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Transient dynamics in plant-pollinator networks: Fewer but higher quality of pollinator visits determines plant invasion success

Abstract: Invasive plants often use mutualisms to establish in their new habitats and tend to be visited by resident pollinators similarly or more frequently than native plants. The quality and resulting reproductive success of those visits, however, have rarely been studied in a network context. Here, we use a dynamic model to evaluate the invasion success and impacts on natives of various types of non-native plant species into thousands of plant-pollinator networks of varying structure. We found that non-native plants producing high amounts of floral rewards but visited by few pollinators at the moment of their introduction were the only plant species able to invade the networks. This result is determined by the transient dynamics occurring right after the plant introduction, when the pollinator species visiting the introduced plant are low in abundance so it takes them a large amount of foraging effort to deplete the non-native rewards to the reward threshold that determines the equilibrium of the system. This large increase in foraging effort strongly increases the quality of their visits to the introduced plant which allows the plant to invade. Native pollinators visiting the successful invader increased their abundance but the reallocation of their foraging effort from the native plants to the invader reduced the quantity and quality of visits to native plants and made the networks more modular and nested. These effects were buffered by plant richness. Interestingly, changes in visitation structure only caused a minimal decline in native plant abundance and no extinctions. Our results call for evaluating the impact of invasive plants not only on visitation rates and network structure, but also on processes beyond pollination including seed production and recruitment.

Keywords: Species invasions, impacts on natives, adaptive foraging, floral rewards dynamics, pollinator visit quality, mutualism models.

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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 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 reproductive success of invasive plants (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 quantity of 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).

The effect of these two key factors (i.e., pollinator efficiency and reproductive success) on plant invasions 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

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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 many pollinator visits not necessarily will persist in its new community because those visits might not contribute to its reproduction success. Indeed, non-native plants receiving few but high quality visits can also persist in their new community. Thompson and Knight (2018) show that non-native plants can exhibit high reproductive success when visited by only one or a few pollinator species. In contrast, other studies find that several invasive species exhibit generalized floral traits (Parra-Tabla and Arceo-Gómez 2021), are visited by many and abundant pollinator species (Bartomeus et al. 2008, Vilà et al. 2009), and tend to be network hubs (Albrecht et al., 2014). Furthermore, these contrasting empirical patterns have been obtained for plant species that had already invaded the networks and not necessarily explain their invasion success from the early stages of their introduction. Therefore, we submit our field lacks a clear understanding of the non-native traits and network characteristics that predict the invasion success of a recently introduced plant species. Here, we develop such predictive understanding by evaluating the effects of non-native traits and network characteristics on the invasion success and impacts on natives of introduced plant species, using the dynamic plant-pollinator network model of Valdovinos et al. (2013). Specifically, we evaluate the effects of the number and abundance of pollinator species visiting the introduced species, the quantity and quality of those pollinators' visits, and the effects of those visits on the reproduction and population growth of the introduced 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.

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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, the mechanisms behind those network changes and the impacts of those network changes on the native species are not entirely understood (Parra-Tabla and Arceo-Gómez 2021). Here, we use our modeling approach to evaluate how adaptive foraging of resident pollinators, differences in floral rewards offered by native and introduced species, and the population growth of the introduced species drive changes in network structure, and how those changes impact native species.

Previous work used the same mathematical model we use here to evaluate the invasion success and impacts of non-native pollinators on plant-pollinator networks (Valdovinos et al. 2018). However, the dynamics of pollinators and plant in this model are very different. That is, the equations describing their population dynamics encapsulate biological mechanisms that differ drastically between pollinators and plants (see Eqs. 1 and 2 in Methods), which result in very different dynamical outputs and effects on other species in the network (Valdovinos et al. 2013, 2016, 2018, Valdovinos and Marsland 2020). Moreover, these differences in modeled population dynamics may provide insights into the mechanisms influencing the invasion processes of pollinators vs. plants in ecological networks. Therefore, we evaluate the invasion success and impacts of non-native plants on plant-pollinator networks by testing three hypotheses: 1) non-

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native plants producing more floral rewards than native plants will attract resident pollinators and secure their reproduction success; 2) non-native plants visited by fewer pollinators but receiving higher quality of visits will more likely invade the networks than non-natives visited by more pollinators but receiving lower quality of visits; 3) changes in network structure produced by the introduction of non-native plant species will not necessarily impact the reproduction success of native plants.

Materials and methods

Binary vs. weighted network structures

The binary structure of networks represents species as nodes and their interactions as binary links, while the weighted structure provides information about the strength of those interactions as weighted links. We use the visitation rate of each pollinator species to each plant species (function V_{ij} in Table 1) to determine the weighted structure, which depends on the abundances of plant and pollinator species, the pollinators' foraging efforts, and visitation efficiency. 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). We used the 1200 binary structures from Valdovinos et al. (2018), 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, and recreate structural patterns of empirically observed networks including their heterogenous degree distribution and nestedness. Half of the networks at each set are nested and the other half, non-nested, with NODFst values ranging

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between -0.33 and 2.3. These networks maintain the empirically observed mean ratio of animal to plant species of 2.5 (Jordano et al. 2003). The weighted structures emerged from the network dynamics (see below).

Network dynamics

We used Valdovinos et al.'s (2013) model to simulate the population dynamics of each plant (Eq. 1) and pollinator (Eq. 2) species of the network, as well as the dynamics of floral rewards (Eq. 3) of each plant species, and the foraging effort (Eq. 3) that each pollinator species (per-capita) assigns to each plant species as follows (see Table 1 for definition of functions, parameters, and their values):

$$\overbrace{\frac{dp_i}{dt}}^{\text{population growth of plant sp } i} = \overbrace{\gamma_i \sum_{j\in A_i} e_{ij}\sigma_{ij}V_{ij}}^{\text{reproduction reduced by plants' competition}} - \overbrace{\mu_i^P p_i}^{\text{mortality loss}} \quad (1)$$

$$\overbrace{\frac{da_j}{dt}}^{\text{population growth of animal sp } j} = \overbrace{\sum_{i\in P_j} c_{ij}V_{ij}b_{ij}\frac{R_i}{p_i}}^{\text{recruit to adults from rewards consumption}} - \overbrace{\mu_j^A a_j}^{\text{mortality loss}} \quad (2)$$

$$\overbrace{\frac{dR_i}{dt}}^{\text{floral-rewards dynamics of plant sp } i} = \overbrace{\beta_i p_i - \varphi_i R_i}^{\text{saturated production of rewards}} - \overbrace{\sum_{j\in A_i} V_{ij}b_{ij}\frac{R_i}{p_i}}^{\text{consumption by pollinators}} \quad (3)$$

$$\overbrace{\frac{d\alpha_{ij}}{dt}}^{\text{adaptive foraging}} = G_j\alpha_{ij}\left(\overbrace{c_{ij}\tau_{ij}b_{ij}R_i}^{R\text{ consumption from plant } i} - \overbrace{\sum_{k\in P_j}\alpha_{kj}c_{kj}\tau_{kj}b_{kj}R_k}^{\text{average } R\text{ consumption from all } j\text{'s plants}}\right) \quad (4)$$

We run the model for 10,000 timesteps prior to the plant introductions and another 10,000 timesteps after the introduction. We analyzed both the transient dynamics immediately after the plant introduction (during the first 2,000 timesteps after the introduction) and the equilibrated dynamics (at 10,000 timesteps). The simulations generally equilibrated at around 3,000 timesteps, so running them longer ensured we captured the dynamics at equilibrium.

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Table 1. Model state variables, functions, and parameters.

Definition	Symbol	Dimension	Mean value
State Variables			
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 of *j* on *i*	α_{ij}	None	$1/k_{aj}$*
Functions			
Visitation rate of *j* to *i* (quantity of visits)	$V_{ij} = \alpha_{ij}\tau_j a_j p_i$	visits area time^{-1}	variable
Quality of visits (per-capita) of *j* to *i* (per-capita)	$\sigma_{ij} = \frac{\varepsilon_i \alpha_{ij} p_i}{\sum_{k \in P_j} \varepsilon_k \alpha_{kj} p_k}$	None	variable
Fraction of seeds *i* that recruit to adults	$\gamma_i = g_i\left(1 - \sum_{l \neq i \in P_j} u_l p_l - w_i p_i\right)$	None	variable
Parameters			
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}**

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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.

Non-native introductions

We introduced 8 types of plant species to each network (one per simulation) based on all combinations of two levels of three properties (see Table 2) at t = 10,000, with density equal to the plant extinction threshold, 0.02, and reward density 0.02 times that of the average native to keep the initial rewards density per plant similar between non-native and native plants. Therefore, 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 $p_i = 0.8, \alpha_{ij} = 0.1$). The extinction threshold was set in previous work based on the Allee effect experienced by plants for the parameter values shown in Table 1 (Valdovinos et al. 2013, 2016, 2018).

The pollinator species that initially visited the introduced plant 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

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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).

Table 2. Properties of the non-native plants introduced.

Factor (property)	Description of level 1	Description of level 2
Generality (# *links*)	Specialist *(average # links of 30% most specialist natives)*	Generalist *(average # links of 30% most generalist natives)*
Pollen attachability ($\boldsymbol{\varepsilon_i}$)	Same as average native	Four times higher than average native*
Rewards production ($\boldsymbol{\beta_i}$)	Same as average native	Four times higher than average native*

*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.

Analysis of the simulation results

We conducted a Classification and Regression Tree (CART) analysis using the software JMP to evaluate which properties of networks and introduced plants contributed most to their invasion success. We used five-fold cross validation to avoid overfitting. Network properties included species richness (S), the ratio of plant to animal species, four measures of link density [connectance ($C = L$ / A×P, where L is the total number of links, A the number of pollinator species, and P the number of plant species), links per species (L/S), links per plant species (L/P), and links per animal species (L/A)], 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

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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.

Results

All introduced plant species either went extinct or dramatically increased their density to that of native plants. Thus, we characterized the result of an introduction as either invasion failure or success. We found that specialist plants with high rewards production and high pollen attachability were the most successful invaders (see "Spec High R&P" in Fig. 1), which partly supports our first hypothesis (see Introduction). 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. Our CART analyses (Table 3) confirm these results, showing 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 finally by having high pollen attachability.

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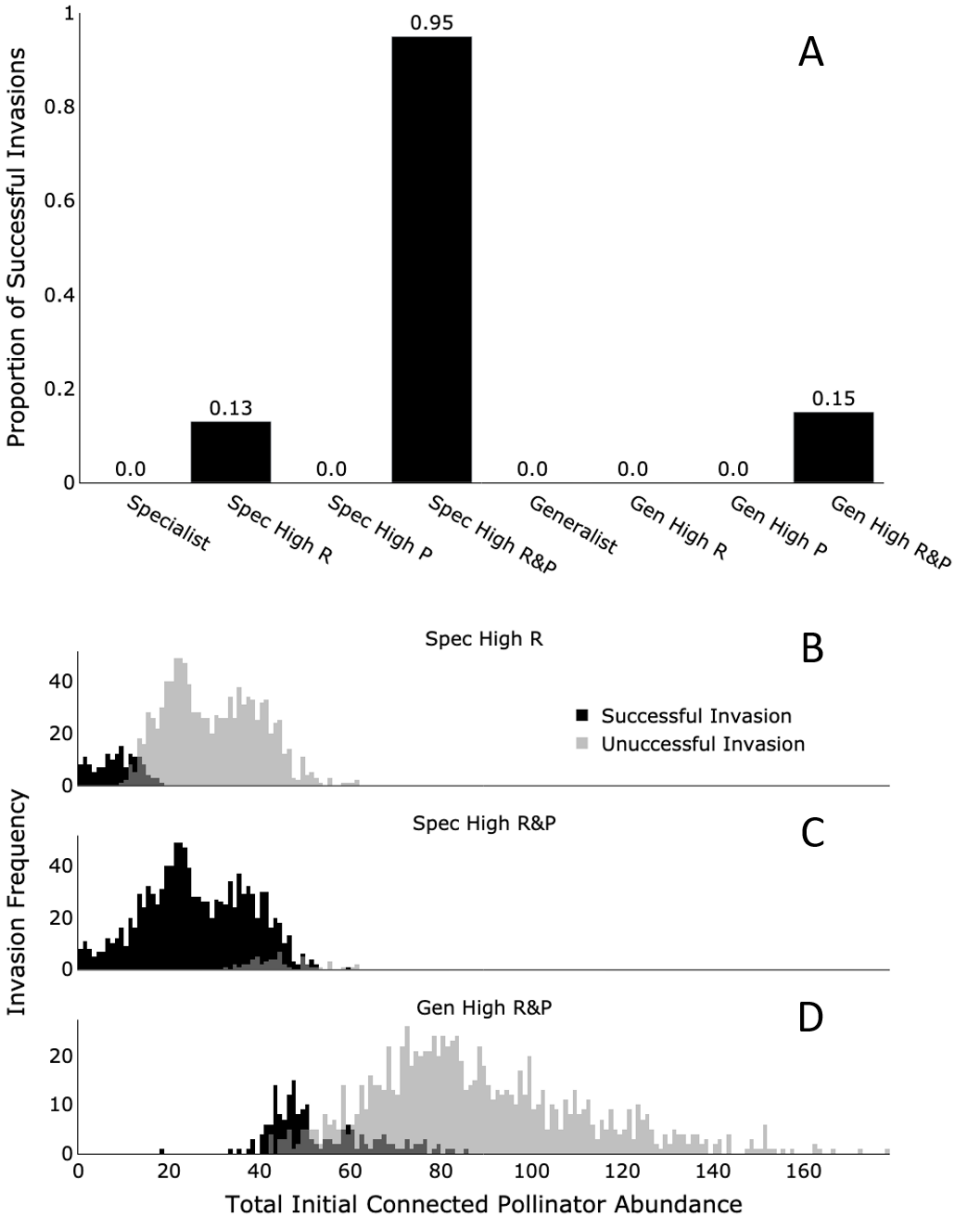

Figure 1. Proportion of successful plant invasions of each introduced species type (A) and the effect of pollinator abundance initially visiting them on their invasion success (B-D). Panel **A** shows (N = 28,800) that introduced plants visited by one or a few native pollinator species (Spec), high reward producers (High R), and with 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 medium gray indicate were those two bar types overlap.

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We found that plants visited by fewer pollinators (in terms of abundance) at the moment of their introduction most likely invaded (Fig. 1B-C), which partly supports our second hypothesis. Therefore, we conducted a second (refined, see Table 3) 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 the total abundance of pollinators visiting the introduced plant species better predicts its invasion success than the number of pollinator species visiting it (note these two variables are strongly and positively correlated Fig. S1).

Table 3. 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).

The explanation for introduced plants visited by fewer pollinators being more likely to invade resides in the reward threshold determining whether a plant species attracts sustained visitation or not (hereafter "reward threshold"; Fig 2, Appendix S1, Fig. S2). When the reward density of a plant species drops from such threshold, the pollinators stop visiting it and the plant species declines in abundance which, in turn, declines the reward density of its population even further (i.e., fewer flowers available for pollinators). This vicious cycle causes the irreversible process of plant species going extinct once their rewards density drops below the reward threshold. All plant species have the same reward threshold at each simulation (Eq. S2 in Appendix S1, R* in Fig S2), as a result of the "ideal-free distribution" caused by pollinators being adaptive foragers (Valdovinos et al. 2013), and its value is determined by the parameter

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values drawn randomly prior to running each simulation. However, the dynamics of floral rewards differ among plant species given that they have different per-capita production rate of rewards and are visited by different pollinator species with different abundances and foraging efforts.

If the reward density of the introduced species stays at or above this reward threshold (black curve in Fig. 2A), the plant population keeps attracting pollinators for long enough to receive high quality of visits (black curve in Fig. 2B), which ensures its population growth and, therefore, its invasion success (Figs. S3A-D). If the reward density of the plant population drops from this threshold (gray curve in Fig. 2A) due to high consumption by pollinators, the pollinators stop visiting it and reassign their visits to other plant species in their diet whose rewards are at or above the threshold. Consequently, pollinators do 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; Fig. S2) needed for its invasion, and the plant species goes extinct. See Appendix S1 for a mathematical analysis demonstrating that our results are general.

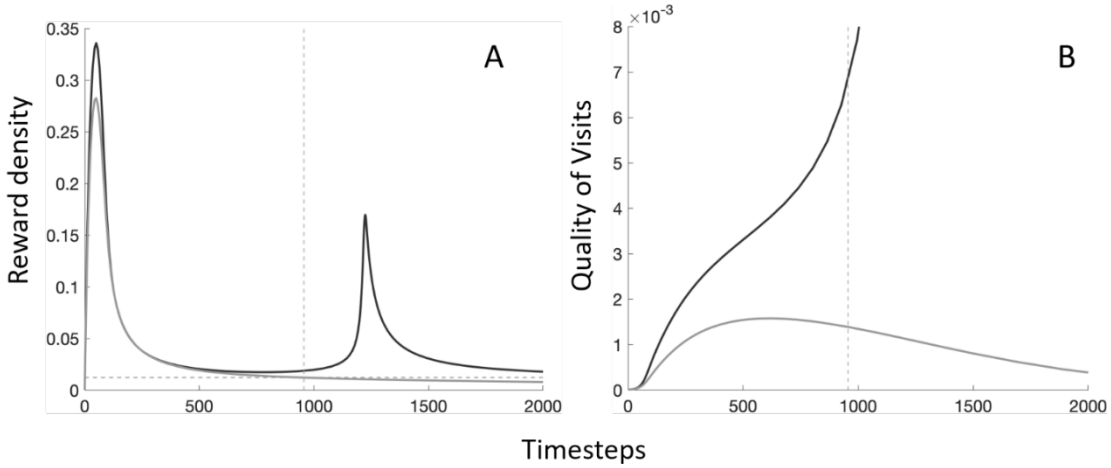

Figure 2. Reward threshold that determines invasion success during the transient dynamics. Transient dynamics are defined as the non-asymptotic dynamical regimes that persist for less than one to 'as many as tens of generations' (Hastings et al. 2018). Two simulations (one of the successful, black curves, and one of the failed, gray curves, 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.

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1C, to illustrate: **A.** An introduced plant species fails to invade (gray curve) when its rewards drop from the reward threshold (horizontal dashed line). The vertical dashed line indicates the timestep at which the reward threshold was crossed for the failed invasion. **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. The second peak observed in panel A corresponds to the increase floral rewards due to the increase in abundance of the introduced species that successfully invades, but then get depleted again to the reward density determining the system's equilibrium (see Eq. S2 in Appendix S1). All successful and failed invasions look qualitatively the same as these figures.

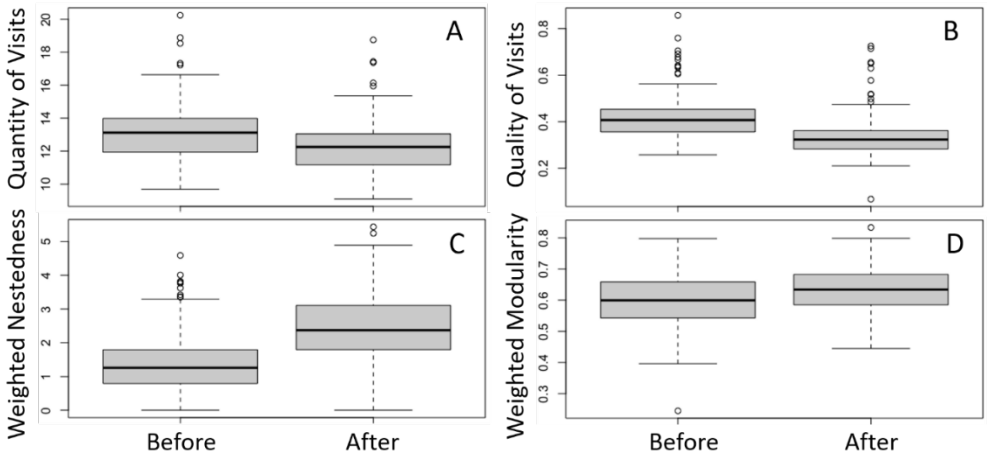

Figure 3. Effect of plant invasions on the quantity (A) and quality (B) of visits received by native plants and the networks' weighted nestedness (C) and modularity (D). Box plots for these variables before (at 10,000 timesteps) and after (at 20,000 timesteps) the plant introduction for all the networks 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).

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. 3A and 4A) and quality (Figs. 3B and 4B) 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. 4D). However, the native plants only slightly decreased their density (Fig. 4C) and never went extinct (data not shown) as a consequence of the invasion. The magnitude of this negative effect on the density of native

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plants was reduced by the number of plant species in the network (Fig. 4G). Conversely, the plant invasions increased the density of native pollinators (Fig. 4F), effect that was also attenuated by the number of plant species in the network (Fig. 4H). Finally, the plant invasions increased the networks' weighted nestedness (Fig. 3C) and modularity (Fig. 3D). See Table S1 for all the statistics of the Welch Two Sample t-test comparing weighted nestedness and modularity for all networks, groups of networks, and by the plant types introduced. Table S2 conceptually summarizes Table S1 for easy understanding of the trends.

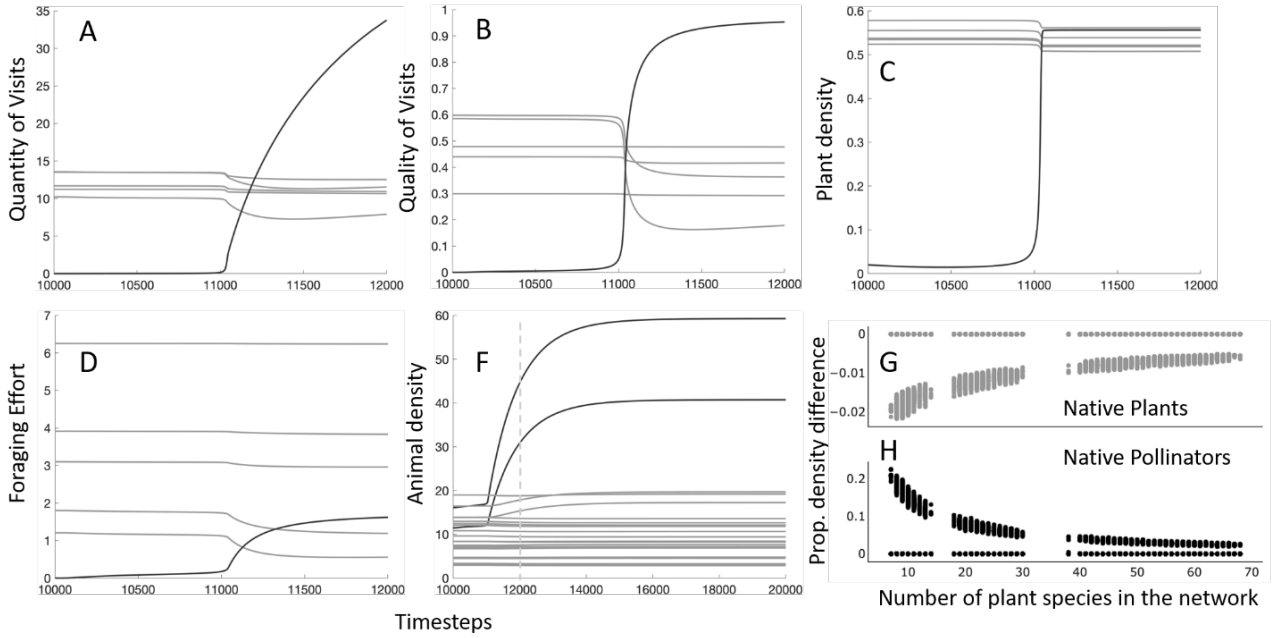

Figure 4: Effects of plant invasions on native plants (A-D, G) and pollinators (F and H) right after the plant introduction. Panels A-F show time series for only one simulation chosen from a successful invasion of Spec High R&P, but all simulations with successful invasions show qualitatively similar patterns. 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 species decrease. Panel F shows the increase in density of pollinator species (black) visiting the invasive species in comparison to those (gray) not visiting the invasive. Panels G-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. 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.

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Discussion

Ecologists are increasingly calling for theory focusing on transient as opposed to equilibrium dynamics (Hastings et al. 2018, 2021, Morozov et al. 2020, Francis et al. 2021, Abbott et al. 2021). Many ecological phenomena occur before the system reaches an equilibrium, which may never be reached due to the effects of stochasticity and perturbations (Hastings et al. 2018, Abbott et al. 2021). The latter strengthens the importance of studying ecological transients especially for evaluating how ecological systems respond to perturbations caused by global change. Dynamical transients are defined as the non-asymptotic dynamical regimes that persist for less than one to 'as many as tens of generations' (Hastings et al. 2018). To the best of our knowledge, our work is one of the first revealing a dynamical transient in ecological networks, as theory on ecological networks has traditionally focused on equilibrium dynamics (e.g., Bascompte et al. 2006, Bastolla et al. 2009, Pascual-García and Bastolla 2017, Valdovinos and Marsland 2020). Specifically, we found that — due to the transient dynamics that occur right after the plant introduction — non-native plants producing high amounts of floral rewards but visited by few pollinators at the moment of their introduction were the only plant species able to invade the networks. These dynamics occur when the pollinator species visiting the introduced plant species are low in abundance so it takes them a large amount of foraging effort to deplete the rewards of the plant to the reward threshold that determines the system's equilibrium. This large increase in foraging effort strongly increases the quality of visits received by the introduced plant which allows the plant to invade the network, and increases the abundance of the pollinators visiting the successful invader.

The transient dynamics we found in our study support our three hypotheses, that is: 1) introduced plant species producing more floral rewards than natives were more likely to invade,

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2) introduced species visited by more pollinators but receiving lower quality of visits were less likely to invade, and 3) changes in visitation network structure caused by plant invasions minimally (if at all) affected the reproduction success of native plants. In addition, we found that among the 22 factors evaluated (see Methods), 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 magnitude of the invasions' impacts on natives. Below, we discuss each of our results with respect of the empirical evidence found in the literature.

Our finding of higher invasion success of plants offering higher amounts of floral rewards is consistent with 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). Our finding of higher invasion success of plants attracting fewer pollinator species is 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). This finding is also consistent — although due to a different biological mechanism — with empirical data showing that too many pollinator visits can reduce the fitness of the plant receiving those visits (Morris et al. 2010, Aizen et al. 2014), especially when the abundance of pollinators is disproportionally higher than that of the plant population. Our work shows that non-native plants that are introduced at very low abundances but visited by abundant pollinators receive too many visits that are low in quality and, therefore, go extinct after their rewards are depleted below the reward threshold capable to attract pollinators.

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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, the field still lacks research on how those effects on visitation rates translate to effects on the reproduction success and population growth of native plants (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), 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

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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 cause changes in network structure, particularly on the weighted structure, as pollinators respond to the plant invasion by reassigning 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

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work can guide future empirical research by identifying mechanisms that can be affecting the invasions success of non-native plants and their impacts on natives.

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 during the transient dynamics of ecological networks, 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.

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