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RESEARCH ARTICLE

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Pollen transfer networks reveal alien species as main heterospecific pollen donors with fitness consequences for natives

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Abstract

1. The ecological dynamics of co-flowering communities are largely mediated by pollinators. However, current understanding of pollinator-mediated interactions primarily relies on how co-flowering plants influence attraction of shared pollinators, and much less is known about plant–plant interactions that occur via heterospecific pollen (HP) transfer. Invaded communities in particular can be highly affected by the transfer of alien pollen, but the strength, drivers and fitness consequences of these interactions at a community scale are not well understood.
2. Here we analyse HP transfer networks in nine coastal communities in the Yucatan Mexico that vary in the relative abundance of invasive flowers to evaluate how HP donation and receipt varies between native and alien plants. We further evaluate whether HP donation and receipt are mediated by floral traits (e.g. display, flower size) or pollinator visitation rate. Finally, we evaluated whether post-pollination success (proportion of pollen tubes produced) was affected by alien HP receipt and whether the effect varied between native and alien recipients.
3. HP transfer networks exhibit relatively high connectance (*c*. 15%), suggesting high HP transfer within the studied communities. Significant network nestedness further suggests the existence of species that predominantly act as HP donors or recipients in the community. Species-level analyses showed that natives receive 80% more HP compared to alien species, and that alien plants donate 40% more HP than natives. HP receipt and donation were mediated by different floral traits and such effects were independent of plant origin (native or alien). The proportion of alien HP received significantly affected conspecific pollen tube success in natives, but not that of alien species.
4. *Synthesis*. Our results suggest that HP transfer in invaded communities is widespread, and that native and alien species play different roles within HP transfer networks, which are mediated by a different suite of floral traits. Alien species, in particular, play a central role as HP donors and are more tolerant to HP receipt than natives—a finding that points to two overlooked mechanisms facilitating alien plant invasion and success within native co-flowering communities.

KEYWORDS
interaction networks, plant invasion, pollinator sharing, pollinator-mediated interactions, unipartite networks

1 | INTRODUCTION

The study of biotic interactions at the community level has provided insight into the processes and mechanisms that mediate the assembly of plant communities (e.g. Bascompte & Jordano, 2007; Petanidou et al., 2008; Sargent & Ackerly, 2008). In particular, the study of plant–pollinator networks has shown that generalized interactions are common in plant–pollinator systems (e.g. Bascompte et al., 2003; Petanidou et al., 2008; also see Herrera, 1996; Waser et al., 1996). This, in turn, has generated renewed interest in the role of pollinator-mediated interactions in co-flowering community assembly (McEwen & Vamosi, 2010; Sargent & Ackerly, 2008; Tur et al., 2016), with most studies focusing on the outcomes of indirect plant–plant interactions via pollinator attraction (competition and facilitation; e.g. Gibson et al., 2012; Ghazoul, 2006; Sargent & Ackerly, 2008). Increasing evidence suggests, however, that plants often interact more directly through heterospecific pollen (HP) transfer, and that HP receipt can have detrimental effects on plant fitness (e.g. Ashman & Arceo-Gómez, 2013; Fang & Huang, 2013; Morales & Traveset, 2008). Hence, characterizing the extent, intensity, mediators and effects of HP transfer at the community level is a necessary step to fully understand the processes that govern the assembly of co-flowering communities.

Heterospecific pollen transfer is not only common (Arceo-Gómez et al., 2019; Ashman & Arceo-Gómez, 2013; Fang & Huang, 2013; Morales & Traveset, 2008), but can have significant effects on male (HP donor) and female (HP recipient) fitness (Arceo-Gómez & Ashman, 2016; Moreira-Hernández & Muchhala, 2019). For instance, it is well known that the HP receipt can reduce the number of conspecific pollen tubes and seeds in recipient plants (reviewed in Ashman & Arceo-Gómez, 2013; Morales & Traveset, 2008). Moreover, HP effects on recipient plants can increase with increasing HP diversity, or depend on HP donor identity (Arceo-Gómez et al., 2016; Arceo-Gómez & Ashman, 2011). Thus, changes in the incidence and/or diversity of HP transfer can have strong community-level effects on plant reproductive success (e.g. Bergamo et al., 2020). Nevertheless, studies that link HP intensity and diversity with its effects on pollination success at the level of entire communities are still scarce (but see Emer et al., 2015; Lopezaraiza-Mikel et al., 2007; Tur et al., 2016).

Plant species invasion could further intensify HP transfer since alien species commonly have a generalized pollination system (Albrecht et al., 2014; Bartomeus et al., 2008; Muñoz & Cavieres, 2008; Traveset & Richardson, 2014), and/or are wind-pollinated (Culley et al., 2002). For instance, Johnson and Ashman (2018) found that alien species donated significantly more HP than native species across 15 invaded communities (but see Emer et al., 2015 for a study where alien HP transfer was restricted to a subset of all species in invaded communities). Thus, we could also expect that pollen transfer networks will exhibit higher connectance with increasing abundance of invasive flowers (hereafter, invasion intensity). It is also possible that differences in floral and pollination attributes between alien and native species will lead to differences in their capacity to donate and receive HP. For instance, higher levels of pollinator generalization and/or a high reliance on generalist pollinators in invasive plants may heighten their role as HP donors and recipients compared to natives. These differences may, in turn, determine the ability of invasive plants to compete and succeed in invaded communities. However, to date, it is still unclear whether native and alien species differ in their roles as HP donors or recipients, and how these roles may change across different levels of plant invasion intensity. Studies that evaluate how HP transfer network structure and individual species roles within a network change across a gradient of plant invasion are thus central not only for understanding the drivers of HP transfer network structure but also its role in plant invasion success.

Evaluating the factors that mediate HP transfer dynamics is also crucial when predicting community responses to plant invasion. In this sense, studies have shown that floral traits can be important predictors of HP donation and receipt (i.e. pollen removal and deposition; e.g. Campbell et al., 2010; Galen & Newport, 1987; Montgomery & Rathcke, 2012; Morales & Traveset, 2009). For instance, plants with large floral displays or with large corolla size have higher rates of pollinator visitation and pollen removal (e.g. Arceo-Gómez et al., 2016; Eckhart, 1991; Galen & Newport, 1987). Moreover, alien plants typically have large flowers and floral displays, thus increasing their attraction to pollinators and potentially their pollen dispersal abilities (Johnson & Ashman, 2018; Lopezaraiza-Mikel et al., 2007; Muñoz & Cavieres, 2008). It is thus likely that floral traits such as flower size and floral display, as well as pollinator visitation rates, mediate HP interactions between native and invasive plants (e.g. Emer et al., 2015) and their potential roles as HP donors and recipients in a community (Daniels & Arceo-Gómez, 2019; Gibson et al., 2012, Johnson & Ashman, 2018; but see Charlebois & Sargent, 2017). Knowledge of the drivers of HP transfer is key to achieve a more predictive understanding of its potential effects in natural communities, particularly as a result of plant species invasion.

The study of plant–pollinator networks based on flower visitation has further suggested that co-flowering communities are robust to species invasion (e.g. Parra-Tab la et al., 2019; Vilà et al., 2009 but see Albrecht et al., 2014). However, if the arrival of alien plant species exacerbates HP transfer, it could affect the robustness of co-flowering communities and their long-term stability independently of changes in pollinator visitation (see Fang & Huang, 2016). Thus, it is important not only to gather evidence on the dynamics of HP transfer in invaded communities but also on their effects on post-pollination success (e.g. pollen tube and seed production; e.g. Suárez-Mariño et al., 2019). This latter step is imperative if we aim not only to determine the overall effects of plant invasion on co-flowering communities but also to uncover the mechanisms that underlie such effects. However, to our knowledge, only a few studies have evaluated the extent of HP transfer in invaded communities (Emer et al., 2015; Johnson & Ashman, 2018), and none have evaluated alien HP effects on post-pollination success at a community level. Such studies would help advance our understanding of the effects of plant invasion on native plant community structure and stability.

This study examines HP transfer networks in nine coastal co-flowering communities that have experienced recent invasion (<30 years) of alien plant species, but with varying degrees of invasion intensity across sites (Parra-Tab la et al., 2018). Plant–pollinator networks in these communities have revealed that alien plants are well integrated, and that their presence does not seem to compromise network structure and robustness (Parra-Tab la et al., 2019). However, the effects of plant species invasion on HP transfer networks and its potential post-pollination consequences are unknown. Here we ask the following specific questions: (a) Do HP transfer network structure changes as a result of increasing plant invasion intensity (invasive flower abundance); (b) Do native and alien plant species differ in their HP donor/receiver roles within HP transfer networks?; (c) Are HP donor/receiver roles mediated by floral traits (e.g. increase with increasing flower size and floral display) and/or pollinator visitation rate? and (d) Does alien HP receipt decreases post-pollination reproductive success and is the effect stronger on native compared to invasive recipients?

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in pioneer sand dune plant communities within a 205-km stretch along the northern coast of the Yucatan Peninsula, Mexico (Figure S1). The average temperature is 26°C with a mean annual precipitation of 700 mm (Orellana et al., 2009). The soil is sandy and uniform along the entire coast (Orellana et al., 2009). The sand dune plant community is composed of annuals and perennial herbs and small shrubs including, *Cakile edentula* (Brassicaceae), *Sesuvium portulacastrum* (Aizoaceae), *Lycium carolinianum* (Solanaceae), *Scaevola plumieri* (Goodeniaceae), *Suriana maritima* (Surianaceae) and *Ipomoea pes-caprae* (Convolvulaceae), which are the most abundant species (Espejel, 1987; Parra-Tab la et al., 2018). However, these communities have been highly invaded by both annual and perennial herbs such as *Alternanthera microcephala*, *Amaranthus dubius*, *Melanthera nivea* and *Bidens pilosa* (Parra-Tab la et al., 2018). Alien species represent around 30% of total plant richness (Parra-Tab la et al., 2018) and a high percentage of all the flowers available to pollinators in these communities (76% ± 30, *M* ± *SD*), but with high variability among sites (12%–99%; Table 1). Alien plant species also share a high proportion of the primary insect pollinators with native plant species (Albor et al., 2019; Suárez-Mariño et al., 2019; Parra-Tab la et al., 2019). Following Parra-Tab la et al. (2018), we considered as invasive those plant species with known detrimental impacts on native plants, as well as exotic species whose origin resides outside the Yucatan Peninsula but whose effects on native plant populations remain unknown. For consistency in this study we refer to both categories as alien species.

2.2 | Sampling design

We selected nine study sites 10–105 km apart (average = 31 km; Figure S1). Flower abundance of native and alien species was determined by establishing ten 20 m^2 plots at each site, each plot separated by 20 m. Within each plot, we recorded the number and identity of all flowering species and the total number of open flowers per species. In species with numerous small flowers (<1 cm), we estimated the total number of flowers by averaging the number of flowers on three inflorescences × total number of inflorescences on a plant (seven species: *Atriplex tampicensis*, *Alternanthera microcephala*, *Amaranthus greggii*, *Suaeda linearis*, *Bidens pilosa*, *Flaveria linearis* and

TABLE 1 Pollen transfer network descriptors in nine co-flowering communities. The percentage of alien flower abundance for each community is also shown. Sites are ordered from top to bottom according to their proportion of alien flower abundance. Network metrics (nestedness and modularity) that are significantly different from random are shown in bold ($p \le 0.02$)

Sites	Number of plant interacting species (alien species)	Network size	Linkage density per species	Connectance	Modularity	Nestedness	Percentage of alien flower abundance
Chapo 1	18 (6)	14, 20	2.61	0.21	0.014	**33.15**	11.29
Playa Maya	15 (4)	10, 16	1.81	0.18	0.053	**57.81**	40.69
Chapo 2	16 (5)	14, 18	1.76	0.20	0.180	**32.42**	78.08
Telchac	22 (6)	20, 23	2.06	0.14	0.194	**20.63**	79.42
Cancunito	18 (8)	11, 19	1.41	0.09	0.187	40.56	90.08
Punta Meco	17 (6)	14, 19	1.83	0.10	0.001	**49.32**	92.15
Sisal	17 (6)	13, 19	1.70	0.12	0.303	24.01	95.63
Charcas	18 (5)	14, 20	1.66	0.16	0.207	**25.51**	97.10
Chabiahu	18 (7)	16, 20	2.31	0.22	0.097	**38.12**	99.36

Melanthera nivea). A complete list of native and alien plant species is shown in Table S1. It is also important to note that there is no spatial correlation in plant community composition among sites (Parra-Tab la et al., 2018). Each site was monitored approx. every 10 days in random order. The study was carried out during peak flowering time, corresponding to the rainy season in this coastal dune system (September to November) in 2016.

2.3 | Conspecific and heterospecific pollen transfer and pollination success

To evaluate patterns of pollen transfer dynamics (conspecific and heterospecific pollen) and alien HP effects on post-pollination success (i.e. pollen tube growth), we collected 3–4 styles per plant for all plants present within each plot each time we visited a site (average per species 48.5 ± 68.95, ±*SD*). Styles were collected from senesced flowers in the afternoon (≈1,500 hr), after pollinator activity had ceased (Parra-Tab la et al., 2019), and were stored in formalin-acetic alcohol (FAA). For each style collected, the number of CP and HP grains on stigmas, and the number of pollen tubes at the base of the style were scored with a fluorescence microscope (Nikon e2010). We used pollen tube number as a *proxy* of post-pollination success because it is an intermediate phase between pollen arrival and seed production and thus excludes the potential effects of resource availability (e.g. water and soil nutrients) on fruit and seed development (Ashman et al., 2020). To perform pollen grain and pollen tube counts, each style was first softened in 8 M NaOH and stained with decolorized aniline blue and mounted on a slide following standard procedures (Kearns & Inouye, 1993). To identify CP and HP pollen grains from plot-collected styles/stigmas, a pollen library was first created from mature floral buds (3–5) collected from each species present in the community following Kearns and Inouye (1993). Pollen grains were photographed with an optical microscope equipped with a digital camera that allowed for the morphological characterization of pollen grains (Motic BA310). This pollen library was then used as a reference to identify pollen loads on stigmas and to record CP and HP abundance on each stigma (Suárez-Mariño et al., 2019). A total of 4,500 styles were collected (average per site: 498.22 ± 348.32, ±*SD*) corresponding to 1,273 individual plants. Sampling completeness (i.e. observed number of unique HP donor–recipient species interactions) was verified via rarefaction analysis using EstimateS 9.1 (Arceo-Gómez, Alonso, et al., 2018; Colwell, 2013). Rarefaction curves were constructed with 500 randomizations and sampling without replacement (Oksanen et al., 2015; see Table S2).

2.4 | Pollinator visit rate

To evaluate the influence of pollinator visitation rate in mediating plant species HP donor/recipient roles, we recorded pollinator visitation by observing each sampling plot for 5 min, three times per day for a total of 15 min/plot/day, and a total of 150 min per site. All observations were carried out during peak pollinator activity between 08:00 and 12:00 hr (see Campos-Navarrete et al., 2013; Parra-Tab la et al., 2019). This sampling effort has proved to be adequate in the studied communities to characterize plant–floral visitor interactions (Parra-Tab la et al., 2019). Pollinator censuses were performed on the same days as style collections (see above). The short height of the vegetation (<50 cm tall) and the low density of plants allowed us to accurately record all floral–visitor interactions within each plot (Parra-Tab la et al., 2019). Total flower counts for each species within each plot were conducted at the beginning of each day before pollinator censuses. Overall pollinator visit rate (all pollinator species combined) was estimated as the average number of observed visits/flower/15 min throughout the sampling period.

2.5 | Floral traits

We evaluated the role of floral display, flower size, floral colour and herkogamy in mediating plant species role as HP donor or recipient. These floral traits were selected as they are related to pollinator attraction, pollinator generalization (e.g. Eckhart, 1991; Galen & Newport, 1987; Kantsa et al., 2017) and with pollen delivery and receipt (e.g. Arceo-Gómez et al., 2016; Barrett et al., 2000; Fang & Huang, 2013; Montgomery & Rathcke, 2012). Flower size (floral length, corolla diameter and corolla tube opening) was estimated by measuring flowers in the field with a caliper (±0.01 mm). Three to five open flowers per plant were measured in at least five individuals per species. Floral length was measured as the distance between the calyx and the tip of the corolla. Corolla diameter refers to total corolla width and corolla tube opening refers to the diameter of the corolla opening; for non-tubular flowers this value was recorded as zero. Because the three flower size measurements (i.e. floral length, corolla diameter and corolla tube opening) were correlated ($r \geq 0.6$, $p \leq 0.01$), we performed a principal component analysis, and used the scores of the first PCA for each species, which explained 85% of the variance, as a surrogate of flower size. Herkogamy was measured as the minimum distance between anthers and the stigma. In all cases, the anthers were above the stigma. Floral display size was calculated as the average number of open flowers/day throughout the sampling period.

We evaluated flower colour by measuring flower reflectance spectra (300–700 nm) from the dominant corolla colour in 1–3 flowers per species with a BLUE-Wave field spectrophotometer (StellarNet INC) under standardized light conditions (i.e. shaded). Estimation of the trichromatic colour-hexagon vision proposed by Chittka (1992) was carried out with the PAVO package in the R 3.2 software (R Core Team, 2016). Then, following Kantsa et al. (2017), we described the dominant colour of the corolla using colour saturation (r) or 'spectral purity', a measure of how much grey or white is mixed with pure colour, and tonality (angle θ; 0–360°). Because variation in the amplitude of the reflectance for each species was small, we randomly selected one reflectance curve for the construction of the bee colour vision model (van der Kooi et al., 2016). We omitted floral symmetry (radial vs. bilateral) from our analyses, even though it can contribute to among-species variation in HP receipt (Arceo-Gómez et al., 2019) because in our communities only two species showed bilateral symmetry (*Scaevola plumieri* and *Canavalia rosae*).

2.6 | HP transfer network structure

We constructed HP transfer networks for each site (e.g. Fang & Huang, 2013; Johnson & Ashman, 2018). Directed networks represent each plant species as a node, with the links between each node representing HP donation and receipt between two species in the network (Bastian et al., 2009). We calculated the following network parameters (a) network size, which represents the total number of interacting species (either donating or receiving HP), (b) linkage density, which is the average number of links (i.e. interactions) per species, (c) connectance, which reflects the proportion of possible links that are realized and (d) modularity, which indicates whether species are structured into subsets of species within the network that are more densely connected to one another than to species outside the module (see White & Harary, 2001). Connectance and modularity were calculated with the IGRAPH package (Csardi & Nepusz, 2006; R Core Team, 2016), using the *edge_density* function and the algorithm *cluster_walktrap* (version 1.2.3; Csardi & Nepusz, 2006), respectively. The *edge_density* function computes the proportion of present edges from all possible edges in the network (Csardi & Nepusz, 2006) and the *cluster_walktrap* searches for densely connected subgraphs (i.e. modules) via a random walk process in which shorter random walks between nodes will indicate the existence of modularity (Fortunato & Hric, 2016). Additionally, we estimated overall network nestedness using wNODF, which incorporates weights of network edges (Almeida-Neto & Ulrich, 2011), using the function wnodf in the MBI package (version 1.0; Youhua, 2012). To test whether modularity and nestedness values deviate significantly from random, we simulated 1,000 random networks and calculated nestedness and modularity of each simulated network. We then compared random to the observed nestedness and modularity values for each site. Randomizations were conducted by randomizing weights (i.e. interaction frequency) while keeping the number of species and interactions (i.e. source–target association) fixed (see Vázquez & Aizen, 2004).

2.7 | Species-level roles as pollen receivers and pollen donor

To evaluate the contribution of each plant species in the pollen transfer network as a 'pollen receiver' and as a 'pollen donor', we calculated the number of links as a HP recipient (degree 'in') and as a HP donor (degree 'out') for each species at each site. Metrics of degree 'in' and 'out' were weighted by the intensity of the interactions (i.e. number of pollen grains donated/received). In addition, we calculated a 'hub' and 'authority' score for each species at each site (Kleinberg, 1999). A 'hub' species donates many pollen grains to other well-connected species within the communities and an 'authority' species receives many pollen grains from other well-connected species (see Johnson & Ashman, 2018). All these species-level metrics (i.e. degree 'in', degree 'out', hub and authority) were estimated using Gephi ver. 9.1 (Bastian et al., 2009).

3 | STATISTICAL ANALYSES

3.1 | Spatial variation and plant origin effects on conspecific and heterospecific pollen loads

We tested the effect of site and plant origin (i.e. native and alien) on the proportion of CP (CP/total pollen grains) and HP (HP/total pollen grains) received as well as HP richness (i.e. number of different HP donor species on a stigma). For this, a generalized linear mixed model (GLMM) was conducted for each response variable using SAS 9.1 (SAS, 2002). Site and plant origin were considered as fixed effects and species identity was included as a random effect. The models were run using a Binomial error distribution for CP and HP proportion and a Poisson distribution for HP richness. These error distributions had the best fit while minimizing over-dispersion. To evaluate if HP proportion or HP richness increased with increasing invasion intensity in the community, linear regressions were conducted to evaluate the relationship between average HP proportion and richness (per site) and the proportion of alien flowers (alien flowers/total flowers at a site) present (log transformed) in each community. These regressions were done in SAS (SAS, 2002).

3.2 | HP transfer network structure and drivers of HP receipt and donation

To determine whether HP network structure changes with invasion intensity, linear regressions were applied to test the relationship between each network parameter (i.e. network size, linkage density connectance, modularity and nestedness) and the proportion of alien flowers present at each site (log transformed). Regressions were performed in SAS (SAS, 2002).

To test the drivers of HP receipt and donation, a GLMM was conducted separately for each response variable (degree 'in', degree 'out', hub and authority) considering site and plant origin (i.e. native vs. alien) as fixed effects, and species identity as a random effect. To test whether floral traits and/or pollinator visitation rate mediates HP donation and receipt, in each model we included flower size (first PCA axis), flower colour (tonality and saturation), herkogamy, floral display size and mean pollinator visitation rate as covariates. The response variables were ($\log X + 1$) transformed. These analyses were carried out using the LME4 package in R 3.2 using a Gaussian error distribution with an identity link function (R Core Team, 2016). To avoid over-parametrization of the models, we started with the complete model and conducted backwards stepwise regression using

Akaike information criterion (AIC) to identify the models with the best fit (see Table S3 for the complete initial model). The AIC and ΔAIC of each model were estimated using the AICcmodavg package (Mazerolle, 2013).

3.3 | Alien HP effects on pollination success

A GLMM was performed to evaluate the effects of alien HP (only that from alien plant species), site and recipient origin (native vs. alien) on the proportion of pollen tubes that reach the base of the style (number of pollen tubes/number of conspecific pollen grains). Site and plant origin were considered fixed effects, and the proportion of alien HP and HP richness was included as covariates. The identity of the recipient plant was included as a random effect in the model. We also included the interactions of site and origin with each one of the covariates. To optimize the models, we applied backwards stepwise regression following the same procedure described above (see Table S4 for the complete initial model). When differences among sites or due to plant origin were found, multiple comparisons were conducted via paired t tests. The GLMM was performed using lme4 package in R 3.2 (R Core Team, 2016) using a binomial error distribution with a logit link function.

We did not consider phylogenetic effects in our analyses (e.g. Arceo-Gómez & Ashman, 2016; Morales & Traveset, 2009) because only four of the 19 plant families present were represented by more than one species (Table S1).

In all cases, means ± *SD* are presented unless otherwise specified.

4 | RESULTS

4.1 | Spatial variation and plant origin effects on conspecific and heterospecific pollen loads

A total of 312,773 pollen grains were counted. On average, the proportion of CP (CP/total pollen grains on stigma) received across all plant species was high in all communities (88% ± 22.9; Figure S2a). We did not find significant differences on the proportion of CP received due to site, plant origin (alien vs. native) or their interaction ($F \leq 1.4$, $p \geq 0.2$ for all). Average HP proportion (HP/total pollen load) across species was relatively low (11.8% ± 22.9). Although we observed large among-site variation on HP proportion (2.3%–20.8%, Figure S2a), no significant effects of site, plant origin (alien vs. native) or their interaction were observed ($F \leq 1.9$, $p \geq 0.07$ for all). Species receive a relatively low HP donor per stigma (3.5 ± 2.0). Although HP richness varied by site (2.3–5.5 HP donor species, Figure S1b), no significant effects of site, plant origin (invasive vs. native) or their interaction were detected ($F \leq 1.89$, $p \geq 0.07$ for all). Furthermore, we found no correlation between average HP proportion or HP richness at a site and plant invasion intensity (i.e. the proportion of total floral abundance from alien species; $r \leq 0.35$, $p > 0.05$, in both cases).

4.2 | Pollen transfer networks

Rarefaction analyses showed that on average we captured a high percentage of all expected plant–plant interactions via HP transfer (89% ± 13.7; Table S2). Pollen transfer networks included from 15 to 22 native plant species, and from four to eight alien plant species. Network size ranged from 10–16 species (Playa Maya) to 20–23 species (Telchac; Table 1) and the mean number of links per species was relatively low (1.9 ± 0.34) with little among-site variation (Table 1). Network connectance showed that on average, 15% of all possible plant–plant interactions (via HP transfer) occurred (0.15 ± 0.04; range 9%–22%, Table 1). Nestedness was significant in seven co-flowering communities and modularity was not significant in any community (Table 1). We found no significant correlation between network size, linkage density, connectance or nestedness with the proportion of alien flowers present at a site ($r \leq 0.6$, $p > 0.05$, in all cases) suggesting that invasion intensity does not affect the structure of HP transfer networks.

4.3 | Floral traits as drivers of HP receipt and donation

We observed interaction asymmetry in HP donation and receipt (Figure 1). Across communities, the majority of species that were frequent HP recipients were poor HP donors (Figure 2; all HP transfer networks are shown in Figure S3). For instance, while the natives *Cakile edentula* and *Lycium carolinianum* were predominantly HP recipients, the alien *Alternanthera microcephala* was mainly an HP donor (Caed, Lyca, and Almi in Figure 2, respectively). Nevertheless,

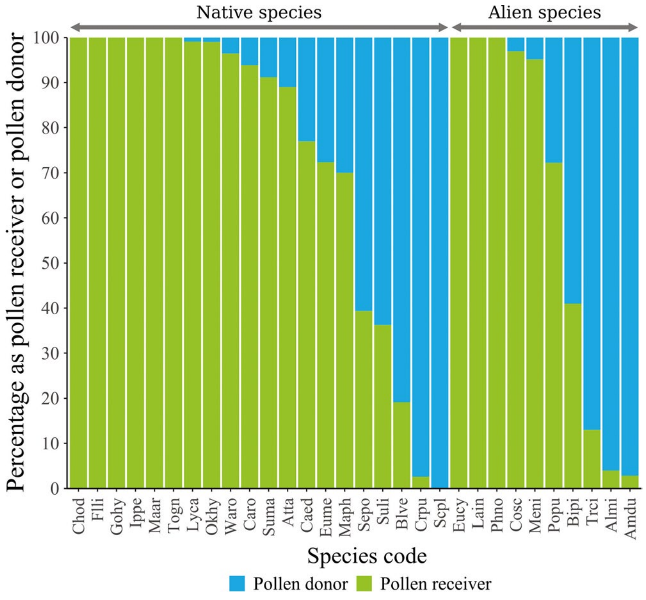

FIGURE 1 Alien and native species proportional role as a heterospecific pollen receiver (degree in) or as a heterospecific pollen donor (degree out) across the studied co-flowering communities. Plant species codes are shown in Table S1

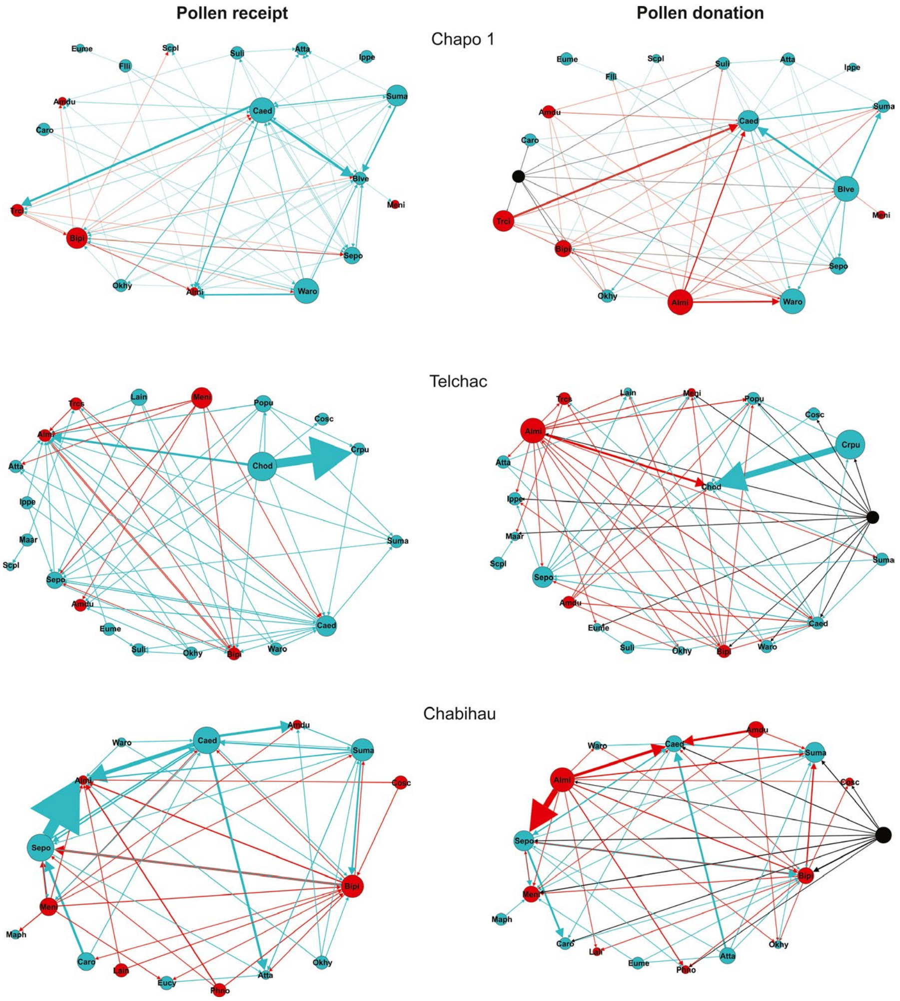

FIGURE 2 Heterospecific pollen transfer networks at three coastal sand dune plant communities with contrasting alien floral abundance (only three out of nine sites are shown for illustrative purposes: Chapo 1, Telchac and Chabiahu; see Table 1). All HP transfer networks are shown in Figure S3. Networks are divided into HP donation and receipt only for clarity and for better visualization of the patterns observed. Circles represent individual plant species (blue circles = native species, red circles = alien species; black circle represents unknown pollen in pollen receipt networks). Only species that received or donated pollen are shown. The size of the circle represents a weighted quantitative value as a pollen receiver or pollen donor (see methods). The arrow represents the target (pollen recipient) and the pollen source (pollen donor) for each species. Species codes are shown within circles (see Table S1). The position of each species is the same for the pollen receipt and pollen donation networks

neither ‘degree out’ (HP donation) and ‘degree in’ (HP receipt) nor ‘hub’ and ‘authority’ were significantly correlated with each other ($r \leq -0.25$, $p \geq 0.2$, in all cases).

However, we did find a significant effect of plant origin determining plant species role as an HP donor or recipient. Specifically, plant origin significantly affected species degree in ($F_{1,46} = 5.16$, $p < 0.05$; Table 2). Native species had 40% more interactions (links) as HP recipients compared to aliens (Figure 3a). Furthermore, across sites, four native species accounted for approximately 80% of all HP recipient interactions, with *L. carolinianum* (32%) and *C. edentula* (18%) being the species with the highest percentages (Lyca and Caed in Figure 2; also see Figure S3). The proportion of HP interactions was also positively affected by flower display size and negatively affected by flower colour (corolla tonality; Table 2). Our analyses further revealed a significant effect of plant origin on species ‘authority’ ($F_{1,46} = 4.7$, $p < 0.05$; Table 2). In this case, native plants species received 34% more HP grains than alien species (Figure 3a). Species ‘authority’ index was also positively related to floral display size and negatively related to flower tonality (Table 2).

Plant origin (native vs. alien) also influenced species degree out ($F_{1,46} = 7.5$, $p < 0.01$). Specifically, alien species had 44% more interactions as HP donors than native plants (Table 2; Figure 3b). Furthermore, plant origin had a significant effect on species ‘hub’ ($F_{1,46} = 2.36$; $p < 0.05$), as alien plants donated 45% more pollen to other species than natives (Figure 3b). Across all sites, *Alternanthera microcephala* accounted for *c.* 55% of the total HP donated (Figure S3). Species degree out and ‘hub’ increased with flower size and floral display size and species ‘hub’ was also positively affected by pollinator visitation rate (Table 2). Finally, both degree out and ‘hub’ were significantly affected by the plant origin × herkogamy interaction (Table 2) showing that increasing herkogamy increased HP donation in alien species but not in natives. Degree in and hub, and degree-out and authority had a weak correlation with each other ($r < 0.28$, $p < 0.05$ for both).

4.4 | Alien HP effects on pollination success

A total of 21,163 pollen tubes in 4,500 styles were scored. On average, 19% (±0.23, pollen tubes/total CP) of pollen grains on a stigma formed tubes that reached the base of the style across all species. The proportion of conspecific pollen tubes significantly differed among sites, but not differences were observed due to plant origin (Table 3). Furthermore, we found a significant negative effect of the proportion of alien HP received on the proportion of conspecific pollen tubes produced (Table 3; $\beta = -2.04 \pm 1.0$ *SE*; $p = 0.01$). Interestingly, we

TABLE 2 Results from mixed models (GLMM) to evaluate the effect of floral traits and pollinator visitation rate on plant species 'roles' (HP recipient and donor) in nine co-flowering communities. Slopes (*β*) for each variable included in the optimized models are shown. Significant effects are shown in bold type. AIC and ΔAIC values for the best-fit models and the full models for each response variable are shown. ND = variables excluded from the model via stepwise backwards model comparisons

Floral traits and visitation rate	Receiver		Donor		Authority		Hub	
	β (±*SE*)	*p*	*β* (±*SE*)	*p*	*β* (±*SE*)	*p*	*β* (±*SE*)	*p*
Origin	**1.10 (0.35)**	**0.05**	**−0.54 (0.32)**	**0001**	**0.09 (0.03)**	**0.05**	**−0.46 (0.02)**	**0.001**
Flower size	−0.77 (0.52)	0.81	**0.30 (0.26)**	**0.01**	0.08 (0.04)	0.96	**0.01 (0.02)**	**0.01**
Herkogamy	−0.79 (0.59)	0.64	−1.07 (0.37)	0.11	−0.06 (0.04)	0.61	−0.08 (0.02)	0.06
Flower colour								
Saturation	ND	ND	−0.33 (0.14)	0.18	ND	ND	−0.02 (0.01)	0.25
Tonality	**−0.18 (0.18)**	**0.03**	ns	ns	**−0.01 (0.01)**	**0.03**	ND	ND
Log floral display size	**0.51 (0.21)**	**0.02**	**0.90 (0.16)**	**0.001**	**0.03 (0.01)**	**0.01**	**0.06 (0.01)**	**0.001**
Log flower visitation rate	0.28 (0.21)	0.09	0.03 (0.17)	0.08	ND	ND	**0.03 (0.01)**	**0.01**
Origin × herkogamy	ND	ND	**0.68 (033)**	**0.03**	ND	ND	**0.06 (0.02)**	**0.01**
AIC (ΔAIC) values	Best model: 687.6 (Δ0.0)	Full model: 692.8 (Δ9.7)	Best model: 640.3 (Δ0.0)	Full model: 645.4 (Δ0.2)	Best model: −52.6 (Δ0.0)	Full model: 55.0 (Δ121.2)	Best model: −23.8 (Δ0.0)	Full model: −131.26 (Δ121.4)

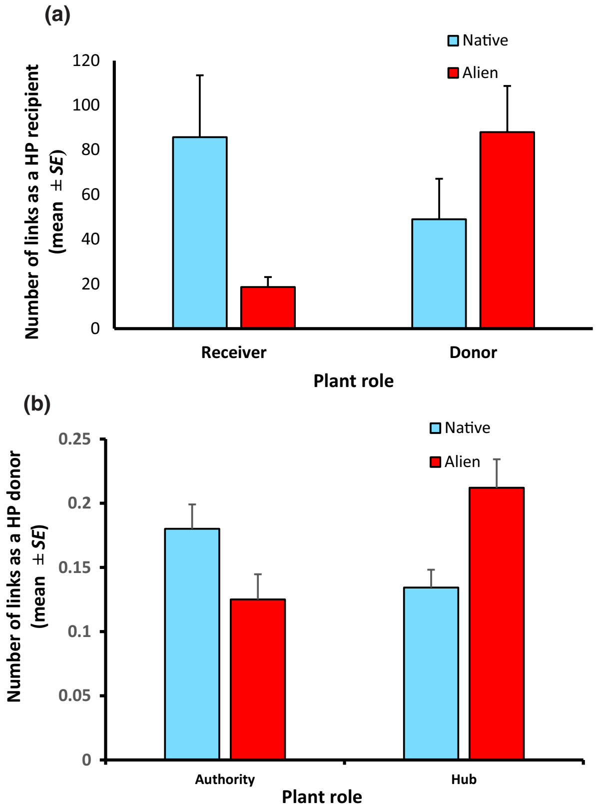

FIGURE 3 Average native and alien species (±*SE*) values as a (a) pollen receiver (number of links as a HP recipient 'degree in') and pollen donor (number of links as a HP donor 'degree out'), and as (b) authority and hub across sites. Statistically significant differences were found in all cases ($p < 0.01$)

TABLE 3 Results from the mixed model (GLMM) used to evaluate the effects of site, origin and proportion of alien heterospecific pollen (HP) on the proportion of pollen tubes (number of pollen tubes/number of conspecific pollen grains) across nine co-flowering communities. Significant effects are shown in bold. AIC and ΔAIC values for the best-fit and full models are shown

	Proportion of pollen tubes		
Effect	*F*	*df*	*p*
Site	**2.13**	8,70	**0.03**
Origin	0.82	1,70	0.36
Site × Origin	ns	ns	ns
Alien HP proportion	**5.74**	1,70	**0.01**
HP richness	ns	ns	ns
Alien HP proportion × Site	ns	ns	ns
HP richness × site	ns	ns	ns
Alien HP proportion × Origin	14.79	1,70	**0.001**
HP richness × Origin	ns	ns	ns
Log floral display size	0.01	1,60	0.09
AIC (ΔAIC) values	Best model: 93.94 (Δ0.0)	Full model: 139.87 (Δ82.8)	

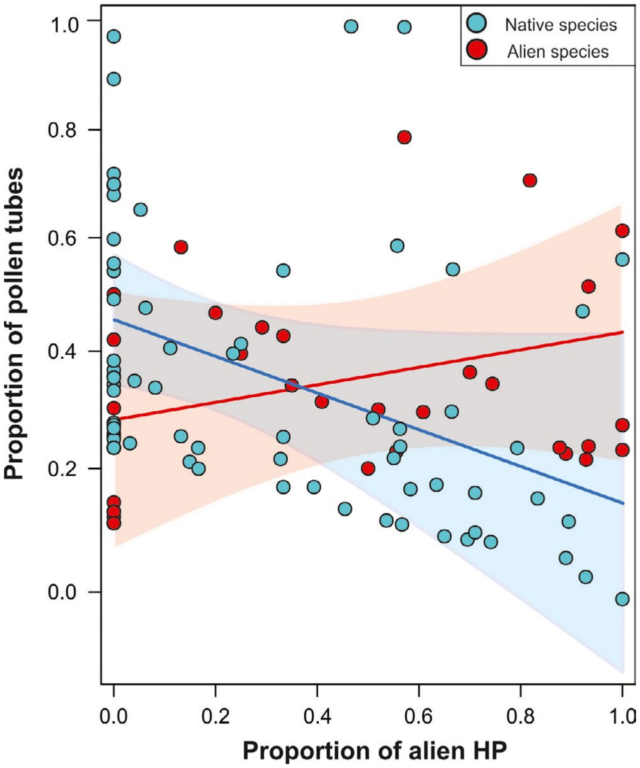

FIGURE 4 Regression analysis between the proportion of conspecific pollen tubes (number of pollen tubes/conspecific pollen) and the proportion of alien heterospecific pollen received in native and alien recipient species. The relationship was statistically significant for natives ($F_{1,78} = 11.83$, $p < 0.001$) but not for alien species ($F_{1,37} = 1.65$, $p = 0.20$)

also found a significant plant origin × alien HP interaction (Table 3; Figure 4). This interaction showed that pollen tube production in native species was negatively affected by an increasing proportion of alien HP ($F_{1,78} = 11.83$, $p < 0.001$), whereas other alien plants were unaffected by alien HP receipt ($F_{1,37} = 1.65$, $p = 0.20$; Figure 4).

5 | DISCUSSION

The study of the effects of alien plant species on plant–pollinator networks has suggested that networks are robust to plant invasion. However, few of these studies have incorporated the potential impacts on native plant communities via changes in pollen transfer dynamics and via direct effects of alien HP on pollination success of native plants. These potential impacts may more directly reflect the overall effects of plant invasion in co-flowering communities. This study revealed that plant–plant interactions via HP transfer are widespread and remain relatively constant regardless of invasion intensity (proportion of alien flowers). However, our results showed that native and alien species play different roles within HP transfer networks, with aliens being more frequent HP donors and natives being frequent HP recipients. These network roles also seem to be shaped by different floral phenotypic traits. Even more important, we found that alien HP significantly reduces pollination success of natives but not that of other alien plant species, suggesting this as a possible mechanism facilitating plant species invasion. Below, we discuss the broader implications of these and other results.

5.1 | Heterospecific pollen transfer networks in invaded communities

Results showed that in our invaded coastal communities 15% of all potential plant–plant interactions via HP transfer occurred, suggesting relatively widespread HP transfer among species compared to other studies (e.g. Bartomeus et al., 2008; Emer et al., 2015; Johnson & Ashman, 2018). These results are also consistent with structural properties observed in invaded plant–pollinator networks (e.g. Padrón et al., 2009, Vilà et al., 2009, Parra-Tab la et al., 2019, but see Albrecht et al., 2014). It has been shown that in invaded ecosystems the presence of 'super generalist' pollinators (e.g. *Apis mellifera*) increases connectivity and reduces modularity in both, plant–pollinator (e.g. Kaiser-Bunbury et al., 2011; Olesen et al., 2002), and HP transfer networks (Johnson & Ashman, 2018). This could also be the case in our communities where *A. mellifera* contributes to a large proportion of floral visits (*c.* 60%, Parra-Tab la et al., 2019). It is important to note that a similar structure (e.g. significant connectance and nestedness) has also been observed in plant–pollinator visitation networks in this same ecosystem (Campos-Navarrete et al., 2013; Parra-Tab la et al., 2019). These results thus emphasize the potential importance of 'super generalist' pollinators in structuring both, plant–pollinator and pollen transfer networks, especially in invaded communities (see Herrera, 2020).

5.2 | Species-level roles and drivers of HP donation and receipt

Understanding the roles that native and alien plants play within HP transfer networks can help uncover the mechanisms that facilitate plant invasion into native co-flowering communities (Emer et al., 2015; Johnson & Ashman, 2018). For instance, if alien species show greater capacity to donate and avoid HP receipt compared with natives, this could aid in their establishment, help them outcompete natives, and hence influence co-flowering community assembly. Our results lend support to this prediction by revealing that native and alien plants play different roles within HP transfer networks. Specifically, alien species interact more often as HP donors and donate more HP compared to native species. In contrast, native species interact more often as HP recipients and receive more HP than alien species. For instance, alien species *A. microcephala* and *B. pilosa*, donated high quantities of pollen (*c.* 95%–60%, respectively), but received much less HP (*c.* 5%–40%, respectively). In contrast, the natives *C. edentula* and *L. carolinianum* received high HP loads (*c.* 95%–75%, respectively), but proportionally donated much less pollen to other species (*c.* 5%–25%, respectively). It is also important to note that four native species (*Lycium carolinianum*, *Cakile edentula*, *Chromolaena odoratum* and *Atriplex tampicensis*) contributed to a high percentage of HP receipt (80%) in the studied community. Interestingly, these species possess large floral displays (Parra-Tab la et al., 2019), which may make them highly susceptible to HP receipt, either by increasing pollinator visitation or by creating a larger target for wind-dispersed pollen. Across all species, floral display size was also positively associated with HP receipt. In the only other study published to date in which the role of invasive and native species in HP transfer networks was evaluated, Johnson and Ashman (2018) found that alien species also donated more pollen than natives, but no differences in pollen receipt were observed. One potential reason for the high contribution of alien species as HP donors at our study sites is that most alien species seem to be at least partially wind pollinated. For instance, *A. microcephala*, a predominantly wind-pollinated alien species (Parra-Tab la et al., 2019), contributed to more than half (55%) of total HP donated to other species across all sites. Furthermore, *A. microcephala* was the species with the highest 'hub' value across sites and we recorded pollen from this species on the stigmas of more than 66% of all other species present (native and alien). This suggest, that in coastal communities that are commonly exposed to high and constant winds (Orellana et al., 2009), the importance of wind-pollinated species in HP transfer networks, particularly alien, may be greater than that of animal-pollinated species (also see Whitehead, 1968). As such, wind-pollinated species could be considered 'super HP donor species' and drive HP transfer network structure, perhaps even in the absence of animal floral visitors. This prediction has received little attention and deserves further study (Culley et al., 2002), particularly in invaded and coastal ecosystems. Overall, our results and those by others (e.g. Emer et al., 2015; Johnson & Ashman, 2018; Suarez-Mariño et al., 2019) suggest that differences in the role invasive species play in HP transfer dynamics could aid in their success invading native communities, thus highlighting the need for more studies to evaluate their importance and functional role within HP transfer networks.

We also found that HP recipient and donor roles are influenced by a different set of floral traits regardless (with the exception of herkogamy) of plant origin (native or alien). This last result could reflect the high similarity in floral traits observed between alien and native species (*c*. 80%, Parra-Tab la et al., 2019) at our study sites. Specifically, while HP recipient and donor roles were positively affected by floral display size, HP donation was additionally affected by flower size and visitation rate. Both floral display and flower size have been associated with an increase in flower visits and pollen removal (Arceo-Gómez et al., 2016; Eckhart, 1991; Fang & Huang, 2013; Galen & Newport, 1987). An increase in visitation rate may thus result in increasing likelihood of HP transfer to other species. However, as discussed previously, in our co-flowering communities, wind-dispersed HP may also have the potential to contribute to the amount of HP donation observed. Thus, floral display size may not only influence HP donation via pollinator attraction but may also act as a platform for pollen release (and a target for HP deposition), thereby increasing the amount of wind-borne pollen that can be dispersed.

On the other hand, HP pollen receipt was negatively affected by flower colour (i.e. corolla tonality). Specifically, species with white/cream/yellow/green pale flowers (low tonality e.g. *Lantana involucrata* and *Melanthera nivea*) received more HP than species with blue/purple/pink corollas (high tonality; e.g. *Sesuvium portulacastrum*, *Ipomoea pres-capre*, *Canavalia rosea* and *Okenia hypogea*). Previous plant–pollinator networks at the study sites showed that plant species with white-pale flowers are visited by nine insect species on average (range: 4–18), while species with purple/pink corollas are visited by less than five species (range: 1–9; Parra-Tab la et al., 2019). Thus, it is possible that a higher number of pollinator species visiting white-pale flowers (more generalized) leads to higher amounts of HP on stigmas compared with the more specialized purple-pink flowers. In this sense, differences in the degree of pollinator specialization associated with flower colour could help mediate differences in HP transfer dynamics independently of plant origin (native or alien). There are just a few empirical studies that have examined the effects of functional floral traits in mediating pollen transfer dynamics (e.g. Emer et al., 2015; Johnson & Ashman, 2018; Montgomery & Rathcke, 2012), and even fewer have analysed whether such relationships depend on plant origin (native or alien). For instance, Johnson and Ashman (2018) found that native species with longer stamens were strong HP donors, but the opposite was true for invasive species. In our study, however, we observed the opposite pattern, while alien species with longer stamens (high herkogamy) were strong HP donors, stamen length did not seem to influence HP donation in native plants. What is clear, however, is that more experimental evidence is needed to understand the degree to which floral traits play a role in mediating pollen transfer dynamics in native and alien species, and how this may affect the success of alien plants in novel co-flowering communities (see Daniels & Arceo-Gómez, 2019; Gibson et al., 2012).

5.3 | Alien HP effects on post-pollination success

An increasing number of studies have highlighted the ubiquity of HP transfer in co-flowering communities (e.g. Arceo-Gómez et al., 2016, 2019; Emer et al., 2015; Fang & Huang, 2013; Tur et al., 2016) and its importance in pollination processes (Ashman et al., 2020; Ashman & Arceo-Gómez, 2013; Morales & Traveset, 2008). However, few have linked HP transfer dynamics with its effects on post-pollination success at the community level (e.g. Tur et al., 2016). Our results showed a negative effect of alien HP on the proportion of pollen tubes produced. Interestingly, this negative effect was only observed in native species, while other alien species remain unaffected by alien HP receipt. This difference in alien HP effects suggests that tolerance and avoidance of HP receipt may be important strategies determining whether alien plants can establish and become invasive (Arceo-Gómez & Ashman, 2016; Suárez-Mariño et al., 2019). In a meta-analysis, Arceo-Gómez and Ashman (2016) found that invasive HP donors reduced fruit and seed production of recipients to a greater degree than native HP donors did. Interestingly, the effect of native HP donors on the post-pollination success of invasive species remains far less studied. For instance, Suárez-Mariño et al. (2019) found that although the alien *B. pilosa* received more HP than native species, this had a weaker impact on reproductive success compared to that of natives. Overall, our results support the idea that higher HP donation and increased tolerance for its effects may help facilitate Alien species invasion, and thus highlight the need to evaluate reciprocal HP transfer and effects between native and alien species.

Evidence from the study of plant–pollinator networks has suggested that co-flowering communities are robust to species invasion (e.g. Bascompte & Jordano, 2007; Memmot et al., 2004; Parra-Tab la et al., 2019; Vilà et al., 2009). However, our results suggest that alien plant species could diminish overall post-pollination success of invaded communities, and their long-term robustness, via HP transfer. These effects can even occur independently, or in the absence of, alien species effects on patterns of pollinator visitation. These results also emphasize the need to integrate information on pollen transfer dynamics and pollination success into the study of plant–pollinator networks. For instance, a recent study showed that an increase in plant–pollinator network specialization within nested communities might lead to increasing HP transfer, as specialists tend to interact more frequently with generalist species (Arceo-Gómez, Jameel, et al., 2018). Thus, integrating information across all levels of the pollination process is key if we aim to gain a more complete understanding of the ecological and evolutionary consequences of changes in the structure of plant–pollinator networks. It is also important to note that historical records indicate that plant invasion in the studied communities has taken place during the last 30 years (Espejel, 1987; Parra-Tab la et al., 2018), suggesting that the invasion process and its negative effects can occur during relatively short time scales. Overall, our results suggest that the combined study of HP transfer networks and their effects on post-pollination success has the potential to advance our understanding of the mechanisms that facilitate plant species invasion and their integration into native plant–pollinator communities.

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AUTHORS' CONTRIBUTIONS

V.P.-T., G.A.-G., C.A., T.-L.A. and R.A.R. designed the experiment; V.P.-T., P.S., C.A. and D.C. performed experiments, acquired data and analysed data; V.P.-T. wrote the first version of the manuscript. All authors participated in the preparation of the final version of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qv9s4mwcs (Parra-Tabla et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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