modules as hypothesized by Olesen *et al.* [8] but rather resulted in larger modules that were more strongly connected through interactions. At the community level, this increase of realized new links in invaded modules did not compensate the lack of overall realized links associated with the significantly higher number of species of invaded networks, resulting in a tendency towards lower overall network connectance.

Thus, high pollinator attraction and level of generalization of the plant invader showed to be a key predictor of changes in modularity. Indeed, most of the principal alien plant invaders acted as super-generalists [*sensu* 29] in the invaded plant–pollinator networks, such as *Carpobrotus affine acinaciformis* or *Opuntia stricta* in Spanish continental mainland [21], *O. maxima* in Balearic island communities [22], and *Impatiens glandulifera* in temperate riparian communities [50]; the only exception seems to be *Opuntia dillenii*, which showed to act as a specialist in the invaded networks in the Canary Islands [22] and tended to increase modularity when compared to uninvaded communities. However, the mechanistic process driving changes in network compartmentalization revealed here for plant invasions may also apply more generally to processes by which mutualistic communities become dominated by a single or a few species showing particularly high abundance and/or attractiveness, e.g. by species with boom and bust cycles, irrespective of whether this dominant species is alien or not. Such positive correlations between species abundance, interaction frequency and generalization is predicted by the theory of interaction neutrality and frequently observed in plant-pollinator networks (see [30] and references therein). Conversely, we show that if alien species do not become dominant (i.e. invasive *sensu* [27]) – as in the studies analysed here –, strong effects on compartmentalization appear unlikely.

While compartmentalization in antagonistic interaction networks such as food webs may increase their persistence and resilience [2,15], partly by buffering the propagation of species extinctions throughout the webs [2], recent research suggests that, in contrast, the persistence of mutualistic networks may decline with higher levels of modularity [15]. Here, we found that the modules of invaded plant–pollinator networks were more connected by links with each other, probably making the networks more cohesive and robust against fragmentation into weakly or not at all connected modules. However, the effects of modularity on the functioning and stability of networks is still not fully understood [51]. We tentatively explore this avenue with a simple secondary species extinctions simulation. Our analysis suggests that increased numbers of pollinator species, which tended to act more often as connectors of modules in invaded networks, was a key driver of enhanced robustness against secondary species extinctions of invaded networks. Interestingly, this effect depended on the extinction order and topological role of the removed species: while present when the extinction order was from the least to the most connected species, which may be considered as a realistic extinction scenario in many real-world situations [52], it disappeared if the most connected species, i.e. network hubs, were removed first from the networks. In the latter case, networks collapse faster because the impact of the early loss of key species accounting for most of the network coherence is so strong that subtle differences in the interaction structure between invaded and uninvaded networks is no longer relevant. This corroborates findings of modelling studies identifying connectivity of alien plants as a principal driver of the persistence of species in plant-pollinator networks following simulated alien removal (e.g. [12]). Hence, it is important to note that despite invasive plants appear to enhance some aspects of network robustness, it makes the networks also more dependent on them and hence more vulnerable [53], if the invasive plants have boom and bust cycles [54] or in the face of eradication programs, although flexibility in foraging behaviour of pollinators may mitigate this vulnerability to some degree [42-44].

Topological role shifts of plant and pollinator species

The overall proportions of the four different topological roles species were very similar in the uninvaded communities to those reported in other plant–pollinator networks [8,11,12]. Plant species – as a logical consequence of the typically several times higher number of pollinator than plant species in plant–pollinator networks [e.g. 30] – played on average more topologically important roles than pollinator species, which were more often peripherals [8]. Indeed, not pollinator species acted as a module hub; this topological role was exclusively occupied by generalist plant species.

Most of the principal plant invader species (73%) played topologically important roles, while approximately every fourth played only a peripheral role in the invaded networks, largely confirming previous findings that abundantly flowering invasive plants are generally well integrated in native plant–pollinator networks [12,19-25]. The well-connected principal invaders formed mostly new modules and became module hubs, but also linked existing modules as connectors or did both as super-generalist network hubs. Closer inspection of the network pairs revealed that the invaders either displaced natives from these roles or, in one third of the network pairs, played new important roles as network or module hubs – roles that were not occupied by native species prior to invasion especially in some of the smaller networks. Yet, invasion may also cause individual species to shift their topological role with potentially important dynamical implications for individual species. Although with this dataset we could not directly compare species' roles prior and after invasion, our study of paired networks suggests that a considerable proportion of native pollinator species (approximately 20%), and an even higher proportion of native plant species (roughly 30%) present in both the invaded and the uninvaded network within a geographic pair showed such a role shift. Our analysis also reveals that plant and pollinator species differed in the direction of role shifts. Thus, invasion resulted in a shift in the trophic composition of the connector role that forms the "glue" [8] holding different modules together. While the first finding is in agreement with several studies showing that attractive invasive plant species can usurp some generalized pollinator species from native plants [17], the second result suggests that present pollinators include resources of the invasive plants in their diet and thus become more generalized in their visits of plant species across modules (diet expansion hypothesis). Ecological network data available to date notoriously lack sample completeness, affecting most network descriptors [55-57]. This almost certainly affected the number of unconnected, true compartments detected in the analysed networks. However, sampling effort was identical for the uninvaded and the invaded communities within a site pair. Thus, even though the absolute numbers of true compartments may not precisely represent actual numbers, the significantly lower numbers of such compartments in invaded compared to uninvaded networks sampled with the same effort should provide a robust, "coarse" indication for lower compartmentalization of invaded communities.

Super-generalist invaders are predicted to play central roles for the evolution and co-evolution in mutualistic networks by enhancing trait convergence [58]. Indeed, since modules might reflect units of co-evolution in mutualistic assemblages [8,11] and may have functional and stability consequences [3,15], several of our key findings with respect to how plant invasion altered the way plant–pollinator communities are compartmentalized may have important dynamical implications. In particular, the blurred module boundaries and reduced compartmentalization in networks invaded by highly generalized alien invader species and the increase in module size and pollinator-plant ratio of invaded modules may alter pollination functions and community dynamics, and influence multi-species reciprocal selection regimes and co-evolutionary processes in the longer term.

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Data accessibility

Data sets supporting this article: Dryad doi:10.5061/dryad.m26h2

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Figure legends

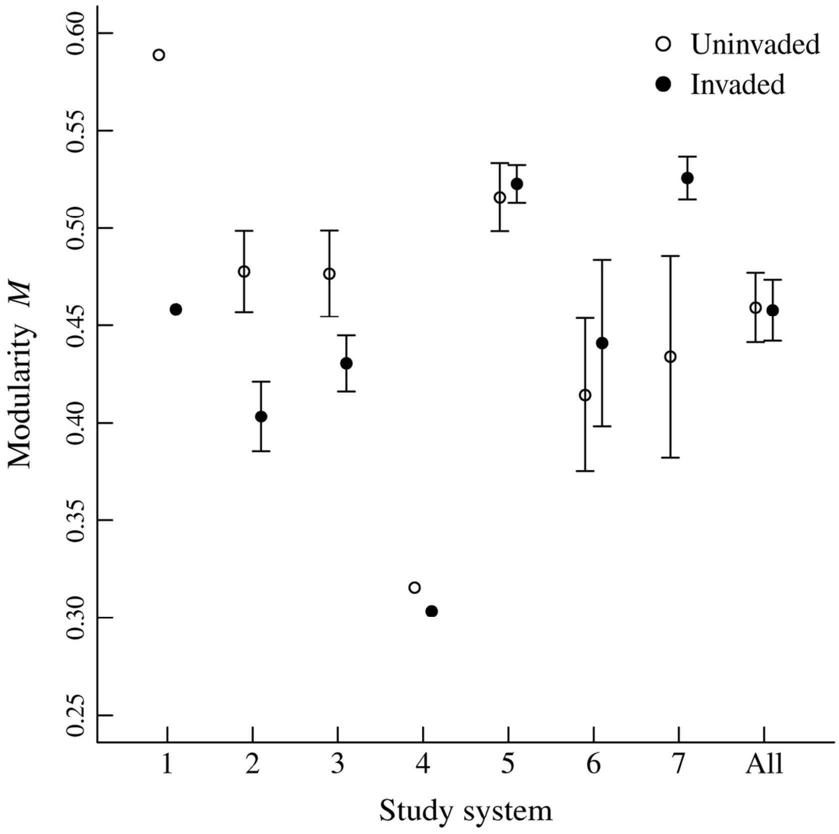
Fig. 1 Mean (± 1 standard error) modularity (*M*) of "uninvaded" plant–pollinator networks and networks invaded by one or several alien plant species plotted against the seven study systems. *M* is a measure of the degree to which a network is organized into clearly delimited modules. "Uninvaded" networks contained no aliens (16 networks) or a significantly lower proportion of alien plant species (study system 3) than invaded networks. Information about study systems is given in Electronic Supplementary Information 1a.

Fig. 2 Relationship between species generalization of the principal invader plant, measured as standardized degree (*SD*), and modularity (*M*) of invaded plant–pollinator networks.

Fig. 3 Example of the modular structure of **(a)** an uninvaded plant–pollinator network and **(b)** a network invaded by an alien plant invader (*Carpobrotus affine acinaciformis*; large red square). Interaction networks represent Mediterranean shrubland communities sampled at two locations at Cap de Creus, Spain [for details see 24]. Plants are represented by squares whereas pollinators by circles. Different colours represent different topological species' roles: peripheral species (yellow), connector (green), module hub (pink), network hub (red).

Fig. 4 Mean (± 1 standard error) module size (i.e. the number of species forming a module) of modules of uninvaded plant–pollinator networks (n = 92), modules of invaded networks not containing alien plant species (n = 68) and modules of invaded networks containing alien plant species (n = 32).

Fig. 5 Proportion of topological species' roles in uninvaded (open circles) and invaded plant–pollinator networks (closed circles). Roles are defined according to their position in the parameter space of within-module degree z and between-module connectivity c: a network hub ($z > 2.5$, $c > 0.62$) is highly linked to species within its own module and is well connected to species of other modules, making it important for the coherence of both, its own module and the entire network; a module hub ($z > 2.5$, $c \leq 0.62$) plays an important role within its own module whilst weekly connected to species of other modules; a connector ($z \leq 2.5$, $c > 0.62$) species is important for among-module connectivity, and consequently network coherence, but plays an inferior role within its own module; a peripheral species($z \leq 2.5$, $c \leq 0.62$) plays a topologically inferior role in the network (Olesen *et al.* 2007).



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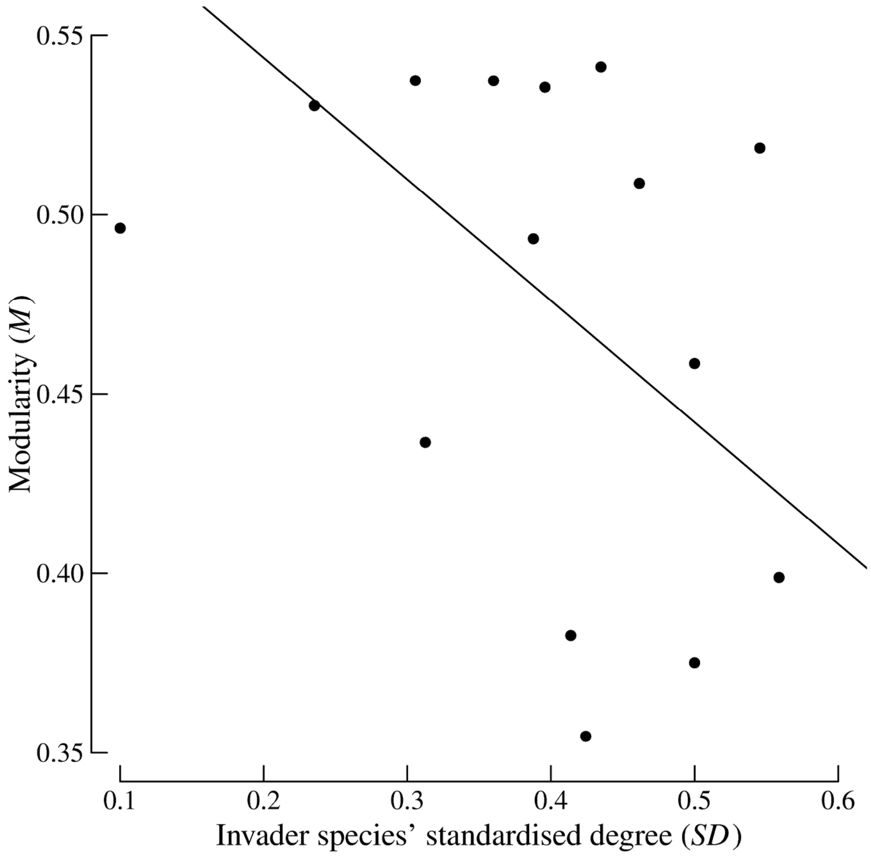

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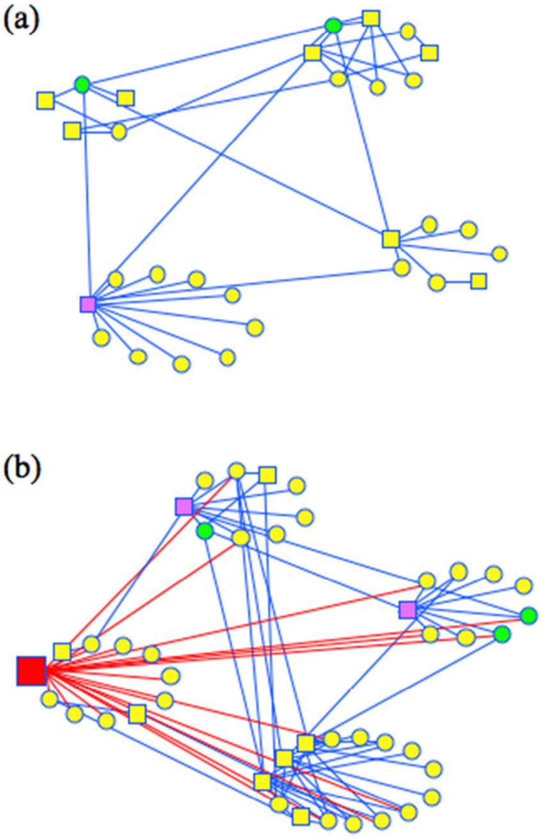
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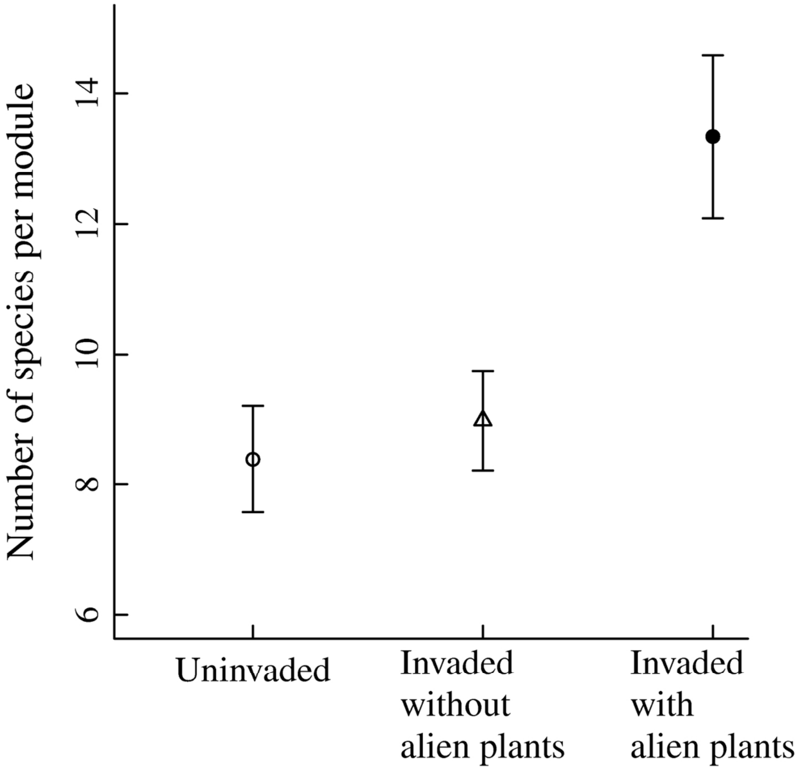

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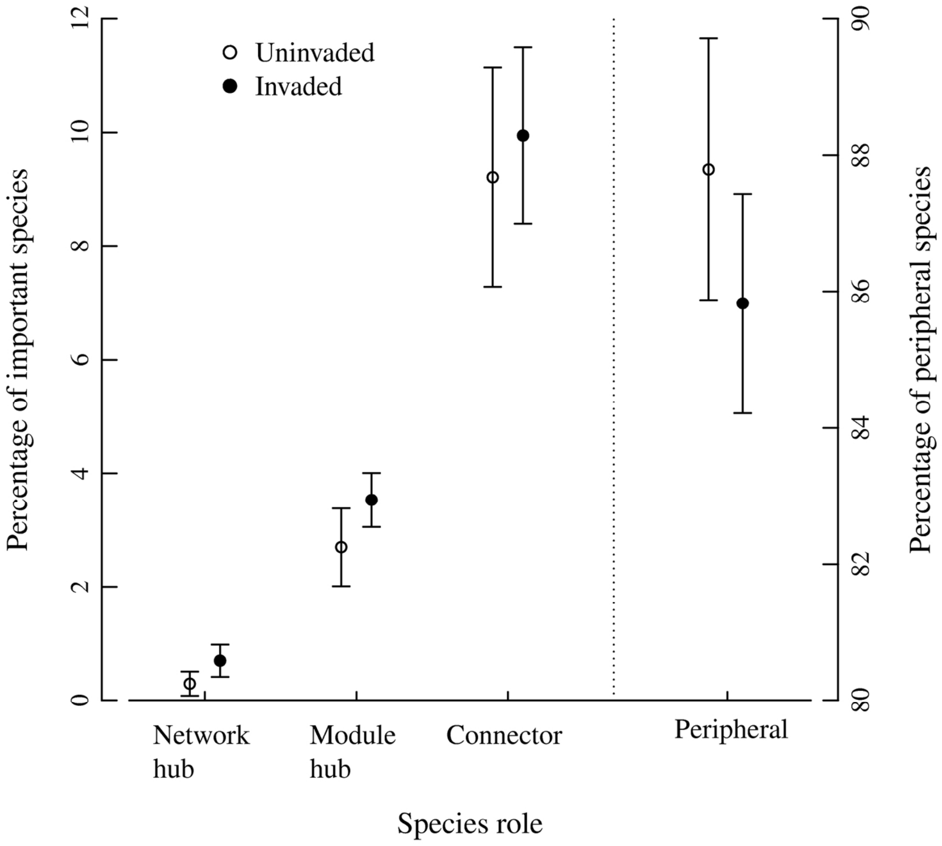

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