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ARTICLE

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No evidence for missed mutualists in an invasive plant with the buzz pollination syndrome

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Abstract

The missed mutualist hypothesis predicts that the absence of mutualistic partners poses a barrier to introduced species becoming invasive. Yet, some alien plants thrive despite potential dependence on certain pollinators. For example, buzz-pollinated plants typically have specialist floral morphologies and benefit from buzz pollinator behavior for pollination. Despite this apparent specialization, some buzz-pollinated plant species have become invasive. To understand this contradiction, we undertook field observations at three sites in one native region (Mexico), and at five sites in one invaded region (Australia), of an invasive plant with the buzz pollination syndrome (*Senna obtusifolia*; Fabaceae), to (1) identify the floral visitors and pollinators, (2) determine whether pollinator assemblages differ between regions, and (3) assess whether *S. obtusifolia* relied on specialized buzzing behavior for pollen transfer in both the native and invaded populations. We identified 15 different insect species (native region) and 11 species (invaded region) that contacted the stigma or carried pollen and classed these as potential pollinators. We calculated a pollination importance index based on the relative abundance, pollen load, pollen fidelity, stigma contact, and body size match index of each morphospecies; the most important pollinators were non-buzzing bees (*Apis mellifera* and Meliponini species) in both regions. We observed buzzing behavior infrequently (<9% of visits), and it was 3.8 times more common in the invaded region compared to the native region. The dominance of non-buzzing behaviors suggests that *S. obtusifolia* does not rely on a distinct pollinator niche. We found no evidence for the missed mutualist hypothesis.

KEYWORDS
bee pollination, behavioral ecology, biotic interactions, ecological specialization, floral visitor, melittophily, nonindigenous, non-native, plant–pollinator network, poricidal anther, tropics

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INTRODUCTION

When species are introduced into new regions, they are typically removed from their coevolved mutualists, such as protective and defensive partners, microbial mutualists, seed dispersers, or pollinators (Mitchell et al., 2006). The missed mutualist hypothesis predicts that the loss of mutualistic partners when a species is introduced to a new area can inhibit invasion success (i.e., to spread outside their native range and negatively affect native biodiversity; Mitchell et al., 2006; Moles et al., 2022). For example, Anemonefish are common in aquaria and frequently released into seas around the world (Schofield & Akins, 2019), but they have not established populations outside the Indo-Pacific region where their mutualistic partners, sea anemones, are native (discussed in Moles et al., 2022). Similarly, plants are commonly introduced into new regions, but many introduced species never become naturalized or invasive (Richardson & Pyšek, 2012). Alien plants may fail to become invasive if they lack a useful mutualist, such as their pollinators, and have no other means of obtaining what the mutualist provided (Moles et al., 2022).

Over 90% of flowering plants require a biotic pollinator for outcross pollen transfer (Ollerton et al., 2011), thus, invasion success for many flowering plants may require that pollinators are present and attracted to the newly introduced plant (Traveset et al., 2020). Yet, the extent to which pollinator attraction influences invasion success depends on the reproductive strategy of the plant species, including the plants' dependence on pollinators to transfer pollen, the plants' reliance on sexual reproduction, the plants' degree of self-compatibility, and the plasticity of each of these traits (reviewed in Traveset et al., 2020). We lack data on the reproductive biology and ecology for many invasive species in either or both their native and introduced regions (see reviews: Lopresti et al., 2024; Traveset et al., 2020) which has prevented accurate predictions as to the importance of pollinator interactions in plant invasions.

Specialist plant–pollinator interactions may increase genetic diversity by increasing outcross conspecific pollen transfer (Waser & Ollerton, 2006), and in turn, increase seed production (Armbruster, 2017), or by reducing the risk of pollen wastage during transport (Wilcock & Neiland, 2002). Although plants with specialist pollinator mutualisms are theoretically less likely to find their pollinator match compared to plants with generalist mutualisms when introduced into new regions (Lopresti et al., 2024; Richardson et al., 2000; Rodger et al., 2010), the evidence remains inconclusive. While some broadly distributed invasive plants exhibit an apparent specialized plant–pollinator mutualism in their native and invaded regions, studies have found that plants are more likely to attract generalist pollinators in their new range compared to specialist pollinators (Chitchak et al., 2024; Parra-Tabla & Arceo-Gómez, 2021; Richardson et al., 2000; Rodger et al., 2010). However, we lack empirical studies assessing what factors enable these species to become naturalized and invasive, including whether they benefit from generalist pollinators, which has prevented a detailed understanding as to the factors influencing invasion success (see reviews: Lopresti et al., 2024; Traveset et al., 2020).

Pollination syndromes are based on common floral traits that have been driven by pollinator-mediator selection (Dellinger, 2020). The buzz pollination syndrome is considered both a phenotypic and functional-group specialized pollination syndrome (sensu Armbruster, 2017). Buzz-pollinated flowers have restricted pollen access, commonly encased by poricidal anthers (Buchmann et al., 1983). Poricidal anthers are specialized floral structures that have convergently evolved multiple times in an estimated 6%–10% of angiosperm species (Russell et al., 2024). The most efficient way to remove pollen from a flower of a species with the buzz pollination syndrome is through floral vibrations (see reviews: Cooley & Vallejo-Marin, 2021; Lopresti et al., 2024). Vibrations are typically produced by female bees, although one fly species also can buzz pollinate (Buchmann et al., 1983; Vallejo-Marín, 2019). Despite this apparent specialization, at least 131 (of 4, 630) invasive plants (CABI, 2022) exhibit the buzz pollination syndrome (Lopresti et al., 2024).

However, our recent review showed that buzz-pollinated plants may be pollinated by non-buzzing species (Lopresti et al., 2024). Alternative foraging behaviors by floral visitors include biting the anthers to access the pollen, using their legs to squeeze the pollen out of the anthers (milking), and pushing their proboscis inside the apical slit to extract the pollen (licking) (reviewed in Lopresti et al., 2024). Yet, we are still in the early stages of understanding the relative importance of these non-buzzing behaviors for plant reproduction. To the best of our knowledge, no previous studies have compared the behaviors of pollinators of invasive buzz-pollinated plants both in their native and invaded regions to determine whether the alien plant has found suitable specialist pollinators in its invaded region and whether non-buzzing behaviors have adequately provided pollination services.

We used *Senna obtusifolia* (L.) Irwin & Barneby (Fabaceae) as a model system to test the missed mutualist hypothesis and to elucidate how invasive plants overcome the theoretical barrier of having specialized pollination mutualisms. *Senna* species have poricidal anthers, exhibit the buzz pollination syndrome, and are pollinated by bees that exhibit buzz pollination behavior (Laporta, 2005; Williams, 1998; Wolowski & Freitas, 2010). Specifically, we (1) identified the floral visitors and pollinators in each region; (2) determined whether floral visitor and pollinator assemblages differ between regions; and (3) assessed whether *S. obtusifolia* relied on specialized buzzing behavior for pollen transfer in either the native or the invaded regions. To test the missed mutualists hypothesis, we compared whether the absolute effective diversity of potential pollinators (floral visitors that contacted the stigma or carried pollen) was significantly reduced in the invasive region compared to the native region.

METHODS

Study species and sites

S. obtusifolia (Fabaceae) is a globally broadly distributed invasive plant (CABI, 2021). It has common traits of buzz-pollinated plants, including poricidal anthers and nectarless flowers. Plants typically flower under 2 m in height (CSIRO, 2025), and plant height does not exceed 2.5 m (DPI, 2025). The *Senna* genus is a large buzz-pollinated one that contains 250–300 accepted species with very similar floral structures to *S. obtusifolia* (Oladeji et al., 2021). *S. obtusifolia* is native to tropical America, and it has been introduced to six continents, becoming highly invasive in North and South America (beyond the tropics), Africa, and Australasia (CABI, 2021). It was introduced to Australia in the 1940s and declared invasive across tropical Australia by the 1960s (Mackey et al., 1997). *S. obtusifolia* has had far-reaching effects in its invaded regions, including altering the structure and composition of native plant communities (e.g., Gebrekiros & Tessema, 2018). Its introduction in Australia has affected agroecosystems, national parks, and indigenous areas (Mackey et al., 1997), and its management has been economically expensive (DPIRD, 2020).

Modeling suggests that *S. obtusifolia* will continue to expand its range poleward into currently unoccupied regions (Dunlop et al., 2006). Hand pollination experiments showed that *S. obtusifolia* is fully self-compatible but that it can set little seed in the absence of pollinators in both the native and invaded regions (Lopresti et al., unpublished). Uniparental reproduction is expected to be beneficial in the early stages of colonization where mates and pollinators are more likely to be scarce, but over time, finding a pollinator match can be critical for outcross pollination and population health (Rodger et al., 2013 and references therein).

We conducted this study in Mexico and Australia during the respective *S. obtusifolia* flowering seasons. We undertook pollinator observations between September and November 2023 at three sites in Yucatan, Mexico: Chochola, Tekik de Regil, and Xmatkuil (Appendix S1: Table S1, Figure S1). We undertook pollinator observations between May and July 2022 at five sites in Queensland, Australia: White Rock, Kamerunga, Trinity Beach, Lakeland, and the West Normanby River (Appendix S1: Table S1). Sites in each location were located at least 6.5 km apart and separated by either suburbia, farmland, native vegetation, or a combination of the three. Each site contained at least 50 *S. obtusifolia* plants.

Field observations

We assessed floral visitors with a combination of direct observations and digital video recordings for a total observation time of 65 h across regions and sites (Appendix S1: Table S2 details the sampling effort at each site). For both direct observations and recordings, we sampled the accessible part of the plant canopy, with the flowers housing mature androecium or gynoecium. Both sampling methods were conducted within 2 m of the ground. We surveyed on days with minimal cloud cover, no rainfall, calm winds (maximum wind gusts did not exceed 54 km h^{-1}), and temperatures ranging between 17 and 30°C (Australia) or 24 and 36°C (Mexico).

We directly observed and captured floral visitors during defined time periods and areas to ensure similar sampling effort across sites. The exception was at Lakeland (Australia) where, due to time and distance constraints, we did not undertake direct observations. At all seven of the other sites, trained volunteers assisted with the floral visitor observations. Two observers conducted assessments in 30-min blocks resulting in a total observation time of 5–6 h per site (Appendix S1: Table S2). In Australia, surveys were done evenly over one day at each site, between 08:00 and 16:30. In Mexico, surveys were done over two days between 07:00 and 11:00, because floral visitors were not active after this time, potentially due to the hot climate. We observed fixed sections of the flowering stand (80 cm × 80 cm), referred to as the "arena" (following Dafni, 1992). We determined this 80 × 80 cm arena size based on the observer's ability to confidently track the movements of floral visitors. We captured floral visitors in specimen jars or using insect sweep nets after their foraging bouts within the arena and euthanized them on ice for subsequent identification and pollen analysis. We identified captured specimen with the help of entomologists Rei Asai, Matthew

Connors, and Abiel Sansores using the keys: Houston (2018), Mexico: Ayala (1999), Ayala-Barajas (2016), Michener (1994, 2007), and Packer (2023). Specimens are vouchered in the Insect Ecology Laboratory (James Cook University, Cairns, Australia) and in the Department of Tropical Ecology (Universidad Autónoma de Yucatán, Mexico).

At all eight sites, we used digital video recordings to increase total observation time and observe species that may be deterred by human presence (as described by Dafni, 1992). We set GoPro HERO10 Black and Zero-X ZX-40 UHD Action Cameras to record in 3000 resolution up to two flowers that had mature anthers and a receptive stigma, in 1-h time block commencing between 07:00 and 12:00, over three days at each site throughout the flowering season. Due to technical issues, we obtained data from one, two, or three days at each site. We did not record in the afternoon due to cameras overheating (human observations showed peak pollinator activity was between 09:30 and 10:00 in Australia and between 07:30 and 08:00 in Mexico).

We documented the foraging behavior of each floral visitor. We defined floral visitors as species contacting any part of the flower. We assessed whether each floral visitor contacted the stigma while foraging and whether it produced audible floral vibrations to extract pollen. For every floral visitor, we recorded the behavior the individual used to extract pollen (buzzing or not buzzing) and where possible, we noted what non-buzzing behavior (see Lopresti et al., 2024) (Appendix S1: Table S3).

Pollinator diversity calculations

To assess whether the pollinator assemblages differed between regions, we calculated, for each site, an individual absolute effective diversity biodiversity index (Gatti et al., 2020) using the *vegan* package (Oksanen et al., 2024) in R (version 4.1.1). We classed any floral visitor that contacted the stigma while foraging or carried pollen on their body as a potential pollinator. Absolute effective diversity describes the species of a community by incorporating Hill's N_0, N_1, and N_2 metrics, but it is less affected by estimation errors (Gatti et al., 2020). To assess whether pollinator assemblages statistically differed between regions, we undertook a generalized linear model with a Gaussian distribution in R (version 4.4.1), where absolute effective diversity of potential pollinators at each site was the response variable, and region was the fixed variable. In this model, we do not include site as a random factor, because each site contributed only a single absolute effective diversity value, providing no within-site replication to estimate a random-effect variance.

We compared the beta diversity of potential pollinator communities among sites within each region by calculating a Bray–Curtis dissimilarity matrix using the *vegdist* function from the *vegan* package (Oksanen et al., 2024) in R (version 4.1.1). This method calculates pairwise dissimilarities between sites based on differences in species composition and their relative abundances. We then visually compared the pollinator communities within each region by generating an ordination plot, where the Bray–Curtis dissimilarity values were used to represent the similarity among communities.

Calculating pollination effectiveness

We assigned a pollination importance value (PIV) to each morphospecies in each region for which we obtained data for all variables in the equation (modified from Lindsey, 1984; Equation 1).

$$\mathrm{PIV} = A \times \mathrm{PCC} \times F \times \mathrm{PE(a)} \times \mathrm{PE(b)} \tag{1}$$

where A is abundance, calculated by the number of visits per flower per observation time in each region for floral visitors observed by either direct observations or digital video recordings.

PCC is the pollen carrying capacity, calculated as a count of *S. obtusifolia* pollen grains from the individual (presented as a mean per morphospecies on the logarithmic scale). We placed each euthanized specimen on a sterile slide under a stereomicroscope and swabbed it with basic fuchsin stain gels cut into 1 mm^3 on a stainless-steel pin (Kearns & Inouye, 1993; Razanajatovo et al., 2024). We did not assess the pollen contained within the scopa and took care to not contact the scopa because tightly compact pollen grains in the scopa remain on the bee if it contacts the stigma (Parker et al., 2014), and we were only interested in pollen available for pollination. We swabbed each of the body parts until no pollen remained visible on the insect under 40× magnification (Mexico: Motic SMZ168; Australia: Nikon SMZ800). We warmed the cubes to melt the jelly and identified and counted the pollen grains under a standard light microscope (40× or 100× magnification) (Mexico: Motic BA310; Australia: Nikon Eclipse 200). There were two instances when more than two swabs were taken for each body part, and there were too many grains for a complete count to be practical. In these cases, we used a sterile dissecting needle to stir the melting jelly and ensure the pollen grains were homogenous through the mix. We counted half of the area of the mix and multiplied this by two to estimate the total pollen count in these cases.

F is fidelity, calculated as the proportion of *Senna* pollen compared to non-*Senna* pollen carried by each captured individual, presented as an average per morphospecies per region. To calculate the pollen fidelity, we classified pollen as either *Senna* or not *Senna* using reference slides we created at the start of the analysis. It is not possible to distinguish many *Senna* species by pollen morphology under a standard light microscope (Nnamani & Onu, 2014), and we could not distinguish floral pollen in our reference collection between *S. obtusifolia* and *Senna uniflora* (which also presented the buzz pollination syndrome (Marazzi et al., 2006) and was a common co-flowering species at sites in the native region). However, we never observed an individual visit both *S. obtusifolia* and *S. uniflora* in a single foraging trip when they co-flowered within the arena.

PE is pollinator efficiency. To calculate the pollinator efficiency, Lindsey (1984) assigned each broad taxonomic group a value between 0 and 1 based on estimates of insect size, foraging behavior in relation to anther and stigma contact, and the consistency of movement within and between inflorescences. This value is subjective, and therefore, to reduce the error and bias for this calculation, we split the pollinator efficiency score into two categories:

PE(a) is pollinator efficiency (size-match index), calculated whether the thorax width was less than, equal to, or greater than the mean *S. obtusifolia* anther-stigma distance (herkogamy) following Mesquita-Neto et al. (2021). We measured the width of the thorax for all captured specimen with a digital caliper (Australia: Q1382, Dick Smith; Mexico: 6in, RexQualis). To obtain the mean anther-stigma distance in each region, we haphazardly selected five individual plants at each site and measured the distance between the anther and stigma from one flower that had a receptive stigma. If the specimens' thorax width was within the mean (±SD) anther-stigma distance, we assigned the specimen a "2," if the individual was outside this region, we assigned it a "1." We present the size match index as an average per morphospecies per region. The size-match index is an assessment of the likelihood of each morphospecies to contact the stigma when foraging on plants with the buzz pollination syndrome (Mesquita-Neto et al., 2021). We did not assess floral visitor body size as a measure of pollen removal efficacy for buzzing species, because we are still in the early stages of understanding whether, and how, insect body size correlates to buzz frequency and amplitude, and in turn, pollen removal from plants with poricidal anthers (see Vallejo-Marin & Russell, 2024).

PE(b) is pollinator efficiency (stigma contact), calculated as the proportion of floral visits during which contact with the stigma was observed for each morphospecies within each region.

We then assigned each morphospecies a pollination importance index (PII), which represents the relative importance of the floral visitor compared to other floral visitors within the same region. We calculated the PII for each morphospecies by dividing its PIV by the total PIV for all morphospecies in the same region ($\text{PII} = \text{speciesPIV}/\sum\text{PIVregion}$).

Visitors for which we could not obtain information on all parameters were excluded from this pollination effectiveness calculation. Consequently, floral visitors that were not captured could not be included. Typically, excluded species were infrequent floral visitors which we only observed once throughout the entire survey period (Appendix S1: Table S4). There is potential that the infrequent visitors that contacted the stigma while foraging did pollinate *S. obtusifolia*. As such, we still included them as potential pollinators, although we could not assign these species a pollinator importance index.

RESULTS

We observed 19 floral visitor morphospecies in the native region and 20 in the introduced region (Appendix S1: Table S4). Hymenopterans were the most species-rich taxon (native region: 18 morphospecies; introduced region: 14 morphospecies). Non-Hymenoptera visitors consisted of a single Lepidopteran in the native region. Non-Hymenoptera floral visitors were comparatively more diverse in the introduced region, consisting of six morphospecies from the Lepidoptera, Blattodea, Coleoptera, and Diptera orders. We classed 15 (native region) and 11 (invaded region) floral visitor morphospecies as potential pollinators because they contacted the stigma when foraging or carried pollen (Appendix S1: Table S4). We assigned a pollinator importance value to six species in the native region and eight species in the invaded region because we obtained all the necessary data for these floral visitors (Table 1).

We found no evidence that *S. obtusifolia* was missing pollinator mutualists in its introduced region. More morphospecies were potential pollinators in the native region (15 morphospecies) compared to the invaded region (11 morphospecies). Yet, the absolute effective diversity of potential pollinators did not significantly differ between the regions ($t = 1.42$, $p = 0.20$). Absolute effective diversity varied among sites, and two sites with the lowest pollinator diversity were both in the native region (Chochola: absolute effective diversity = 2.2 and Tekik de Regil: absolute effective diversity = 2.4) (Appendix S1: Figure S2). There was little variation in pollinator diversity among the remaining six sites, with absolute effective diversity values distributed between 5.0 and 8.4 (Appendix S1: Figure S2).

TABLE 1 Floral visitors and pollinators of *Senna obtusifolia* in its native region of Mexico and invaded region of Australia.

Floral visitor morphospecies	*A*	PCC	*F*	PE(a)	PE(b)	PIV	PII
Native region							
Apis mellifera	21.18	7.13 (5)	0.99 (5)	1 (5)	0.89 (354)	134.34	88.38
Trigona fulviventris	2.08	6.09 (5)	1 (5)	1.4 (5)	0.55 (40)	9.73	6.40
Frieseomelitta nigra	0.82	5.43 (5)	0.99 (5)	1.8 (5)	0.44 (9)	3.58	2.35
Melipona beecheii	0.40	8.08 (5)	0.99 (5)	1 (5)	1 (4)	3.18	2.09
Eulaema polychroma	0.13	8.90 (3)	0.99 (3)	1 (3)	1 (1)	1.17	0.77
Nannotrigona perilampoides	0.53	3.82 (2)	1 (2)	2 (2)	0 (11)	0	0
Invaded region							
Tetragonula species	8.74	7.89 (6)	1 (6)	1 (6)	0.32 (152)	22.05	54.22
Apis mellifera	1.06	7.42 (6)	0.99 (6)	1 (6)	1 (1)	7.76	19.09
Xylocopa species	0.53	10.18 (4)	1 (4)	1 (4)	0.88 (5)	4.73	11.63
Lipotriches (*Austronomia*) species	0.29	8.69 (1)	1 (1)	1 (1)	1 (6)	2.50	6.15
Mellitidia species	0.34	8.86 (6)	0.99 (6)	1.33 (6)	0.43 (7)	1.70	4.18
Patellapis (*Pachyhalictus*) *stirlingi*	0.29	9.00 (3)	1 (3)	2 (3)	0.2 (5)	1.03	2.55
Amegilla species	0.19	7.12 (1)	0.85 (1)	1 (1)	0.5 (4)	0.58	1.43
Palaeorhiza species	0.14	3.18 (2)	1 (2)	2 (2)	0.33 (3)	0.30	0.74

Note: The pollination importance index (PII) represents the relative importance of the pollinator importance value calculated within each region, with higher values indicating more effective pollinators, and a value of "0" indicating that the morphospecies does not pollinate *Senna obtusifolia*. Morphospecies for which we were not able to obtain data for every column are omitted from the table but listed in Appendix S1: Table S4. Values in parentheses are *N*.
Abbreviations: *A*, relative abundance; *F*, fidelity; PCC, pollen carrying capacity; PE(a), size match index; PE(b), stigma contact; PIV, pollination importance value.

All pollinator communities were highly dissimilar among sites in the invaded region and comparatively similar among sites in the native region (Figure 1).

The honey bee (*Apis mellifera*) was the most important pollinator in the native region, followed by non-buzzing stingless bees (*Trigona fulviventris* and *Frieseomelitta nigra*) (Table 1). In the invaded region, non-buzz pollinating stingless bee (*Tetragonula* species) had the greatest pollinator importance value, followed by the honey bee (*A. mellifera*). Buzzing pollinators were present in both regions (Figure 2) and carried nine times more pollen grains per individual (7458 ± 2383 pollen grains; mean ± SE) than non-buzzing pollinators (812 ± 364 pollen grains) (Appendix S1: Table S5). Nonetheless, buzzing pollinators visited *S. obtusifolia* less frequently than *A. mellifera* and non-buzzing stingless bees (Table 1), which contributed to their lower pollinator importance values.

Potential pollinators that vibrated flowers when foraging were uncommon in both regions, but they were proportionally more frequent in the invaded region compared to the native region (Figure 3). Overall, most potential pollinators did not produce floral vibrations, but we could not confidently define the specific non-buzzing behavior for 73.3% of non-buzzing pollinator visits (native region) or 57.8% of non-buzzing pollinator visits (invaded region). For each interaction in which we confidently assessed visitor behavior, 1.96% of floral visitors in the native region produced floral vibrations ($N = 177$) compared to 7.34% ($N = 153$) in the invaded region, a 3.8-fold difference (Figure 3). Three non-buzzing behaviors were used by pollinators to extract pollen: gleaning, biting, and licking (Appendix S1: Table S3; Video S1). Biting damages the anthers, whereas the other behaviors do not. In the native region, most potential pollinators for which we could confidently assign non-buzzing behaviors exhibited the passive, gleaning behavior (94.11%), while in the invaded region, most potential pollinators bit the anther heads (89.27%) and, in turn, damaged the anthers while foraging (Figure 3).

DISCUSSION

We found no evidence for the missed mutualist hypothesis because effective pollinators were present in both the native and invaded region. We classed 15 different bee species (native region) and 11 species (invaded region) as potential pollinators because they contacted the stigma while foraging or carried *S. obtusifolia* pollen. We observed buzzing behavior infrequently (<9% of visits), and it was 3.8 times more common in the invaded region than the native region. Our results contradict the few

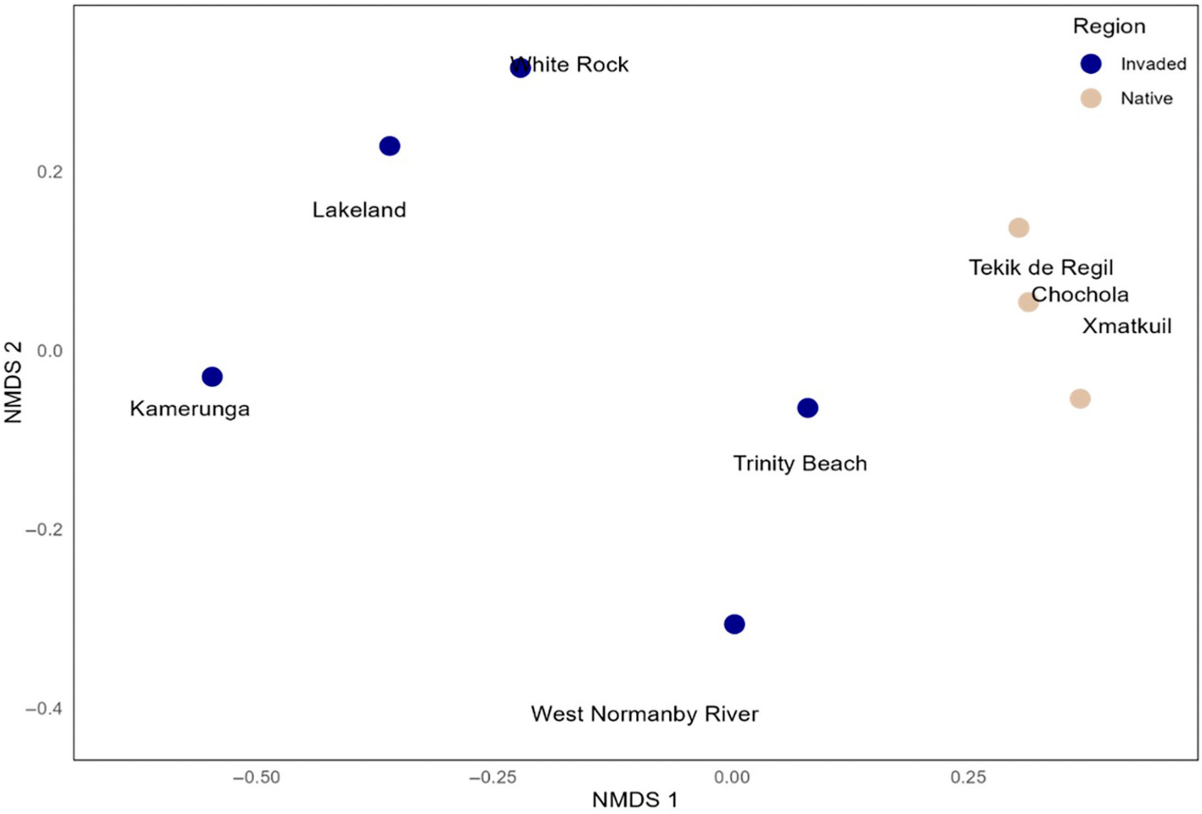

FIGURE 1 Nonmetric multidimensional scaling (NMDS) ordination plot of Bray–Curtis dissimilarity indices for potential pollinator assemblages of *Senna obtusifolia* among sites in the native (Mexico) and invaded (Australia) regions.

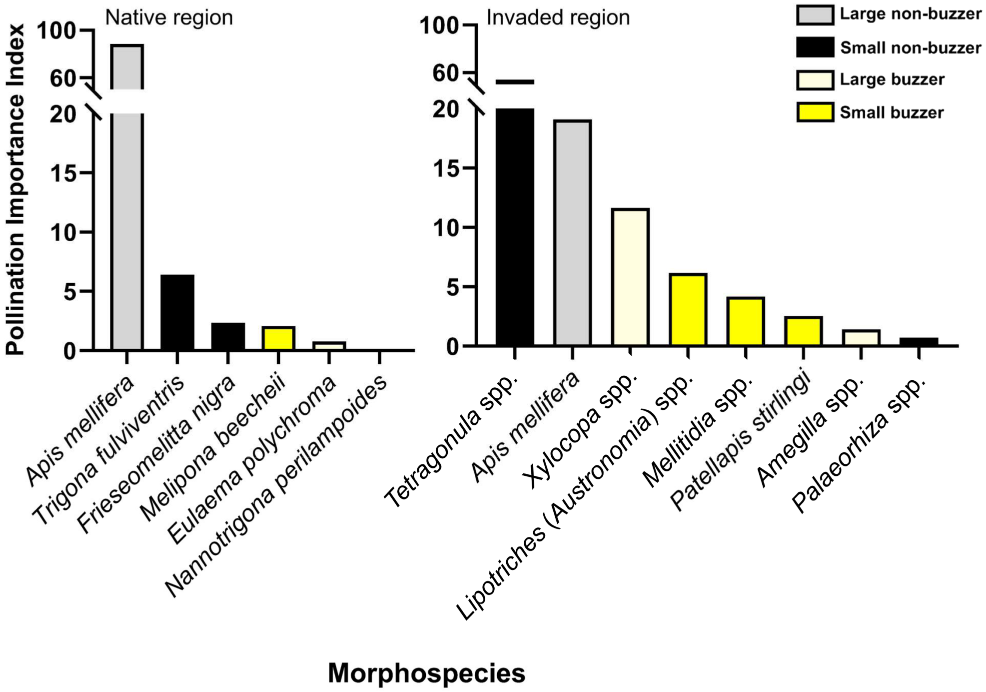

FIGURE 2 Pollinators of *Senna obtusifolia* (based on observed foraging behaviors) ranked by pollination importance index, in one native (Mexico) and one invaded (Australia) region.

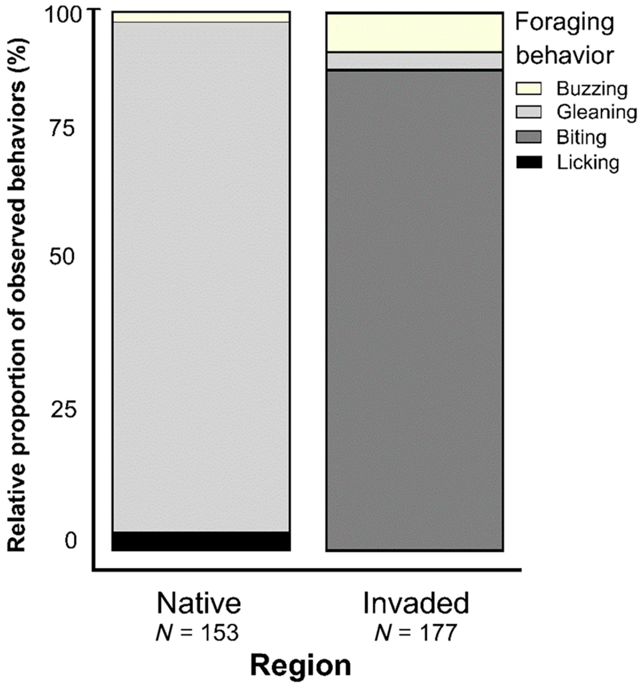

FIGURE 3 The proportion of pollen extraction behaviors observed by potential pollinators when foraging on *Senna obtusifolia* in each region pooled across both sampling methods (digital video recordings and direct observations). *N* is the number of pollinator visits in each location in which we confidently described a non-buzzing behavior. Note that we could not confidently define the specific non-buzzing behavior for 73.3% of non-buzzing pollinator visits (native region) or 57.8% of non-buzzing pollinator visits (invaded region).

other studies that have compared species richness or visitation rates of mutualists in a species' native and invaded regions. For example, a recent meta-analysis found that in their native regions, plants have 2.3 times more interactions with mutualists (both pollinators and seed dispersers) per unit time than in their invaded regions (Moles et al., 2022).

We found that, despite exhibiting the specialized buzz pollination syndrome, *S. obtusifolia* is predominantly visited and pollinated by non-buzzing bees in both its native and invaded regions. The diversity of pollinator behaviors likely contributes to its success as an invader and suggests that *S. obtusifolia* does not require specialist buzzing behavior for successful outcross pollen transfer (but see Baker, 1974; Richardson et al., 2000; Rodger et al., 2010). Contrary to our expectations, we observed specialist buzzing behavior 3.8 times more frequently in the invaded region than the native region, albeit buzz-pollination played a very small role in both regions (<9% of overall observed pollinator behaviors).

Interestingly, non-buzzing species were the most important pollinators in both regions, largely due to their high abundance. The most common species which we observed foraging (*A. mellifera* and stingless bees) are eusocial bees which potentially contributed to their high abundances. Animals are motivated to collect pollen for the protein source it provides to them and their young (Hargreaves et al., 2009). Poricidal anthers have evolved, in theory, to protect and hide pollen from pollen thieves and robbers (Arceo-Gómez et al., 2011; Buchmann & Hurley, 1978). However, non-buzzing insects are often observed to collect pollen from poricidal anthers. Studies typically find that non-buzzers are not highly effective pollinators (see reviews: Cooley & Vallejo-Marin, 2021; Lopresti et al., 2024), or a priori discard non-buzzing floral visitors as pollinators based on the behavior alone (e.g., Cardoso et al., 2018; Oliveira et al., 2016; Tavares et al., 2018). Many non-buzzing insects in our study were observed to bite and damage the anther while foraging. Floral damage can reduce pollinator attraction in some species (e.g., Kessler et al., 2013; Suárez et al., 2009; Tsuji & Ohgushi, 2018), including buzz-pollinated plants (Rego et al., 2018). Yet, we observed some insects, particularly in the invaded region, that frequently bit and damaged the anthers while contacting the stigma, likely pollinating the flower. Future studies of plants with poricidal anthers that detail the non-buzzing behaviors of floral visitors and pollinators will allow a better understanding as to which specialized behaviors may contribute to effective pollination, and in turn, whether buzz-pollinated plants are truly ecologically specialized.

A. mellifera cannot buzz-pollinate and is not native to either region of our study, but *A. mellifera* frequently visited *S. obtusifolia* flowers in both the native and invaded regions. *A. mellifera* was introduced to Australia around 200 years ago (DCCEEW, 2021) and to Mexico around 250 years ago (Baena-Díaz et al., 2021), because of its importance in honey production and crop pollination. It has since established outside of apiaries in both regions. *A. mellifera* is the most common visitor to exotic plants around the world, in part due to its generalist foraging habits and high abundance as a eusocial species (Chitchak et al., 2024). Feral *A. mellifera* populations may compete with native pollinators for floral resources and in turn can disrupt established plant–pollinator networks (Parra-Tabla et al., 2025; Worthy et al., 2023). Investigating the pollinator communities where *A. mellifera* is absent, or actively excluded, would enable an assessment of whether it has deterred buzzing pollinators from visiting *S. obtusifolia* in both its native and invaded regions.

Non-buzzing pollinator behaviors could still be considered specialized, which highlights the ambiguity of the definition of an ecological "specialization." For example, poricidal anthers may rely on pollinators specialized in one of seven behaviors including buzzing, licking, or biting (Lopresti et al., 2024). The dominance of non-buzzing pollinator behaviors in our study poses interesting questions about the evolution and maintenance of specialized floral morphologies that restrict pollen access, such as whether poricidal anthers still offer a fitness advantage for the plant when visited by many non-buzzing pollinating insects. Defining specialization has important implications in invasion ecology because species with specialist mutualisms are often expected to be co-introduced with a mutualistic partner, to change mutualistic partners, or to increase the number of mutualistic partners upon introduction to a new region, thereby ensuring populations can establish and become invasive (Le Roux et al., 2017). While rarely examined, it is critical to confirm that theoretical specialist interactions are indeed specialists, to produce a holistic understanding of how mutualisms unfold to influence the spread of invasive alien species.

There is no doubt that buzzing behavior is efficient and removes the greatest amount of pollen in only a few seconds. In our study, large buzzing bees, such as *Eulaema polychroma* (native region) and *Xylocopa* species (invaded region), carried the most pollen grains of any species, exceeding an average of 7300 pollen grains per individual bee. Our result aligns with some other pollinator studies that have found buzzing bees to carry many more pollen grains than non-buzzing bees when assessing pollinator efficiency for plants with the buzz pollination syndrome (Estravis-Barcala et al., 2021; Gross, 1993; Moquet et al., 2017; Solís-Montero et al., 2015). *Xylocopa* species had the greatest pollinator importance value when we used the raw count of pollen grains to calculate the PII. However, we analyzed the pollen carrying capacity on the logarithmic scale because pollen carrying capacities were highly variable among species, and most pollinators (>70%) carried more than 1000 pollen grains. *S. obtusifolia* pods typically contain fewer than 32 ovules and seeds (Lopresti et al., unpublished), so maximum seed set can be obtained with pollen deposit magnitudes smaller than the 1000 pollens which bees were found to carry. To obtain a greater understanding of whether individuals carrying 1000 pollen grains compared to 7300 pollen grains are equally effective as pollinators, future studies should compare seed set following single floral visits by each pollinator.

We found pollinator assemblages to be highly dissimilar among sites in the invaded region, which further demonstrated that *S. obtusifolia* is not restricted to a distinct pollinator niche. We expected similar pollinator communities within the invaded region because sites were located on disturbed habitats with comparable weedy adjacent vegetation communities and abiotic conditions. Logically, the diverse behaviors that pollinators can use to access pollen from poricidal anthers (Lopresti et al., 2024) potentially explain the variable pollinator assemblages among sites. Plants with poricidal anthers may be more likely to find a pollinator match when introduced into a new region if they are not reliant on specialist buzz pollinator behavior.

In conclusion, we found no evidence that *S. obtusifolia* was missing its pollinator mutualists. The ability to attract suitable pollinators has potentially contributed to *S. obtusifolia*'s invasion success upon introduction to a new region. Importantly, our findings indicate that the buzz pollination syndrome may be less specialized than previously assumed, underscoring the importance of evaluating floral visitor efficacy, rather than relying on foraging behavior, in future studies of buzz-pollinated plants.

AUTHOR CONTRIBUTIONS

Laura C. Lopresti, Lori Lach, and Daniel Montesinos designed the study. Laura C. Lopresti collected the data and analyzed the data. All authors contributed substantially to the manuscript and gave final approval for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lopresti et al., 2026) are available from Research Data JCU: https://doi.org/10.25903/zx8c-0q24.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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