Fewer but higher quality of pollinator visits determines plant invasion success in simulated plant-pollinator networks

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Abstract

1. Invasive plants often use mutualisms to establish and spread in their new habitats. These plants tend to be well-integrated into plant-pollinator networks in terms of being visited by resident pollinators similarly or more frequently than the native plants.
2. The long-term persistence of non-native plants, however, not only depends on the quantity of visits they receive but also on the visit quality and the resulting reproductive success, which have been rarely studied in a network context.
3. We evaluated the potential of non-native plants to invade and impact plant-pollinator networks based on their ability to attract pollinators via production of floral rewards, to produce and attach pollen on pollinators, and the consequent seed production and population growth.
4. We simulated the introduction of different types of non-native plants into thousands of different networks using a model that includes population dynamics of plants and

pollinators, quantity and quality of pollinator visits, the dynamics of floral rewards, and pollinators' adaptive foraging.

5. We found the counterintuitive result that introduced plants visited by fewer pollinators were more successful at securing the high-quality visits necessary to invade. These plants did not experience the depletion of floral rewards that plants visited by too many pollinators experienced, which caused pollinators to reassign their visits to other plants and, therefore, dilute the conspecific pollen they carried.
6. Native pollinators increased their abundance with the plant invasions, but the reallocated foraging effort concentrated on invaders reduced the quantity and quality of visits to native plants and made the networks' visitation structure more modular and nested. These effects were buffered by plant richness.
7. Interestingly, the significant changes in visitation structure only caused a minimal decline in native plant abundance and no extinctions.
8. Our results call for evaluating the impact of invasive plants not only on visitation rates and network structure, but also on the demographics of native plants, which depend on other processes beyond pollination including seed production and recruitment.

Keywords: Species invasions, impacts on natives, adaptive foraging, floral rewards dynamics, seed production, plant recruitment, mechanistic models, transient dynamics.

Introduction

Species invasions are one of the six global change drivers threatening biodiversity worldwide (Tylianakis et al. 2008). Plants consist of the largest and most studied group of invasive species globally (Pyšek et al. 2008, Downey and Richardson 2016), which often use mutualisms to establish and spread in their new habitats (Richardson et al. 2000, Traveset and Richardson 2014, Parra-Tabla and Arceo-Gómez 2021). In particular, the interaction of non-native plants with resident pollinators (native or non-native) plays an important role in the plants' invasion success (Ghazoul 2002, Traveset and Richardson 2014, Parra-Tabla and Arceo-Gómez 2021). Studies analyzing the interactions of non-native plants within plant-pollinator networks indicate that these species are well-integrated into the networks by showing that they share flower visitors with native plants (Aizen et al. 2008, Bartomeus et al. 2008, Kaiser-Bunbury et al. 2011, Traveset et al. 2013, Montero-Castaño and Vilà 2017) or that they are visited either similarly or more frequently than the natives (Lopezaraiza–Mikel et al. 2007, Montero-Castaño and Vilà 2017, Parra-Tabla et al. 2019, Seitz et al. 2020). However, the long-term persistence of non-native plants not only depends on the visits they receive from pollinators in their new community but also on the efficiency of those pollinators in transporting their pollen and their consequent reproductive success (Parra-Tabla and Arceo-Gómez 2021). These other two key factors for plant invasion success (i.e., pollinator efficiency and reproductive success) have been rarely studied in the context of plant-pollinator networks (Parra-Tabla and Arceo-Gómez 2021).

Pollinator efficiency (in terms of pollinator contribution to seed production) has recently been studied in the context of plant-pollinator networks, but not associated with plant invasions. De Santiago-Hernández et al. (2019) shows that networks built using pollinator efficiency data are not nested, and are more modular and specialized than networks built with visitation data.

This study also shows that only 59% of floral visitors contributed to seed production. These findings suggest that a non-native plant receiving similar or more pollinator visits than the natives not necessarily will persist in the invaded community because those visits might not contribute to the plant reproduction success. Moreover, Thompson and Knight (2018) show that non-native plants can exhibit high reproductive success when visited by only one or a few pollinator species. That is, high quality of visits even when performed by one pollinator species can allow a non-native plant to get established and persist within the network. Here, we use a dynamic model to evaluate the potential of non-native plants to invade and persist in plant-pollinator networks based on their ability to attract pollinators via production of floral rewards, ability to attach pollen in the body of the pollinators, and the quality of pollinator visits they receive, as well as, their reproductive success and population growth. We also use this model to evaluate the impact of invasive plants on native species.

Invasive plants can affect plant-pollinator networks negatively by competing with native plants for pollinators or by increasing heterospecific pollen transfer (Traveset and Richardson 2006, 2014, Morales and Traveset 2009, Arceo-Gómez and Ashman 2016, Kaiser-Bunbury et al. 2017, Parra-Tabla et al. 2021), but also have null (Kaiser-Bunbury et al. 2011) or even positive effects on the networks via increased abundance of native pollinators (Lopezaraiza–Mikel et al. 2007, Bartomeus et al. 2008, Carvalheiro et al. 2008, Valdovinos et al. 2009). These plants can also affect the networks' structure by modifying the strength (Kaiser-Bunbury et al. 2017) and number (Bartomeus et al. 2008, Valdovinos et al. 2009) of species interactions, the natives' position within the network (Aizen et al. 2008, Albrecht et al. 2014), as well as, the network-level metrics such as modularity, nestedness, or connectance (Bartomeus et al. 2008, Valdovinos et al. 2009). However, research is needed to elucidate the mechanisms behind those changes in

network structure, including mechanisms driven by the adaptive foraging of pollinators, the differences in rewards offered between native and invasive plants, and the population growth of the invasive (Valdovinos 2019, Parra-Tabla and Arceo-Gómez 2021).

Building off the study by Valdovinos et al. (2018) that evaluates the invasion success and impacts on natives of non-native pollinators, we simulate the introduction of different types of non-native plants into thousands of different networks using a model that includes population dynamics of plants and pollinators, quality and quantity of pollinator visits, the dynamics of floral rewards, and pollinators' adaptive foraging. We ask: 1) What are the mechanisms allowing a non-native plant to invade and persist in a plant-pollinator network? 2) What are the mechanisms by which invasive plants affect the native species and the network structure?

Materials and methods

Network binary and weighted structures

Following Valdovinos et al. (2016), we define network structure as the binary interactions between plant and pollinator species, while network dynamics as the change in abundance of interacting species and the strength of those interactions. Additionally, we define the weighted structure of the networks as the frequency of visits each pollinator species perform to each plant species of the networks, which depends on the abundances of plant and pollinator species, the pollinators' foraging efforts and flying efficiency (see definition of variable V_{ij}, below). Empirical studies most often use this definition of weighted structures because frequency of visits is what researchers most often record in the field (e.g., Bartomeus et al. 2008, Vilà et al. 2009, Kaiser-Bunbury et al. 2011, 2017). Network binary structures were generated using Thébault and Fontaine's (2010) stochastic algorithm (see Appendix S1), which recreates

structural patterns of empirically observed networks including their heterogenous degree distribution and nestedness. The weighted structures emerged from the network dynamics (see below). We generated 1200 networks composed of three sets of 400 networks centered at three combinations of richness (S) and connectence (C), with values: S = 40 and C = 0.25, S = 90 and C = 0.15, and S = 200 and C = 0.06. These combinations represent three points in the empirically observed relation between richness and connectance (Fig. S1). Half of the networks at each set were nested and the other half, non-nested, with NODFst values ranging between -0.33 and 2.3. These networks maintained the empirically observed mean ratio of animal to plant species of 2.5 (Jordano et al. 2003).

Network dynamics

We use Valdovinos et al.'s (2013) model to simulate the population dynamics of each plant (Eq. 2, see below) and pollinator (Eq. 3) species of the network, as well as the dynamics of floral rewards (Eq. 4) of each plant species and the foraging effort (Eq. 5) that each pollinator species (per-capita) assigns to each plant species. An important advance of this model that is key to our study is that it tracks the quality of visits (per-capita) of pollinator species *j* to plant species *i* (per-capita) as:

$$\sigma_{ij} = \frac{\varepsilon_i \alpha_{ij} p_i}{\sum_{k \in P_j} \varepsilon_k \alpha_{kj} p_k} \tag{1}$$

This function is part of the plants' population dynamics (Eq. 2, below) and accounts for the dilution of plant *i*'s pollen when *j* visits other plant species. That is, pollinators visiting many different plant species carry more diluted pollen than the pollen carried by pollinators visiting only one plant species. Parameter ε_i represents the ability of plant *i* to attach pollen to a

pollinator's body relative to the other plant species visited by the pollinators. We varied this trait for the non-native plants that we introduced (see below). The variables α_{ij} and p_i represent the foraging effort of pollinator *j* assigned to plant *i* and the abundance (density) of plant species *i* (whose dynamics are determined by Eqs. 5 and 2, respectively). The entire model is as follows (see Table 1 for definition of parameters):

$$\overbrace{\frac{dp_i}{dt}}^{population\ growth\ of\ plant\ sp\ i} = \overbrace{\gamma_i \sum_{j\in A_i} e_{ij}\sigma_{ij}V_{ij}}^{reproduction\ reduced\ by\ plants'\ competition} - \overbrace{\mu_i^P p_i}^{mortality\ loss} \tag{2}$$

$$\overbrace{\frac{da_j}{dt}}^{population\ growth\ of\ animal\ sp\ j} = \overbrace{\sum_{i\in P_j} c_{ij}V_{ij}b_{ij}\frac{R_i}{p_i}}^{recruit\ to\ adults\ from\ rewards\ consumption} - \overbrace{\mu_j^A a_j}^{mortality\ loss} \tag{3}$$

$$\overbrace{\frac{dR_i}{dt}}^{floral-rewards\ dynamics\ of\ plant\ sp\ i} = \overbrace{\beta_i p_i - \varphi_i R_i}^{saturated\ production\ of\ rewards} - \overbrace{\sum_{j\in A_i} V_{ij}b_{ij}\frac{R_i}{p_i}}^{consumption\ by\ pollinators} \tag{4}$$

$$\frac{d\alpha_{ij}}{dt} = G_j\alpha_{ij}\left(\overbrace{c_{ij}\tau_{ij}b_{ij}R_i}^{R\ consumption\ from\ plant\ i} - \overbrace{\sum_{k\in P_j}\alpha_{kj}c_{kj}\tau_{kj}b_{kj}R_k}^{average\ R\ consumption\ from\ all\ j's\ plants}\right) \tag{5}$$

The function $V_{ij} = \alpha_{ij}\tau_j a_j p_i$ represents the visitation rate of animal species *j* to plant species *i* and connects the dynamics of plants, animals, rewards, and foraging efforts. The function $\gamma_i = g_i\left(1 - \sum_{l\neq i\in P_j} u_l p_l - w_i p_i\right)$ represents the germination rate of the seeds produced by the successful pollination events, where g_i is the maximum fraction of *i*-recruits subjected to both inter-specific (u_l) and intra-specific (w_i) competition. The sums in Eqs. 2-5 are taken over the sets of A_i and P_j of pollinator species that are capable of visiting plant *i*, and plant species that can be visited by pollinator *j*, respectively. Those sets are defined by the network structure taken as model input. Finally, the dynamic foraging efforts of Eq. 5 model adaptive foraging. These foraging efforts are restricted by $\sum_{i\in P_j}\alpha_{ij} = 1$, that is, they sum 1 for each pollinator species.

Table 1. Model parameters and variables with their initial values

Definition	Symbol	Dimension	Mean value
Density of plant population i	p_i	individuals area^{-1}	0.5*| **0.02**
Density of animal population j	a_j	individuals area^{-1}	0.5*
Total density of floral resources of plant population i	R_i	mass area^{-1}	0.5*| **0.01**
Foraging effort	α_{ij}	None	$1/k_{aj}$*
Visitation efficiency	τ_{ij}	visits area time^{-1} individuals^{-1} individuals^{-1}	1
Expected number of seeds produced by a pollination event	e_{ij}	individuals visits^{-1}	0.8
Per capita mortality rate of plants	μ_i^P	time^{-1}	0.001
Conversion efficiency of floral resources to pollinator births	c_{ij}	individuals mass^{-1}	0.2
Per capita mortality rate of pollinators	μ_j^A	time^{-1}	0.001
Pollinator extraction efficiency of resource in each visit	b_{ij}	individuals visits^{-1}	0.4
Maximum fraction of total seeds that recruit to plants	g_i	None	0.4
Inter-specific competition coefficient of plants	u_i	area individuals^{-1}	0.06
Intra-specific competition coefficient of plants	w_i	area individuals^{-1}	1.2
Production rate of floral resources	$\boldsymbol{\beta i}$	**mass individuals^{-1} time^{-1}**	**0.2 | 0.8^{A}**
Attachability of pollen to pollinator's body	$\boldsymbol{\varepsilon_i}$	**None**	**1 | 4^{A}**
Self-limitation parameter of resource production	ϕ_{ij}	time^{-1}	0.04
Adaptation rate of foraging efforts of pollinators	G_j	None	2

Values were drawn from a uniform random distribution with the specified mean, and variances of 10% and 0% of means for plants' and animals' parameters, respectively. The second values in bold for p_i and R_i are the ones used for the introduced plant species. Superscripted A indicates the highest level used for introduced plants. Asterisks indicate initial conditions. k_{aj} is the number of interactions of animal j.

We drew the initial densities for animals, plants, and floral resources from a random distribution with mean 0.5 and variance 0.1. We assigned the initial foraging efforts of each pollinator for each plant species in its diet to be $1/k$, where k is the number of interactions of each pollinator species. Then those foraging efforts change over time depending on the total floral rewards available in each plant species (see Eq. 5, above). We run the model for 10,000 timesteps prior to the plant introductions and another 10,000 timesteps after the introduction. The model simulations generally equilibrated after 3,000 timesteps, so running them for a longer duration ensured that we obtained the response variables at equilibrium. However, we analyzed both the transient dynamics immediately after the plant introduction (during the first 2,000 timesteps after the introduction) as well as the equilibrated dynamics.

Non-native introductions

One plant species per network was introduced at t = 10,000 at a density equal to the extinction threshold of plants, 0.02. This threshold was set in previous work based on the Allee effect experienced by plants (Valdovinos et al. 2013, 2016, 2018), whose abundances always go to zero when below that threshold with the parameter values used here. Substantial changes in parameter values only quantitatively vary this threshold (Valdovinos and Marsland 2021). The initial reward density of the introduced plant species was set to 0.02 times the average reward density of all native plants to keep the initial proportion of the introduced plant and reward densities consistent with that of the natives. Eight types of plant species were introduced to each network based on all combinations of two levels of three properties. First, two levels of generality (specialist vs generalist) that reflect that of the natives. That is, the introduced plant species identified as specialist or generalist were visited by the average number of pollinator

species visiting the 30% most specialist or generalist plant species of the network, respectively. Second, two levels of the plant ability to attach pollen to the pollinator body (same as natives' vs four times higher) either by producing large amounts of pollen or by having specific adaptations. This hereafter "pollen attachability" is described by the parameter ε_i of Eq. 1, which we set as that of the average native plant (Table 1) or four times higher. Third, the ability to attract pollinators (same as natives' vs four times higher) via the production of floral rewards. This hereafter "rewards production" is described by the parameter β_i in Eq. 2, which was set as that of the average native plant (Table 1) or four times higher. We chose the high levels of pollen attachability and rewards production to be four times higher than those of the average natives, because those levels show clear effects of the properties. Different values did not change our qualitative results.

The pollinator species that will initially visit the introduced plant, whose number is determined depending on whether the plant is specialist or generalist (see above), were chosen randomly from: (1) all pollinator species, (2) most-generalist pollinator species, (3) most-specialist pollinator species. These three options of "linkage algorithms" are called hereafter 'random', 'most connected', and 'least connected', respectively. The foraging effort of native pollinators initially visiting the introduced plant was set to 0.0001 (of a total of 1 summed over all the interactions of the pollinator), which was subtracted from the highest effort of the pollinator so the effect of the effort subtraction was null. We conducted a total of 28,800 plant introductions (1200 networks × 8 plant types × 3 linkage algorithms). Following Valdovinos et al. (2018), we used this large number of simulations with plant parameter values drawn randomly, different network structures, and different linkage algorithms as the sensitivity analysis of our results.

Analysis of the simulation results

To evaluate which properties of networks and introduced plants contributed most to their invasion success, we conducted a Classification and Regression Tree (CART) analysis in JMP. We used five-fold cross validation to avoid overfitting. Network properties included species richness, the ratio of plant to animal species, four measures of species connectivity, four measures of degree distribution (power law exponent for plants and animals, the standard deviation of animal generality and the standard deviation of plant vulnerability), four measures of niche overlap (the mean and maximum Jaccardian index for plants and animals), and nestedness (see Supplementary Methods). Introduced plant properties included the generality level, pollen attachability, rewards production, and the linkage algorithm. Network and introduced plant properties totaled 22 contributors for the analysis. We evaluated the effect of successful invasions (i.e., introduced plant species that persisted at high density) on natives' persistence, density, quality and quantity of visits. These variables were measured right before the plant introduction (t = 10,000), during the first 2,000 timesteps after the introductions (to understand the effects on natives of the initial introduction process), and at the end of the simulation (t = 20,000). We evaluated the effect of plant invasions on the networks' weighted structure by calculating the networks' weighted nestedness and weighted modularity before and after the invasion. These metrics were calculated using the nest.smdm() and computeModules() functions, respectively, from the R package bipartite.

Mathematical analysis

Valdovinos and Marsland (2021) show mathematically that the key determinant of plant survival in this model is the quality of visits they receive, σ_{ij} (Eq. 1 above). Moreover, the

authors find a threshold of quality of visits that plants need to meet to persist and the two equilibrium conditions determining such threshold (Eqs. 6 and 7). We use these two conditions to determine when an introduced plant species ($i = x$) will invade the network. First, the rewards at equilibrium of the introduced plant species x is obtained by solving $\frac{dR_x}{dt} = 0$ (Eq. 4), which results in:

$$R_x = \frac{\beta_x p_x}{\varphi_i + \sum_{j \in A_x} \beta_x \tau_{xj} \alpha_{xj} a_j} \tag{6}$$

See parameter definitions in Table 1. This condition indicates that the floral rewards at equilibrium of the introduced plant species is higher when the plant has a higher per-capita production rate β_x, and decreases with the total abundance of pollinators visiting the introduced plant $\sum_{j \in A_x} \alpha_{xj} a_j$. The latter expression is key to our analysis, as it shows that highly abundant pollinators (i.e., high a_j) need to increase less their foraging effort to the introduced plant (i.e., low increase of α_{xj}) to decrease its rewards to levels where the entire system (i.e., all species abundances, rewards, and foraging efforts) equilibrates (see Eq. 7).

Second, the abundance of pollinators visiting the introduced plant species x and their foraging efforts also reach an equilibrium, which Valdovinos and Marsland (2021) showed is guaranteed by:

$$R_x = R_x^* = \frac{\mu_x^A}{c_{xj} b_{xj} \tau_{xj}} \tag{7}$$

This condition together with Eq. 6 indicate that the system reaches a new equilibrium that includes the new plant species when the consumption of the rewards of x by the native pollinators drive the abundance of those rewards to R_x^*. If the rewards of x drop below R_x^*, the native pollinators will re-assign their foraging efforts to the native plants and stop visiting the

introduced species. Importantly, these conditions are general and make our mathematical analysis robust to all parameter values, network structures, and linkage algorithms.

Results

In all our simulations, the introduced plant species either went extinct or dramatically increased its abundance (density) to the density level of native plants, which is consistent with the Allee effect (Valdovinos et al. 2013, 2016, 2018) and quality-of-visits threshold (Valdovinos and Marsland 2021) found by previous work. Thus, we characterized the result of an introduction as either invasion failure or success, respectively. We found that specialist plants with high production of rewards and high pollen attachability were the most successful invaders (see "Spec High R&P" in Fig. 1). These plants invaded 93% of the times they were introduced into the networks, while the same plant type except for being generalist invaded only 18% of the times (see "Gen High R&P" in Fig. 1A). Specialist plants with high production of rewards but average pollen attachability had an invasion success of 12% (see "Spec High R" in Fig. 1A). All other plant types never invaded.

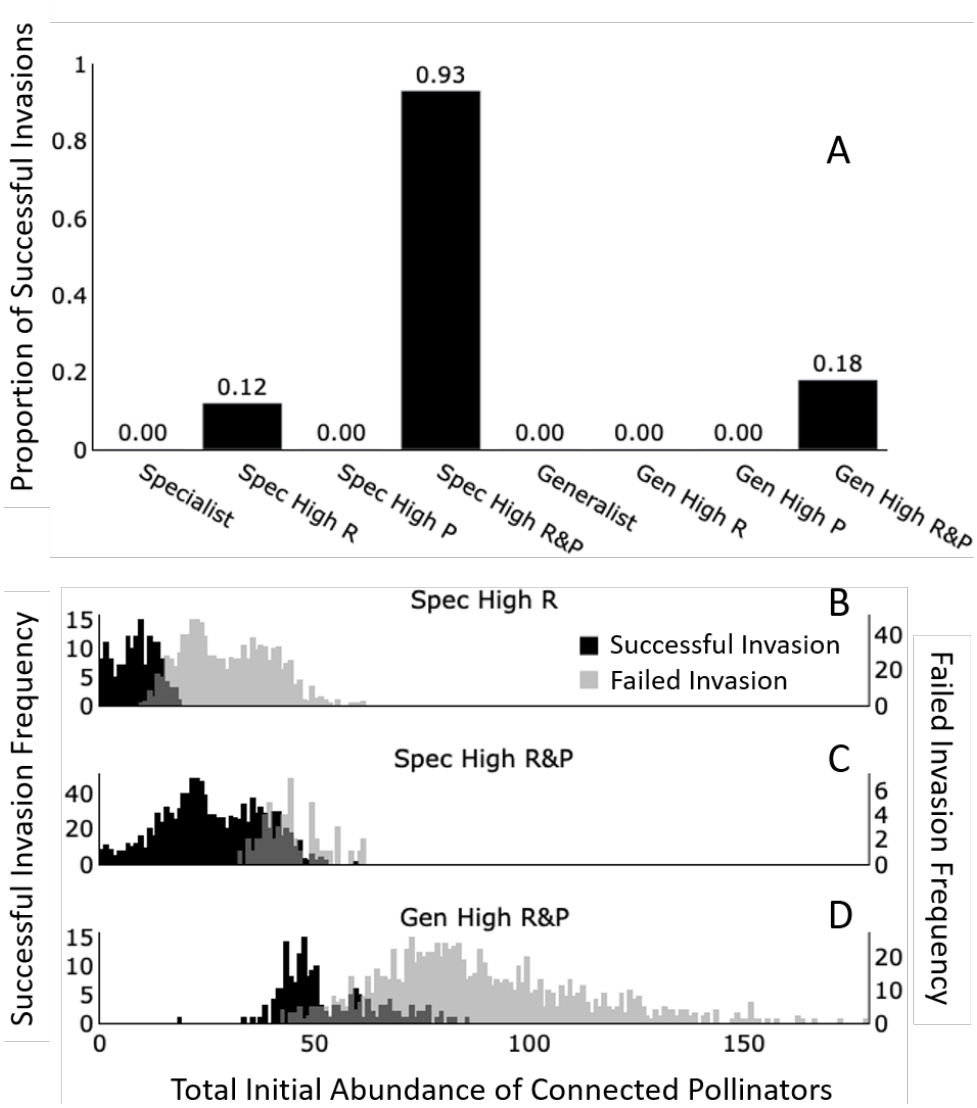

Figure 1. Proportion of successful plant invasions of each introduced species type (A) and the effect of pollinator abundance initially visiting them on their invasion success (B-D). Panel **A** shows (N = 28,800) that introduced plants visited by one or a few native pollinator species (Spec), were high rewards producers (High R), and exhibited high pollen attachability (High P) most frequently invaded. Introduced plants visited by many different pollinator species (Gen) and exhibiting the average level of rewards production or pollen attachability found among native plants (indicated by omitting High R or P) never invade. Panels **B, C, D** show data (N = 3,600; per panel) for the only three species types that successfully invaded the networks, that is, specialist plant species with high production of rewards (Spec High R), specialist plant species with high production of rewards and pollen attachability (Spec High R&P), and generalist plant species with high production of rewards and pollen attachability (Spec High R&P), respectively. Black and light gray bars represent successful and unsuccessful invasion, respectively, while light gray indicate were those two bar types overlap.

These results are corroborated by our CART analyses (Table 2), which shows that among the 22 factors analyzed (see Methods), high production of rewards contributed the most to the variation in invasion success, followed by being a specialist, and by having high pollen attachability. That is, the traits of the introduced plants (i.e., high production of rewards, level of generality, and high pollen attachability) are more important than the network structure to determine the plant invasion success. Finally, among those three types of invasive plants, those visited by fewer pollinators (in terms of abundance) at the moment of their introduction were the most likely to invade (Fig. 1B-C). The latter is a highly counterintuitive result that we explain below using our mathematical analysis. This counterintuitive result led us to conduct a second (refined, see Table 2) CART analysis in which we incorporated the initial pollinator abundance connected to the introduced plant as a contributor for the analysis. This refined analysis shows that it is the total abundance of pollinators visiting the plant (more than the number of pollinator species) what predicts the plant invasion success. Note, however, that these two variables are strongly and positively correlated (**Fig. S3**).

Table 2. Classification and Regression Tree (CART) analyses for invasion success.

	Initial analysis	**Refined analysis***
Five fold R^2	0.82	0.87
Main Contributions	High reward producer (34%) More specialized (25%) High pollen attachability (22%) Linkage algorithm (5%)	High reward producer (36%) *Initial pollinator abundance connected to non-native (33%) High pollen attachability (31%)

The initial analysis followed the simulation design (see Methods). The asterisk indicates that the refined analysis (as opposed to the initial) included the initial pollinator abundance connected to the non-native plant as a new contributor for the CART analysis, which better predicted the plant invasion success than the trait of being more specialized (i.e., visited by fewer pollinator species).

Our mathematical analysis explains our simulation results and demonstrate that they are robust. First, an inspection of Eq. 1 explains why only three types of the introduced plant species were able to invade. This equation shows that the introduced plant species always starts out at a double disadvantage with respect to the native plants because its initial abundance ($p_x = 0.02$), and the foraging effort pollinators assign to it ($\alpha_{xj} = 0.0001$) are very small compared to those of native plants at the moment of its introduction (average $p_i = 0.8, \alpha_{ij} = 0.1$). Those two variables are critical for the visit quality plants receive which, in turn, determines plant persistence (Valdovinos and Marsland 2021). Second, Eq. 6 shows that the higher the production of rewards of the introduced plant (β_x), the higher the amount by which the pollinators' foraging efforts (α_{xj}) assigned to the non-native will increase and, therefore, more likely it is to invade because it will receive higher quality of visits (see Eq. 1). This explains why high rewards producers can invade. Third, Eq. 1 shows the direct relation between the quality of visits and pollen attachability (ε_i), which explains why introduced plants with high pollen attachability are more likely to invade as long as they are capable to attract pollinator visits.

Inspection of the key term $\sum_{j \in A_x} \alpha_{xj} a_j$ in Eq. 6 also explains our counter-intuitive result of Fig. 1B-D. This term indicates that the more abundant the pollinators visiting the introduced plant species initially ($\sum_{j \in A_x} a_j$) the less their foraging effort assigned to the introduced plant (α_{xj}) need to increase to decrease the introduced plant's rewards to the system's equilibrium specified by Eq. 7 (where the rewards of the introduced species, the foraging efforts of pollinators, and the pollinator abundances stabilize). When this increase in foraging efforts is not enough for the introduced species to receive the quality of visits needed to invade (Eq. 1), the introduced plant goes extinct. To illustrate this mathematical finding, we use our simulations and depict the systems' equilibrium (Eq. 7) as a rewards threshold (see horizontal dashed line in Fig

2A). The failed invasion (gray curve in Figs. 2A and 2B) is explained by the introduced plant's rewards decreasing below such threshold (Fig 2A), which causes the pollinators to prefer the native plants after they depleted the introduced plant's rewards. That is, the pollinators did not increase their foraging efforts to the introduced plant fast enough (i.e., before depleting its rewards) to provide the plant with the high quality of visits (compare gray with black curve in Fig 2B) needed for its invasion. See Fig S2 in the Supplementary Information for plots also showing the foraging efforts and resulting plant density for both the successful and failed invasions, with the latter going extinct. This mechanism (Fig. 3) also explains why being a specialist increases the plant invasion success. If only one or a few pollinator species visit the introduced plant species, the total quantity of pollinators $\sum_{j \in A_x} a_j$ is more likely to be small and, therefore, each pollinator species is more likely to reassign their foraging efforts from the natives to the introduced plant species.

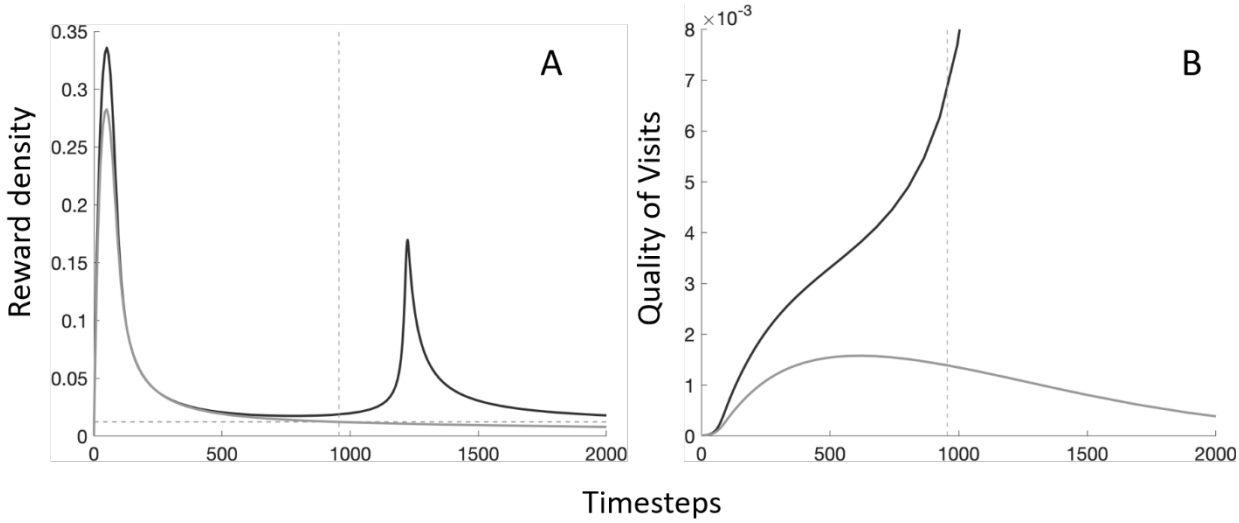

Figure 2. Rewards threshold that determines invasion success during the transient dynamics. Two simulations (one of the successful and one of the failed invasions) for the introduction of specialist plant species with high production of rewards and pollen attachability (Spec High R&P) chosen from the data shown in Fig. 1C, to illustrate: **A.** An introduced plant species fails to invade (gray curve) when its rewards drop from the level at which the system's reaches its feasible equilibrium (Eq. 7). This equilibrium defines a reward threshold (horizontal dashed line) for the introduced plant species that determines its invasion success (i.e., its reward

density remains above this threshold during the transient dynamics) or failure (i.e., its reward density drops below this threshold during the transient dynamics). The vertical dashed line indicates the timestep at which the reward threshold was reached for the failed invasion. The black curve depicts the reward density of a successful invasion for a different simulation (i.e., slightly different parameter values, which are drawn at random for each simulation) by the same type of introduced plant (specialist with high rewards production and pollen attachability) and similar network structure (~40 species and connectance of 0.25). The rewards threshold for the successful invasion is not depicted. **B.** The quality of visits received by the introduced plant species does not increase enough for the failed invasion before the reward threshold is reached, so it goes extinct (see Fig S2). In the successful invasion, the introduced plant species is able to attract the pollinators' foraging effort fast enough during the transient dynamics that obtains enough quality of visits to persist before the threshold is met. All our successful and failed invasions look qualitatively the same as these figures, which we only use to illustrate our mathematical results that are general for all parameter values and network structures.

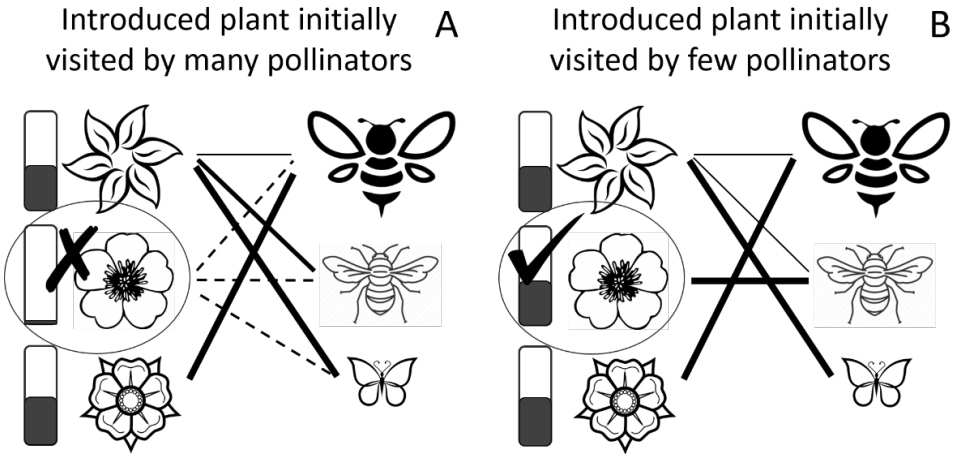

Figure 3. Mechanism explaining the negative relation between total pollinator abundance initially visiting the introduced plant species and its invasion success. Note that total pollinator abundance visiting a plant species depends on both the number of pollinator species visiting the plant species (represented by the three different pollinator drawings) and the abundance of each of those pollinator species (represented by the size of the drawings). **A.** The introduced plant species (circled) is less likely to invade when many pollinators (in terms of number of species and abundance) visit its flowers initially because they will deplete its rewards (bar next to flower) before reassigning their foraging effort (thickness of their links) to the levels the plant needs to receive the quality of visits that will allow its invasion. Dashed lines indicate the interactions that were lost because pollinators preferred native plants over the introduced plant, which resulted in the extinction of the introduced plant. **B.** The introduced plant will likely invade when producing more rewards than the native plants and when visited by few pollinators (in terms of number of species and abundance), which will make the pollinators to more strongly

reassign their foraging effort to the introduced plant and provide the quality of visits the plant needs to invade.

We evaluated the effects of the successful invasions on the native species and on the networks' weighted structure. We found that the native plants that shared pollinator species with the successful invaders received lower quantity (Figs. 4A and 5A) and quality (Figs. 4B and 5B) of visits after the plant invasion, which is explained by pollinators re-assigning their foraging efforts from the native to the invasive plant species (Fig. 5D). However, the native plants only slightly decreased their density (Fig. 5C) and never went extinct (data not shown) as a consequence of the invasion. The magnitude of this negative effect on the density of native plants was reduced by the number of plant species in the network (Fig. 5G). Conversely, the plant invasions increased the density of native pollinators (Fig. 5F), effect that was also attenuated by the number of plant species in the network (Fig. 5H). Finally, the plant invasions increased the networks' weighted nestedness (Fig. 4C) and modularity (Fig. 4D). See Table S2 for all the statistics of the Welch Two Sample t-test comparing weighted nesteness and modularity for all networks, groups of networks, and by the plant types introduced. Table S3 conceptually summarizes Table S2 for easy understanding of the trends.

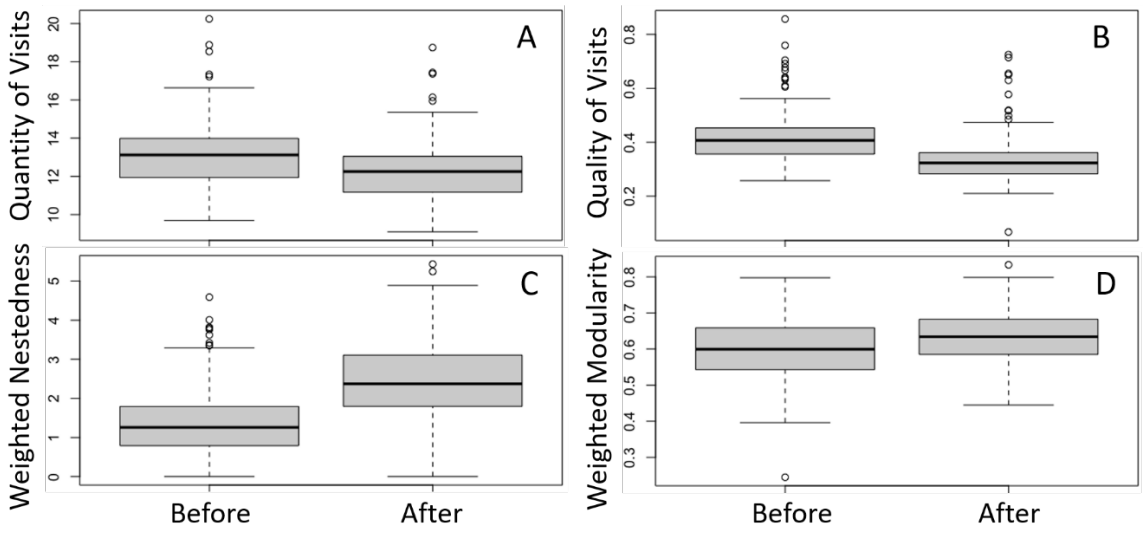

Figure 4. Effect of plant invasions on the quantity (A) and quality (B) of visits received by native plants and the networks' weighted nestedness (C) and modularity (D). Box plots for these variables before (at 10,000 timesteps) and after (at 20,000 timesteps) the plant introduction for all the networks with 40 species and connectance 0.25 that were invaded by the three plant types that successfully invaded the networks (see Fig 1A). The middle bar, box, and error bars represent the mean, interquartile range, and standard deviations of each distribution. Welch Two Sample t-test for A, B, C, and D provided strong evidence for significant differences between the variable means before and after invasion, all of which generated p-values less than 10^{-7}. (see Table S2).

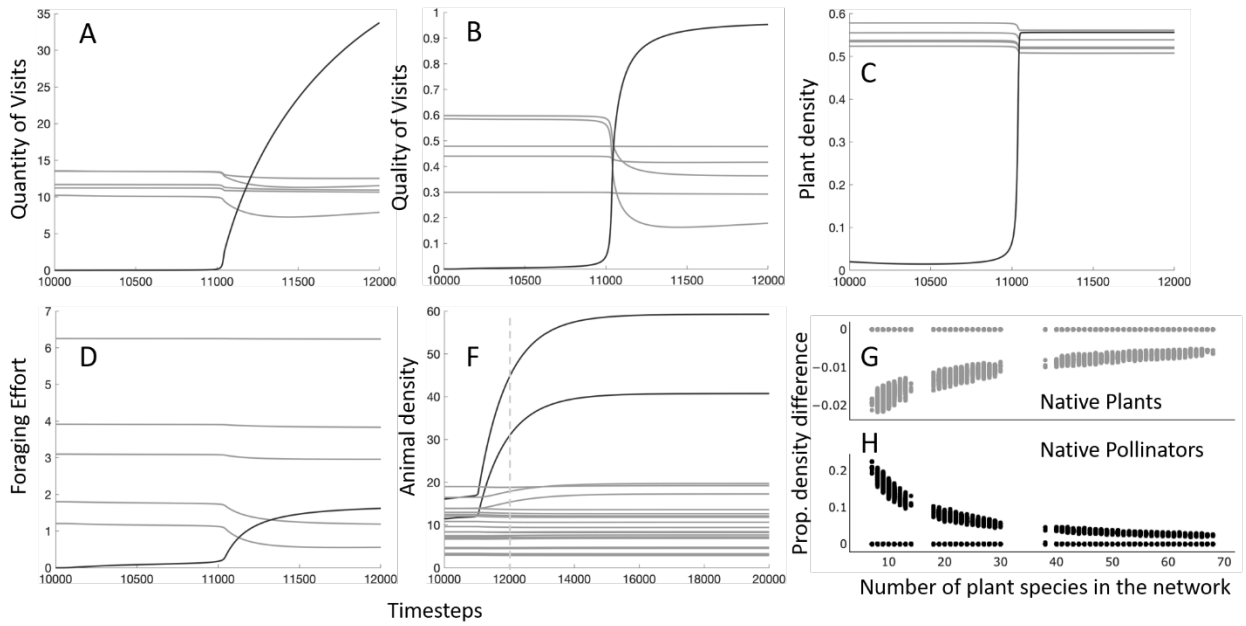

Figure 5: Time-series showing effects of plant invasions on native plants (A-D, G) and pollinators (F and H) right after the plant introduction. Quantity (A) and quality (B) of visits, density (C), and foraging effort assigned to the invasive plant species (black) increase over time, while those of native plant species (gray) sharing pollinators with the invasive decrease. Panel F shows how the pollinator species (black) visiting the invasive plant species increase in density in comparison to those (gray) not visiting the invasive. Plant richness decreases the magnitude of the negative (G) and positive (H) effects of the plant invasion on the native plants and pollinators, respectively, which is consistent with Elton's (1958) prediction of richer systems being more robust to species invasions than poorer systems. Panels G and H show the results of all simulations in which specialist plant species with high production of rewards and pollen attachability (Spec High R&P) were introduced (Fig. 1C), with each dot representing one simulation. Panels A-F show data for only one simulation chosen from a successful invasion of Spec High R&P for illustration purposes. All simulations with successful invasions show qualitatively similar patterns (data not shown).

Discussion

Plant-pollinators interactions enhance the establishment of invasive plants in their new range (Ghazoul 2002, Traveset and Richardson 2014). We used a modeling approach to identify the properties of plant-pollinator networks and non-native plants that influence their invasion success, as well as their effects on native species and network structure. We found that traits of non-native plants (i.e., high rewards production, being visited by only one or a few pollinator species, and high pollen attachability) determined their invasion success, while the number of plant species in the network influenced the invasion effects on natives. We found the counterintuitive result that introduced plants visited by fewer pollinators were more successful at securing the high-quality visits necessary for invading. In addition, plant invasions increased the abundance of native pollinators but the reallocated foraging effort concentrated on invaders reduced the quality and quantity of visits to native plants and made the network's visitation structure more modular and nested. This decline in visitation to native plants only caused a slight decline in their abundance. Below, we discuss each of our results with respect of the empirical evidence found in the literature.

Our results show that plants with higher production of rewards than that of natives were the only introduced plants able to attract pollinators that would reassign their foraging efforts to the extent needed by the non-natives to invade. This is consistent with findings of empirical research showing that plants that successfully invade plant-pollinator networks typically offer large amounts of floral rewards in large, showy flowers (Lopezaraiza–Mikel et al. 2007, Muñoz and Cavieres 2008, Padrón et al. 2009, Pyšek et al. 2011, Kaiser-Bunbury et al. 2011). However, our results also revealed a negative relation between the abundance of pollinators initially visiting the introduced plant and their invasion success. This finding seems counteractive at first,

but makes biological sense after analyzing the dynamics of the non-native floral rewards, and the quality and quantity of visits the plant receives immediately after its introduction. That is, receiving too many visits depletes its floral rewards before the shift in pollinators' foraging efforts is large enough to meet the quality of visits required by the plant to persist. This finding is consistent with previous work showing empirically that too many pollinator visits can damage the plant receiving the visits (Morris et al. 2010, Aizen et al. 2014), especially when the abundance of pollinators is disproportionally higher than that of plants. Our work shows that such dynamics occurs for non-native plants that are introduced at very low abundances but visited by many pollinators. Our finding of higher invasion success of plants offering high rewards but attracting fewer pollinator species is also consistent with empirical work showing that non-native plants can exhibit high reproductive success when visited by only one or a few pollinator species (Thompson and Knight 2018).

Empirical data also support our findings that plant invasions can increase the abundance of native pollinators (Lopezaraiza–Mikel et al. 2007, Bartomeus et al. 2008, Carvalheiro et al. 2008), but decrease the quantity and quality of visits received by native plants (Traveset and Richardson 2006, 2014, Morales and Traveset 2009, Arceo-Gómez and Ashman 2016, Kaiser-Bunbury et al. 2017, Parra-Tabla et al. 2021). However, empirical research analyzing how the effects of plant invasions on the quantity and quality of visits received by native plants translate to effects on the native reproduction success and population growth is still lacking (Parra-Tabla and Arceo-Gómez 2021). Our work can help guide future empirical research by showing that when other stages of plant reproduction are considered beyond visitation (i.e., successful pollination events, seed production, recruitment), the results of a decrease in quantity or quality

of visits does not necessarily translate into a decrease in plant reproduction or reduction of plant growth.

We found that plant invasions made the network structures more modular and nested, which is consistent with previous theoretical (Valdovinos et al. 2009) and empirical (Bartomeus et al. 2008) work, respectively. Valdovinos et al. (2009) using the metacommunity model developed by Fortuna and Bascompte (2006) found that networks with non-native plants where more modular than networks from which the non-natives were removed. Note that here we only evaluated weighted modularity because we are interested in foraging-effort changes driven by adaptive foraging in response to plant invasions, while the model used by Valdovinos et al. (2009) did not incorporate adaptive foraging. In addition, our simulations did not show changes in the binary structure of the networks because none of the species went extinct. That is, all changes in network structure corresponded to changes in visitation rates. Bartomeus et al. (2008) studied the effects of two different non-native plant species on the visits received by native plants and the binary structure of the invaded network. They found that one of the non-native species (*Carpobrotus*) facilitated pollinator visits to the natives, while the other (*Opuntia*) competed for those visits with the natives and made the binary structure more nested.

Other empirical studies did not find a clear relation between plant invasions and changes in the binary structure of the invaded networks (Vilà et al. 2009, Albrecht et al. 2014, Parra-Tabla et al. 2019). For example, Albrecht et al. (2014) found that changes in binary modularity was case specific, with three out of the seven studied systems showing a decrease in modularity (caused by the high level generalism of the invasive plants) and one showing an increase in modularity (not a generalist invasive plant). Our work can guide further research investigating the mechanisms by which these networks may become more (or less) nested and modular due to

plant invasions by showing how adaptive foraging of native pollinators can cuase changes in network structure, particularly on the weighted structure, as pollinators respond to the plant invasion by re-assigning their foraging efforts from the native to the non-native plants.

Our results also show that plant richness increases the robustness of plant-pollinator networks to the introduction of alien plants, which is consistent with Elton's (1958) prediction of richer systems being more robust to species invasions than poorer systems. That is, the more plant species in the network the smaller the effect of the introduced non-native plant on the natives. Finally, to our knowledge, ours is the first study suggesting that the cost of too many visits can affect the invasion success of non-native plants. This initial introduction process into plant-pollinator networks is difficult to study empirically because it would require to conduct the study during the first arrival of the non-native plant, or deliberately introduce the plants, which possess ethical problems. Therefore, our study also exemplifies how theoretical work can promote new thinking and research in areas traditionally studied empirically. Moreover, our work can guide future empirical research by identifying the mechanisms (Fig. 3) that can be affecting the invasions success of non-native plants and their impacts on natives (Figs. 4 and 5).

Our study is limited to the analysis of non-native plants introduced only once and in very small numbers. This type of introduction is at the core of our results showing that generalist plants are less successful to invade the networks than specialist plants. Our results suggest that the common finding of invasive species often exhibiting "highly generalized floral traits" (e.g., radial symmetry; reviewed in Parra-Tabla and Arceo-Gómez 2021), might be explained by those taxa being introduced several times and at larger numbers than those we simulated here. In fact, our results are consistent with those of the analysis conducted by Albrecht et al. (2014) across several plant-pollinator systems showing that generalized invasive plants receive more visits than

specialized invasive plants. The persistence of the generalized invasive plants at early stages right after their introduction (as opposed to our results showing that generalist species introduced slightly above their extinction threshold, receiving too many visits, and not producing enough floral rewards often go extinct) might be explained by frequent introductions or introductions at higher abundance.

Overall, our work contributes in promoting new thinking to integrate theoretical and empirical research, and calls for evaluating the impact of invasive plants not only on visitation rates and network structure, but also on the demographics of native plants, which depend on other processes beyond animal visitation including seed production and recruitment.

Acknowledgements

This research was supported by National Science Foundation grants DEB-1834497 and DEB-2129757 to F.S.V.

Statement of Authorship

F.S.V. conceived the ideas and designed methodology; F.S.V. and S.D. developed the computing code, run the computer simulations, analyzed the simulation results, and produced the figures; R.M. and F.S.V. conducted the mathematical analyses; F.S.V. led the writing of the manuscript. All authors contributed critically to the final drafts and gave final approval for publication.

Data availability statement

All codes used for running simulations, analyzing results, and producing figures are available at: https://github.com/fsvaldovinos/Plant_Invasions

Conflict of interest: The authors declare no conflict of interest.

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