Received: 19 February 2024 | Accepted: 18 April 2024

DOI: 10.1111/1365-2745.14338

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

REVIEW

The specialised buzz pollination syndrome poses a partial barrier to plant invasions

Laura C. Lopresti[1,2,3] | **Lori Lach**[2,3] | **Daniel Montesinos**[1,2,3,4]

[1]Australian Tropical Herbarium, James Cook University, Cairns, Queensland, Australia

[2]Centre for Tropical Biosecurity, James Cook University, Cairns, Queensland, Australia

[3]College of Science and Engineering, James Cook University, Cairns, Queensland, Australia

[4]Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

Correspondence
Laura C. Lopresti
Email: laura.lopresti@my.jcu.edu.au

Handling Editor: Nicole Rafferty

Abstract

1. Plants that exhibit generalised pollination syndromes have been hypothesised to become invasive more easily compared with specialists, yet the degree to which specialised pollination traits inhibit plant invasions is unknown. One such specialisation is the buzz pollination syndrome, which encompasses specialised floral traits that restrict pollen access (typically poricidal anthers) and benefits from specialised insect behaviour for pollen extraction.
2. We reviewed the literature on buzz pollination of invasive plants to assess whether: (1) plant species exhibiting specialised pollination syndromes are underrepresented as invasive species, and (2) species with specialised pollination syndromes that have become invasive can reproduce in the absence of specialist buzzing pollinators.
3. *Synthesis*. We found 2.5% (117/4630) of invasive angiosperms have poricidal anthers, which is an underrepresentation of the proportion of global angiosperms that are estimated to have poricidal anthers (6%–10%). Most invasive buzz-pollinated plants are genetically self-compatible (97%), but only 43% can set fruit in the absence of a pollinator. Our findings highlight the importance of establishing new pollinator mutualisms for sexual reproduction. However, we identified six non-buzzing behaviours used to extract pollen from plants with poricidal anthers, which is important where buzzing pollinators may be absent or not attracted to newly introduced plant species.

KEYWORDS
alien invasive, Baker's law, buzz-pollination, floral sonication, invasion ecology, non-native species, reproductive assurance, specialised plant–pollinator interaction

1 | INTRODUCTION

Invasive species are those that cause ecological harm and threaten native biodiversity, affect human health and livelihoods or cause economic losses (CABI, 2018). To become invasive, angiosperms need to be able to reproduce, and for some that will require establishing new pollination mutualisms within their non-native range. Globally, 89.7% of angiosperms require a pollinator for outcrossed seed set (Tong et al., 2023). Nevertheless, the extent to which pollination interactions are relevant in plant invasions depends on the ability of plant species to reproduce asexually, the plant species' degree of self-compatibility and its dependence on a pollinator to transfer pollen from the anther to a receptive stigma (Traveset et al., 2020).

Plants with generalised pollination systems are hypothesised to become invasive more easily than specialists due to the diversity of fauna that can pollinate them (Baker, 1974; Richardson et al., 2000; Rodger et al., 2010). However, there are multiple definitions of what constitutes generalised or specialised in pollination networks, as specialisation may refer to ecological specialists, functional group specialists or phenotypic specialists (Armbruster, 2017; Ollerton et al., 2007). Ecological specialist refers to the species richness of effective pollinators; functional group specialist refers to the pollinator functional group diversity, typically presented as a mix of functional traits and at a family level or order level (e.g. butterfly pollinated, short-tongued bee pollinated); and phenotypic specialist refers to the floral adaptations, such as specialised morphological structures that attract pollinators (Armbruster, 2017). Defining whether a plant species is a specialist or generalist is subjective, and each type of pollination specialisation is relative and can be placed on a specialist continuum (Armbruster, 2017). For example, at one extreme of that continuum is *Yucca* (Asparagaceae). *Yucca* pollination is considered highly ecologically and phenotypically specialised because each flower has a depressed stigma and requires pollen to be deposited by a single yucca moth species, which has modified tentacles to handle and deposit the pollen on the stigma (Baker, 1986); while, at the other end, eucalypts (Myrtaceae) exhibit generalised plant–pollinator networks as they have an unspecialised floral morphology (Zilko et al., 2017) and can be pollinated by bats (Hingston, 2002), possums (Brundrett, 2021), birds (Zilko et al., 2017) and a diverse suite of insect orders (Brundrett, 2021).

Furthermore, ecological, functional group and phenotypic specialisations are independent of each other (Ollerton et al., 2007). For example, a plant species with high phenotypic specialisation can be ecologically and functionally generalist. In trigger plants (*Stylidium* species; Stylidiaceae), the staminal and pistillate tissues have fused into a column that, when touched at the base, launches onto the dorsal side of the visiting insect, depositing or collecting pollen (Armbruster et al., 1994). Despite *Stylidium* being highly specialised phenotypically, a suite of insect species from five genera and three functional groups (social bees, solitary bees and flies) can pollinate *Stylidium* species (Armbruster et al., 1994), thereby *Stylidium* plants can be classed as ecological and functional generalists.

The ‘buzz-pollination’ syndrome provides a good example of a specialised pollination process because both functional group and phenotypic specialisations occur. Buzz-pollinated flowers have specialised floral traits that restrict pollen access, such as poricidal anthers with a small opening at the tip whereby pollen is released (Buchmann, 1983), or the solanoid flower morphology (De Luca & Vallejo-Marín, 2013; Vallejo-Marin & Russell, 2023). Solanoid flowers lack a nectar reward, contain short, centrally located filaments in a fused cone structure and rarely contain fused petals or sepals into a tube (De Luca & Vallejo-Marín, 2013). Plants containing poricidal anthers are broadly distributed across the angiosperms, from the ancestral complex of the Magnoliales (Buchmann, 1983). Poricidal anthers are a highly specialised floral structure that has convergently evolved in an estimated 6%–10% of angiosperm species (Buchmann, 1983; Russell, Zenil-Ferguson, et al., 2024). The most efficient way to remove pollen from flowers with these specialised traits is through floral vibrations. Vibrations are typically produced by female bees and it is these vibrations that cause pollen release (Buchmann, 1983; Vallejo-Marín, 2019). Bees are the primary taxonomic group known to produce floral buzzes (Buchmann et al., 1978; Pritchard & Vallejo-Marín, 2020; Vallejo-Marín & Vallejo, 2021), making these plants functional group specialists. As such, buzz pollination is commonly considered a specialised pollination syndrome.

In spite of this apparent specialisation, many broadly distributed invasive plants exhibit the buzz pollination syndrome, including species from the Solanaceae, Fabaceae and Melastomataceae families. For example, *Clidemia hirta* (Melastomataceae) exhibits the buzz pollination syndrome and is listed on the ‘100 of the World's Worst Invasive Alien Species’ list (Luque et al., 2014) because it outcompetes native biodiversity and has the potential to cause extinctions for native flora and fauna in its non-native ranges (GISD, 2024). Furthermore, *Solanum torvum* and *Solanum rostratum* (Solanaceae) both exhibit the buzz pollination syndrome and are highly invasive species present on six continents (CABI, 2022; Palchetti et al., 2020). Plants that have specialised pollination syndromes may become invasive if the relevant functional group of pollinators is present in their non-native range, if they switch to a new functional group of pollinators upon introduction to their non-native range or if they do not require a pollinator to reproduce (Rodger et al., 2010 and references therein). The reproductive assurance hypothesis states that selection favours self-pollination or asexual reproduction in flowering plants where pollinators or mates are scarce (Baker, 1955; Darwin, 1876), such as when colonising new habitats (Baker, 1955). Baker's law reiterates the reproductive assurance hypothesis and states that uniparental reproduction is advantageous for species when colonising island ecosystems by long-distance seed dispersal (Baker, 1955; Stebbins, 1957). Currently, evidence for the factors that enable plants with specialised pollination syndromes to become invasive is scarce, and we rarely have data on what species visit or pollinate many invasive plants for either their native or their non-native ranges (Traveset et al., 2020). Consequently, whether species frequently utilise any of these strategies to overcome the barrier of specialist plant–pollinator interactions is largely unexplored.

We reviewed the available literature on invasive buzz-pollinated plants to determine (1) how frequently represented buzz-pollinated plants are as invasive species, and (2) whether buzz-pollinated plants that have become invasive can reproduce in the absence of specialist buzzing pollinators. Specifically, we hypothesised that (1) buzz-pollinated plants will be underrepresented as invasive species. For invasive species that exhibit the buzz pollination syndrome, we expect that (2.1) these invasive plants frequently reproduce in the absence of a pollinator, or that (2.2) these invasive plants can be pollinated by non-vibratile pollen collectors in their non-native range.

2 | INVASIVE SPECIES THAT EXHIBIT THE BUZZ POLLINATION SYNDROME

To determine whether buzz-pollinated plants are underrepresented as invasive species, and in turn, to infer whether the buzz pollination syndrome appears to provide a barrier to plant invasions, we assessed the proportion of known global invasive plant species that have a buzz pollination syndrome. We then compared this to the estimated 6%–10% of angiosperms that have poricidal anthers and, in turn, exhibit the buzz pollination syndrome (Buchmann, 1983; Russell, Zenil-Ferguson, et al., 2024). The proportion of buzz-pollinated plants able to thrive in new regions should be less than the overall number of species exhibiting a buzz pollination syndrome if this specialist interaction poses a barrier to plant invasions. Therefore, we expected that the proportion of invasive buzz-pollinated plants would be less than 6%–10%.

To calculate the proportion of invasive species globally that exhibit the buzz pollination syndrome, we assessed the pollination syndrome of angiosperms listed in the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium Open Data Repository (CABI, 2022). We generated a report of invasive angiosperms listed on the CABI Horizon Scanning Tool in May 2022 using the filters (1) datasheet type: 'invasive species' and (2) sub-phylum: 'Angiospermae'. The search yielded 4807 species from 228 families that are broadly distributed across the angiosperm phylogeny, that are listed as invasive anywhere in the world. We used The Catalogue of Life Checklist Bank (Bánki et al., 2023) to exclude species listed multiple times under synonymous scientific names, resulting in 4630 species; then we extracted the 28 families from this list that are known to contain at least one species that exhibits a buzz pollination syndrome (from De Luca & Vallejo-Marín, 2013). We then conducted visual assessments of the floral morphology from online imagery for the 1231 species from the extracted 28 plant families, to individually examine whether each species had traits consistent with the buzz pollination syndrome (poricidal anthers or solanoid morphology). We reviewed the literature for species for which we could not assess the floral morphology from available online imagery to determine whether these species contained poricidal anthers, exhibited a solanoid floral morphology or had other evidence of buzz pollination recorded. We undertook two independent *Z*-tests to examine whether the proportion of invasive plants that exhibit the buzz pollination syndrome is significantly lower than the overall proportion of angiosperms that contain poricidal anthers. First, we compared only the percentage of invasive plants with poricidal anthers to the 6%–10% global estimate of angiosperms with poricidal anthers. Second, we compared the percentage of invasive plants with any trait representative of the buzz pollination syndrome, including all species with poricidal anthers, a solanoid morphology or species for which we could not infer the pollination syndrome to the 6%–10% global estimate of angiosperms with poricidal anthers. We found that 2.5% (117 of the 4630) of invasive species listed on the CABI Invasive Species Compendium have poricidal anthers, significantly less than global angiosperms with poricidal anthers (6%–10%; $z = -9.951$, df $= 1$, $p < 0.001$). We found that 2.9% (131 of the 4630) of invasive species listed on the CABI Invasive Species Compendium exhibited traits consistent with the buzz pollination syndrome. We were unable to infer the pollination syndrome of a further 31 species from eight families (Table S1; Lopresti et al., 2024); species-specific data on the floral morphology and pollen vectors were unavailable for these species and we could not confidently infer anther dehiscence from available online imagery. If we assumed all 31 of these unclassified species were buzz pollinated, it would bring the total to 162, or 3.5% of the CABI-listed angiosperm invaders ($z = -7.166$, df $= 1$, $p < 0.001$). Therefore, buzz-pollinated invasive plants are approximately two to four times less common than would be expected based on their proportional representation among the generality of angiosperms (2.5%–3.5% of 6%–10%). This supports our first hypothesis that buzz-pollinated plants are underrepresented among invasive species.

We acknowledge that the lack of available data on invasion opportunity and plant reproduction limits a robust test of our first hypothesis. Firstly, multiple complex interactions influence whether an introduced species will become invasive. For example, the number of introduction events (propagule pressure) is strongly and positively correlated with the establishment success of alien invasive species (Cassey et al., 2018). However, we currently lack data as to when many plant species are introduced, intentionally or unintentionally, into a new range (Pigot et al., 2017). Furthermore, pollination syndromes are an oversimplification of the interactions between plants and pollinators (reviewed by Dellinger, 2020). This oversimplification is true for the buzz pollination syndrome because not every plant with a solanoid morphology or poricidal anthers will be buzz pollinated, and some bees will buzz flowers that do not have a solanoid morphology or poricidal anthers (Buchmann et al., 1978). Data on the floral morphology, breeding system and specific pollinators, including the foraging behaviour of floral visitors for many plant species, are currently unavailable. For example, both Buchmann and Russell et al. estimated the number of angiosperm genera that contain at least one species with poricidal anther dehiscence but did not consider solanoid floral morphologies. Nevertheless, we assessed our results against the conservative estimate of 6%–10% of angiosperms that contain poricidal anthers, as this is the most precise estimate of buzz-pollinated angiosperms available. Given these gaps in the available data, a practical and achievable method to test our first hypothesis was to assess the floral phenotypes that typically are associated with the buzz pollination syndrome. However, it would be beneficial for future assessments to obtain a species-specific value of the number of angiosperms that have traits consistent with the buzz pollination syndrome.

3 | THE FACTORS THAT ALLOW BUZZ-POLLINATED PLANTS TO BECOME INVASIVE

3.1 | Uniparental reproduction in buzz-pollinated invasive plants

Some species that exhibit traits consistent with the invasive buzz pollination syndrome have become invasive (131 species listed on the CABI Invasive Species Compendium). Specialised pollination syndromes may not pose a barrier for invasive plants if they can reproduce in the absence of suitable pollinators. Most angiosperms are hermaphroditic (i.e. possess both male and female reproductive organs), but pre- and post-zygotic reproductive barriers can impede effective self-pollination. 'Genetically self-compatible' species are those that can set seed from self-pollen (autogamy). Genetically self-compatible species may still require a pollen vector due to the spatial (e.g. herkogamy or dioecious floral morphologies) or temporal (dichogamy) separation of the androecium and gynoecium. 'Functionally self-compatible' species can set seed autonomously in the absence of pollinators (e.g. apomictic reproduction or spontaneous selfing). Self-compatibility has been reported from at least 30 families of flowering plants, but it is less widespread than vegetative reproduction in vascular plants (Holsinger, 2000). Uniparental reproduction, including self-compatibility and vegetative reproduction, is expected to facilitate colonisation after long-distance seed dispersal of just one or a few propagules (Baker, 1955). However, fewer genotypes are typically present in progeny reared from uniparental reproductive pathways compared to conspecific outcrossed progeny, which can have long-term fitness consequences for populations including inbreeding depression (e.g. see Holsinger, 2000 review).

Baker's Law (Baker, 1955) is frequently cited in the context of biological invasions because uniparental reproduction is expected to help achieve reproductive assurance (Pannell et al., 2015; Rodger et al., 2010). Furthermore, depending on the strength of selection for traits related to higher reproductive assurance, it is expected that some invasive plants will shift towards increased self-compatibility in their non-native range. This shift may occur because genotypes that are more self-compatible will be selected for when suitable pollinators are scarce in the non-native range (Petanidou et al., 2012). Despite the potential long-term fitness consequences associated with uniparental reproduction (Holsinger, 2000), there is some empirical evidence of plants shifting mating systems upon introduction. For example, some populations of *Mimulus guttatus* (Phrymaceae) developed improved selfing ability over five generations after pollinators were excluded (Bodbyl Roels & Kelly, 2011). Yet, the degree to which reproductive assurance and shifts in mating systems enable plant invasions for species with specialised pollination syndromes has been largely unexplored.

To determine whether invasive plant species with a buzz pollination syndrome can reproduce in the absence of a pollinator, or shift towards increased autogamy upon introduction, we examined the reproductive biology of each of the invasive species listed in the CABI Invasive Species Compendium that likely exhibited a buzz pollination syndrome (i.e. species that contained poricidal anthers or a solanoid morphology). We excluded the 39 Araceae and two Mayacaceae invasive species from this subsequent assessment because despite these families commonly containing species with poricidal anthers, these species do not exhibit the buzz pollination syndrome (discussed in Buchmann, 1983). To collate information on the reproductive biology of each species, we searched Scopus and Web of Science using the search terms (Latin species name AND (breed* OR reproduct* OR pollinat*)) and obtained data from each species CABI profile (CABI, 2022). For all species, we included historical names from 1955 in the key search terms to account for studies published under older nomenclature undertaken since Baker's Law was first proposed (Baker, 1955). We also included historical and synonymous species names listed on The International Plant Names Index (IPNI, 2023) (Table S2; Lopresti et al., 2024). We extracted data on each species' breeding system, including assessments of genetic self-compatibility, functional self-compatibility (whether a pollinator is required for seed set), and whether the species can reproduce vegetatively in both its native and non-native ranges.

Breeding system data were available for 32 of the 92 invasive buzz-pollinated species (Table 1; Table S3). Regardless of the range (native or non-native), 97% of species (31 of the 32 species) were genetically self-compatible, that is, capable of setting at least some fruit or seed from pollen sourced from the same parent plant (Table 1; Table S3; Lopresti et al., 2024). This provides support for the reproductive assurance hypothesis. However, only 43% of species (10 of 23 species for which data were available) are functionally self-compatible, that is can set fruit in the absence of a pollinator, regardless of their range. This highlights the importance for some buzz-pollinated plants to establish new pollinator mutualisms for sexual reproduction in their non-native range. Vegetative reproduction data were available for 33 of the 92 species, and 66% (22 of the 33 species) of these species were capable of this form of asexual reproduction (Table 1).

Mating system data were available from both the native and non-native ranges for only three invasive buzz-pollinated species (*Solanum elaeagnifolium*, *S. rostratum* and *Rhododendron ponticum*) (Table S3; Lopresti et al., 2024), limiting our ability to make inferences about how frequently plasticity in the mating system can facilitate plant invasions for buzz-pollinated plants. Hand pollination experiments showed *S. elaeagnifolium* to have a mixed mating system in both native and non-native ranges, but a general shift from self-compatible (native range) to self-incompatible (non-native range) was apparent based on self-compatibility indices (Petanidou et al., 2012). In contrast, no shift in the mating system was apparent for *S. rostratum*, based on a comparison of multilocus

TABLE 1 Synthesis of the relative occurrence of different reproductive systems described for invasive plant species with buzz pollination syndromes.

Reproductive system	% (Total *N*)	Examples	References
Autogamy (genetically self-compatible)	97% (32)	*Solanum elaeagnifolium*	Petanidou et al. (2012)
		Chimaphila umbellata	Standley et al. (1988) and Barrett and Helenurm (1987)
		Ardisia crenata	Cheon et al. (2000)
Apomixis/Agamospermy (functionally self-compatible)	43% (23)	*Ardisia elliptica*	Pascarella (1997)
		Clidemia hirta	Melo et al. (1999)
		Cynoglossum officinale	Upadhyaya et al. (1988)
Asexual vegetative reproduction	66% (33)	Root fragmentation: *Ardisia crenata*	Roh et al. (2005)
		Rhizome: *Polygonatum multiflorum*	Kosiński (2015)
		Tuber: *Liriope spicata*	Nesom (2010)
Lacking data on breeding system	65% (92)	*Senna bacillaris*	Not applicable
		Senna bicapsularis	
		Melastoma septemnervium	

Note: The species richness of invasive buzz-pollinated plants is presented as a percentage (%) of total species for which data were available (Total *N*) and for which the relevant trait (e.g. self-compatibility) had been published. Note that the categories are not mutually exclusive and, thus, that the Total *N* does not equal 92. Species-specific reproductive biology data for each of the 92 buzz-pollinated invasive plants, including the range (native or non-native), is in Table S3 (Lopresti et al., 2024).

outcrossing rates for four populations in the native range (Vallejo-Marín et al., 2013) and 10 populations in the non-native range (Zhang et al., 2017), which suggests a mixed mating system for both ranges. Similarly, a pollinator exclusion experiment replicated in both the native and non-native ranges showed no shift in the mating system of *R. ponticum* (Erfmeier & Bruelheide, 2004). Thus, the few studies comparing the reproductive systems of buzz-pollinated invasive plants in both their native and non-native ranges illustrate two different outcomes: a shift towards reduced autogamy, and no change. However, the low number of studies available preclude any inference about the role of shifting mating systems in the context of plant invasions for buzz-pollinated plants. Future studies should compare the reproductive biology of invasive plants in both their native and non-native ranges to determine the extent to which the species is self-compatible and whether adaptive shifts towards increased self-compatibility in the non-native range could facilitate invasions.

3.2 | Broadening the functional groups of pollinators

Theoretically, pollination barriers for ecological and functional group specialists can be overcome if pollinators in the same functional group are already present in the species' non-native range, or if plants and pollinators are co-introduced (e.g. Liu & Pemberton, 2009; Rodger et al., 2010 and references therein). Females from over 11,600 species of bees can produce vibrations on flowers at a frequency that causes pollen release (vibratile pollen collection) (Vallejo-Marín & Vallejo, 2021) which is estimated to be just over half of the world's bee species (Orr et al., 2021; Pritchard & Vallejo-Marín, 2020). Buzzing bees have a global distribution and are present on every continent, excluding Antarctica (Russell, Buchmann, et al., 2024); therefore, it is likely that the buzz pollination syndrome is a geographically unrestricted specialisation. This could be an important factor in overcoming specialisation barriers for invasive buzz-pollinated plants. However, this requires synchronicity between the non-native plant's floral phenology and vibratile pollen-collecting bees. Local bee species richness and abundance can be highly dynamic and variable (Williams et al., 2001). Consequently, spatiotemporal mismatch may be more likely to occur where the plant is missing its coevolved pollinators in the non-native range compared to its native established pollinators. To our knowledge, whether an introduced plant has become invasive in the absence of buzz-pollinating fauna has not been examined.

Alternatively, invasive species with specialised pollination syndromes may overcome difficulties associated with establishing new mutualistic interactions in their non-native range via an increase in the diversity of functional groups able to pollinate them. This hypothesis implies that the buzz pollination syndrome does not inexorably require functional group specialisation, which has been previously hypothesised for a buzz-pollinated invasive plant (Solis-Montero et al., 2022). However, evidence of invasive plants benefitting from a broader range of their functional groups of pollinators is rare. One example is *Digitalis purpurea* (Foxglove), which exhibits a mellitophilous pollination syndrome: Its tubular flowers are adapted for pollination by long-tongued bees (Mackin et al., 2021). Foxglove is predominantly pollinated by bumble bees (*Bombus* species) in its native range in Western Europe (Best & Bierzychudek, 1982). Foxglove has become naturalised throughout much of the Americas, and a recent study found both bumble bees and hummingbirds to be key pollinators in its non-native range (Mackin et al., 2021).

Hummingbird pollination is resulting in rapid evolutionary shifts for foxglove's floral morphology, as hummingbirds are exerting a selection pressure that causes larger proximal corolla tubes in introduced foxglove flowers than those in the native range (Mackin et al., 2021). This shows that increased pollinator functional group diversity in non-native regions can facilitate plant invasions even for species with specialised pollination syndromes, which leads us to predict that buzz-pollinated plants can be pollinated by non-buzzing floral visitors upon introduction to a new region, in turn facilitating the plant invasion.

Vibratile pollen collection is frequently assumed to be the most efficient method of pollen extraction for plants with a buzz pollination syndrome (Buchmann, 1983); however, there are several other behaviours that insects use to extract pollen from plants with a buzz pollination syndrome. We systematically searched Scopus and Web of Science (March 2023) to obtain data on all known behaviours used to extract pollen from plants with a buzz pollination syndrome and assessed whether these are legitimate pollinators. The search terms 'TITLE-ABS-KEY ((buzz AND pollinat*) OR (poricidal AND anther) OR Solanoid AND behav*)' yielded 109 results. We extracted data on whether floral visitors carried pollen of the target plant, whether species contacted the stigma while foraging or deposited pollen on the stigma, and whether fruit was set following a single species visit to a flower and used these to distinguish floral visitors from the likely pollinators. We excluded studies in which the behaviour of the floral visitors was not described when assessing the pollinating abilities of floral visitors to plants with poricidal anthers because insect species capable of vibratile pollen collection may also exhibit non-buzzing foraging behaviours (e.g. Cortés-Rivas et al., 2022 found that *Bombus terrestris* only vibrated anthers in 45% of floral visits to blueberry crops).

The literature search revealed that pollen can be extracted from plants with a buzz pollination syndrome by two main categories of behaviour: buzzing (vibratile pollen collection) or non-buzzing. We summarised the descriptions of behaviours used to extract pollen from buzz-pollinated plants into eight different subcategories (Table 2). Vibratile pollen collection was the most common behaviour described in the literature. Vibrations can be produced by thoracic vibrations, in which floral visitors contact the flower, anther cone or single anther and vibrate thoracic muscles at high frequencies (~100–400 Hz) to expel pollen (Buchmann, 1983; Larson & Barrett, 1999; Switzer et al., 2016; Vallejo-Marín, 2019). Vibrations can also be produced by head-banging, in which the floral visitor repeatedly taps its head against anthers at a high frequency (~350 Hz) to expel pollen (Switzer et al., 2016). Behaviours for non-buzzing pollen collection included biting the tips of the anther ('biting') until pollen could be accessed, probing the proboscis inside the apical pore of anthers to scrape or lick the pollen ('scraping'), and using mandibles to squeeze the pollen out from the anther ('milking') (e.g. Thorp, 1979, 2000). Despite the range of known behaviours used to extract pollen from buzz-pollinated plants, there has been some assertion that buzz-pollinated plants require a buzzing insect to extract pollen. For example, some studies state that a 'buzzing' or 'sonicating' insect is required to extract pollen from plants with a buzz pollination syndrome (e.g. Olesen & Dupont, 2006; Switzer et al., 2019; Tayal & Kariyat, 2021). Consequently, non-buzzing insects are not always considered pollinators when examining the pollinators of plants with a buzz pollination syndrome (e.g. Cardoso et al., 2018; Oliveira et al., 2016; Tavares et al., 2018), potentially contributing to the under-reporting of pollinator diversity in these studies.

Non-buzzing insects are frequently observed to forage on plants with poricidal anthers, yet few studies have compared the pollinating abilities of both non-buzzing and buzzing insects that forage on plants with poricidal anthers. Our search yielded 12 studies that compared the reproductive success of one or multiple plant species following floral visits by both buzzing and non-buzzing floral visitors. All of these 12 studies found that plants with poricidal anthers benefitted from both pollinator behaviours (Table 3). Studies that examined individual pollen loads or pollen fidelity to assess pollinator efficiency found that non-buzzing pollinators do carry the pollen from the target plant (Cane et al., 1985; Estravis-Barcala et al., 2021; Gross, 1993; Moquet et al., 2017; Solís-Montero et al., 2015). However, buzzing pollinators carried significantly more pollen and demonstrated greater floral fidelity compared to non-buzzing pollinators, for seven of the eight plant species assessed. Similarly, many studies have assessed the effects of managed and wild pollinators on crop species with poricidal anthers and have found that flowers visited by managed honey bees, which do not produce floral vibrations, still result in fruit and seed set in blueberry (*Vaccinium* species; reviewed by Eeraerts et al., 2023) and tomato (*Solanum lycopersicum*; reviewed by Cooley & Vallejo-Marin, 2021) crops. A meta-analysis of fruit set following visits by non-buzzing and buzzing insects to tomato crops found fruit weight to be significantly greater following pollination by buzzing bees, compared to non-buzzing *Apis* species (Cooley & Vallejo-Marin, 2021). Collectively, these studies demonstrate that buzzing is an efficient behaviour to extract pollen from poricidal anthers, but not a requirement to access the pollen.

Furthermore, every assessment of fruit yield (fruit set, size or weight) or seed set following visits by buzzing and non-buzzing pollinators in these 12 studies has shown that fruit set can result from floral visits by non-buzzing pollinators (Table 3). Yet, comparisons of fruit yield and seed set following visits by buzzing and non-buzzing insects have produced variable results. For example, De Araujo Campos et al. (2022) compared fruit yield following a single floral visit and examined whether floral visitors contacted the stigma while foraging to distinguish floral visitors from pollinators. Fruit yield was greatest following pollination by the buzzing *Xylocopa* species; however, there was no significant difference between some other buzzing and non-buzzing floral visitors. The number and size of fruits set when pollinated by the buzzing *Euglossa* species and the non-buzzing *Paratrigona* species did not significantly differ. *Paratrigona* species were observed milking the flowers, and they spent longer foraging on each flower compared to buzzing bees. The authors proposed that longer foraging bouts may compensate for the non-buzzing behaviour by increasing the

TABLE 2 A summary of documented insect behaviours (buzzing and non-buzzing) used to extract pollen from plants exhibiting the buzz pollination syndrome with numbers of published studies (*N*) for each behaviour.

Insect behaviour	Synonym(s)	Explanation	Count (*N*)	Plant fitness metric studied and supported (*N*)			Pollinator
				Carrying pollen	Stigma contact	Fruit set	
Buzzing	Vibratile pollen collection	Floral visitors contact the flower, anther cone or single anther and produce high-frequency vibrations (via thoracic muscles ~100–400 Hz; Vallejo-Marín, 2019, or head-banging behaviour ~350 Hz; Switzer et al., 2016) to expel pollen.	94	20	12	9	Likely
Non-buzzing							
Biting	Cutting Perforating Chewing Slicing	Chewing a new hole or probing an existing hole either through the side of the anther or from the apical tip and extracting pollen with the proboscis (Cane et al., 1983; Harter et al., 2002; Mesquita-Neto et al., 2018; Nogueira et al., 2018; Roubik et al., 1982; Staines et al., 2017; Wille, 1963)	13	2	4	1	Likely
Drumming	–	Drumming flower with forelegs to release pollen (repeated and alternate blows to anther) (Cane, 2014)	1	NS	NS	NS	Unknown
Gleaning	Scavenging Collecting	Collecting residual pollen grains after foraging by another (typically sonicating) species (Baker, 1965; Gao et al., 2006; Harter et al., 2002; Luo & Zhang, 2008; Ranieri et al., 2013; Roubik et al., 1982; Tavares et al., 2018)	12	NS	4	NS	Likely
Licking	Scraping (Santos et al., 2014)	Inserts glossa inside the apical pore and removes the pollen grains directly from the anther	2	NS	NS	NS	Unknown
Milking	–	Squeezing the mandibles around the base of the anther and sliding the trapped pollen towards the apical pore for collection (De Araujo Campos et al., 2022; Luo & Zhang, 2008)	4	NS	1	1	Likely
Non-buzzing (undescribed)	–	No further description was provided (e.g. Cortés-Rivas et al., 2022; Moquet et al., 2017; Roubik et al., 1982)	18	6	5	4	Variable (species-specific)
Scraping	Scratching	Scraping (or scratching) the surface of the anthers to collect pollen (Dieringer & Cabrera, 2022; Udayakumar et al., 2021)	5	1	NS	NS	Unknown

Note: For each behaviour, we list the number of studies (*N*) in which the species carried pollen of the target plant, whether the species contacted the stigma while foraging or deposited pollen on the stigma, or whether fruit was set after a visit to a virgin flower. (NS, not studied). All studies that have included non-buzzing pollinators in these analyses have found, to some degree, support for the relevant pollinator inference (further detailed in Table 3). We assess whether the floral visitor is likely to be a pollinator based on the plant fitness metrics.

TABLE 3 A summary of studies that have included non-buzzing floral visitors in an analysis of pollinators of plants with poricidal anthers.

Non-buzzing foraging behaviour(s)	Likely pollinators	Plant species (family)	Response variable	Buzzing vs. non-buzzing statistical comparison	Notes	Additional factors contributing to the pollination success of non-buzzing floral visitors	Reference
Biting, gleaning, milking	Yes	*Solanum melongena* L. (Solanaceae)	Fruit yield (set and size) following a single floral visit.	Variable	This study included a pollinator exclusion experiment. Visits from non-buzzing floral visitors, and some buzzing floral visitors, did not result in a significantly greater fruit set than the pollinator exclusion treatment	Visitation frequency	De Araujo Campos et al. (2022)
Biting, gleaning	Variable	*Melastoma affine* (Melastomataceae)	Pollen load and stigma contact	Buzzer superior	Most non-buzzing insects were not observed to contact the stigma while foraging and thus are unlikely to be pollinators. Non-buzzing *Apis mellifera* were observed to gather previously deposited pollen from stigmas and did, on occasion contact the stigma, however the authors state these are likely to be robbers, not pollinators	Handling time per flower; Insect size relative to flower size.	Gross (1993)
Biting, gleaning	Variable	*Chamaecrista debilis* (Vogel) H.S.Irwin & Barneby (Fabaceae) *Chamaecrista desvauxii* (Collad.) Killip. (Fabaceae) *Comolia stenodon* (Naudin) Triana (Melastomataceae) *Lavoisiera imbricata* DC. (Melastomataceae) *Leandra aurea* (Cham.) Cogn. (Melastomataceae) *Macairea radula* (Bonpl.) DC. (Melastomataceae) *Miconia albicans* (Sw.) Steud. (Melastomataceae) *Pterolepis alpestris* Triana (Melastomataceae) *Tococa guianensis* Aubl. (Melastomataceae) *Ouratea floribunda* Engl. (Ochnaceae)	Stigma contact	Not assessed	Across all plant species combined, flower-buzzing, anther-buzzing and non-buzzing bees had legitimate visits, touching the stigma in 97%, 28% and 8% of all visits, respectively	Floral constancy	Mesquita-Neto et al. (2018)

TABLE 3 (Continued)

Non-buzzing foraging behaviour(s)	Likely pollinators	Plant species (family)	Response variable	Buzzing vs. non-buzzing statistical comparison	Notes	Additional factors contributing to the pollination success of non-buzzing floral visitors	Reference
Milking	Yes	*Vaccinium stamineum* (Ericaceae)	Pollen load and fruit set following a single floral visit.	Not assessed		Floral constancy; abundance	Cane et al. (1985)
Licking	Yes	*Solanum lycopersicum* L. (Solanaceae)	Fruit yield (size and seed set) following a single floral visit	Variable	Single visit test with non-buzzing *A. mellifera* compared to open control (buzzing or non-buzzing visitors allowed); the number of seeds, and fruit mass was greater in the control compared to single visit test, but the longitudinal diameter of the fruits did not significantly differ between the treatments	Abundance	Bartelli et al. (2021)
Nondescript	Yes	*Vaccinium corymbosum* (Ericaceae)	Conspecific pollen deposition on stigmas following a single visit.	Buzzer superior		Visitation frequency	Cortés-Rivas et al. (2022)
Nondescript	Yes	*Erica tetralix* (Ericaceae) *Vaccinium myrtillus* (Ericaceae) *Vaccinium vitis-idaea* (Ericaceae)	Pollen load and pollen deposition on the stigma following a single floral visit.	Buzzer superior No difference Buzzer superior		Pollen purity	Moquet et al. (2017)
Nondescript	Yes	*Solanum melongena* (Solanaceae)	Fruit yield (size and weight) following a single, or multiple, floral visits.	Variable	Fruit length did not statistically differ between buzzing and non-buzzing floral visits; buzzers produced statistically heavier fruits than non-buzzers in some treatments. Overall, fruit length and weight were greatest when the flower was visited by both buzzing and non-buzzing species		Paschapur et al. (2022)
Nondescript	Yes	*Vaccinium* sp. (Ericaceae)	Pollen deposition on the stigma following a single floral visit and fruit yield (weight, size and seed set) following a single floral visit.	Variable	Significantly more pollen was deposited on the stigma when buzzing insects foraged compared to non-buzzing pollinators; however, fruit yield was variable	Handling time per flower	Sun et al. (2021)

(Continues)

TABLE 3 (Continued)

Non-buzzing foraging behaviour(s)	Likely pollinators	Plant species (family)	Response variable	Buzzing vs. non-buzzing statistical comparison	Notes	Additional factors contributing to the pollination success of non-buzzing floral visitors	Reference
Nondescript	Yes	*Vaccinium corymbosum* 'San Joaquín' (Ericaceae) *Vaccinium corymbosum* 'Emerald' (Ericaceae)	Pollen load.	Buzzer superior	Buzzing pollinators carried 10× more pollen than non-buzzing pollinators	Abundance and floral constancy	Estravis-Barcala et al. (2021)
Nondescript	Yes	*Solanum rostratum* (Solanaceae)	Pollen fidelity and stigma contact.	Not assessed	Illegitimate and legitimate floral visitors were compared; both buzzing and non-buzzing behaviours were classed as 'legitimate' pollinators for some species	Insect size relative to flower size	Solís-Montero et al. (2015)
Nondescript	Inferred	*Rhexia virginica* (Melastomataceae)	Pollen removal	Not assessed	A large amount of pollen could be removed without buzzing (artificial tapping). The authors used this to infer that the non-buzzing visitors observed likely removed pollen		Larson and Barrett (1999)

Note: For each plant species studied the response variable(s) used to evaluate pollinator efficiency (plant fitness metric), and a description of the observed non-buzzing foraging behaviours (referred to as 'nondescript' when the non-buzzing behaviour was not further described for a particular pollinator) are detailed. We assess whether non-buzzing floral visitors are likely to be pollinators based on the reported findings in each study. We indicate whether the plant fitness metrics were significantly different between buzzing and non-buzzing insects. Studies that examined multiple plant fitness response variables and produced inconsistent conclusions we denoted as 'variable' (further details can be found in the Notes column). Additional factors that were assessed or discussed in each study that may have contributed to the success of the non-buzzing pollinators are noted.

amount of pollen deposited on the stigma as the insect milked the anther (De Araujo Campos et al., 2022).

Despite there being few studies that have compared the pollinator efficiency of buzzing and non-buzzing insects for plants with a buzz pollination syndrome, the examples in Table 3 demonstrate that vibratile pollen release is not a requirement for pollination for plants exhibiting the buzz pollination syndrome. These results are consistent with many other studies that have assessed the pollinator efficiency of managed honey bees, which are unable to buzz flowers, in agroecosystems for crop species that have poricidal anthers (e.g. Estravis-Barcala et al., 2021; Goodman & Clayton-Greene, 1988; Macfarlane, 1992; Stubbs & Drummond, 1997). Agricultural studies have been at the forefront of investigating the efficacy of non-buzzing floral visitors on plant reproduction; however unless the foraging behaviour of the floral visitors was described in the study, we excluded it from our systematic search, as species capable of vibratile pollen collection may not exhibit this behaviour every floral visit (e.g. Cortés-Rivas et al., 2022). Non-buzzing insect pollination of buzz-pollinated invasive plants will be relevant where buzzing species may be absent, less abundant or not attracted to newly introduced plant species. Consequently, the use of the terms 'buzz-pollination syndrome' and 'buzz-pollination' warrants caution. Vallejo-Marín (2019) defines 'buzz-pollinated' as 'used implicitly to describe flowers that have obvious features that are likely to be adaptations to buzz-pollination' and 'buzz-pollination' as 'the type of pollination in which bees pollinate flowers while vibrating the flowers to extract pollen.' Based on the results here, we add to this definition that vibrating is only one of several potential behaviours that insects can display to access the pollen of plants presenting the buzz pollination syndrome (De Luca & Vallejo-Marín, 2013; Thorp, 1979, 2000).

Careful observations of foraging behaviour, as opposed to characterisation as buzzing or not buzzing, may yield further insights into which insect species are mere floral visitors and which are pollinators (Solis-Montero & Vallejo-Marin, 2017). Studies comparing the pollination efficiency of all floral visitors, buzzing and non-buzzing, in both the native and non-native ranges of invasive buzz-pollinated plants are currently missing, and will provide further fundamental information about how buzz-pollinated invasive plants overcome difficulties associated with setting outcrossed seed in their non-native range.

4 | CONCLUSIONS

The disproportionate number of invasive plant species that present the buzz pollination syndrome suggests that this specialisation poses a partial barrier to plant invasions; invasive buzz-pollinated plants are approximately two to four times less common than they occur in global angiosperm taxa. Regardless of the floral traits that we use to infer the buzz pollination syndrome (i.e. only poricidal anthers or poricidal anthers, solanoid morphology and species in which we cannot confidently infer their pollination syndrome), plants that exhibit traits consistent with the buzz pollination syndrome are underrepresented as invasive species across the globe, providing support for our first hypothesis.

Our review also highlighted some of the mechanisms that can enable invasive plants with the specialised buzz-pollinated pollination syndrome to effectively reproduce in their non-native range. The success of invasive buzz-pollinated plants may be a consequence of the global distribution of bee species capable of vibratile pollen collection, in what could be considered a geographically unrestricted specialisation. We found that up to 97% (31/32) of invasive buzz-pollinated plants were genetically self-compatible, providing support for the reproductive assurance hypothesis. However, just 43% (10/23) of these genetically self-compatible buzz-pollinated invasive plants set fruit in the absence of a pollinator. As such, most invasive buzz-pollinated plants still need pollinators for sexual reproduction. The success of invasive plants with buzz pollination syndromes may be a result of a combination of buzz pollination behaviour and a diverse range of other behaviours that insects can use to access pollen.

Studies that compare the reproductive biology and ecology of buzz-pollinated plants in both their native and non-native ranges will be most informative for determining the suite of factors that contribute to buzz-pollinated plant invasions. We expected that plants with specialist pollinators may shift their mating systems towards higher self-compatibility during introductions, thereby facilitating plant invasions. To assess the frequency at which species shift their mating system, common pollinator exclusion experiments need to be undertaken in both the native and non-native ranges of invasive buzz-pollinated plants. Furthermore, studies should include a robust analysis to distinguish floral visitors, pollen thieves and effective pollinators in both the native and non-native range of buzz-pollinated plants to assess whether unorthodox pollinator behaviours are more important in the non-native range, thereby facilitating plant invasions. Simultaneous assessments of these processes will shed light onto some of the factors that unfold and contribute to the spread of alien invasive species.

AUTHOR CONTRIBUTIONS

Laura C. Lopresti, Lori Lach and Daniel Montesinos conceived the study. Laura C. Lopresti undertook the data consolidation and drafted the manuscript. Lori Lach and Daniel Montesinos contributed substantially to revisions and gave final approval for submission.

ACKNOWLEDGEMENTS

We thank Lucinda Charles and Anna Page for assistance with the CABI Invasive Species Compendium database, Mario Vallejo-Marin for discussions during the early stages of the review and comments on the manuscript, Stephen Buchmann and Avery Russell for sharing their unpublished list of plant genera containing species with poricidal anthers and two anonymous reviewers for their comments and insights which significantly improved our review. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Laura C. Lopresti was supported by the Australian Government Research Training Program Scholarship.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14338.

DATA AVAILABILITY STATEMENT

The data sets generated during the current study are archived in the Research Data Australia repository and are publicly available: https://doi.org/10.25903/hvd5-v603 Lopresti et al. (2024).

STATEMENT ON INCLUSION

This study was a global review and based on secondary data sourced from both published research and grey literature. Consequently, there was no local data collection. However, we included data from peer-reviewed studies published in local languages (English, Portuguese and Spanish) and ensured the appropriate interpretation of data and results from these studies to support a more global representation in ecology.

ORCID

Laura C. Lopresti https://orcid.org/0000-0002-9016-744X
Lori Lach https://orcid.org/0000-0001-5137-5185
Daniel Montesinos https://orcid.org/0000-0003-2893-0878

REFERENCES

Armbruster, W. S. (2017). The specialization continuum in pollination systems: Diversity of concepts and implications for ecology, evolution and conservation. *Functional Ecology*, *31*, 88–100. https://doi.org/10.1111/1365-2435.12783

Armbruster, W. S., Edwards, M. E., & Debevec, E. M. (1994). Floral character displacement generates assemblage structure of Western Australian Triggerplants (*Stylidium*). *Ecology*, *75*, 315–329. https://doi.org/10.2307/1939537

Baker, H. (1955). Self-compatibility and establishment after 'long-distance' dispersal. *Evolution*, *9*, 347. https://doi.org/10.2307/2405656

Baker, H. G. (1965). Characteristics and modes of origin of weeds. In H. G. Baker & G. L. Stebbins (Eds.), *The genetics of colonizing species* (pp. 147–172). Academic Press.

Baker, H. G. (1974). The evolution of weeds. *Annual Review of Ecology, Evolution, and Systematics*, *5*, 1–24.

Baker, H. G. (1986). *Yuccas* and yucca moths—A historical commentary. *Annals of the Missouri Botanical Garden*, *73*, 556. https://doi.org/10.2307/2399193

Bánki, O., Roskov, Y., Döring, M., Ower, G., Vandepitte, L., Hobern, D., Remsen, D., Schalk, P., DeWalt, R. E., Keping, M., Miller, J., Orrell, T., Aalbu, R., Abbott, J., Adlard, R., Adriaenssens, E. M., Aedo, C., Aescht, E., Akkari, N., … Şentürk, O. (2023). *Catalogue of life checklist* (version 2023-02-07). Catalogue of Life. https://doi.org/10.48580/dfrq

Barrett, S. C. H., & Helenurm, K. (1987). The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Canadian Journal of Botany*, *65*, 2036–2046. https://doi.org/10.1139/b87-278

Bartelli, B. F., Guimarães, B. M. D. C., Borges, N. C. M., & Nogueira-Ferreira, F. H. (2021). Not all about the buzz: Licking, a new foraging behavior of bees in tomato flowers. *Journal of Apicultural Research*, *63*, 1–8. https://doi.org/10.1080/00218839.2021.1954810

Best, L. S., & Bierzychudek, P. (1982). Pollinator foraging on foxglove (*Digitalis purpurea*): A test of a new model. *Evolution*, *36*, 70–79. https://doi.org/10.2307/2407968

Bodbyl Roels, S. A., & Kelly, J. K. (2011). Rapid evolution caused by pollinator loss in *Mimulus guttatus*. *Evolution*, *65*, 2541–2552. https://doi.org/10.1111/j.1558-5646.2011.01326.x

Brundrett, M. (2021). One biodiversity hotspot to rule them all: Southwestern Australia-an extraordinary evolutionary centre for plant functional and taxonomic diversity. *Journal of the Royal Society of Western Australia*, *104*, 91–122.

Buchmann, S. L. (1983). Buzz pollination in angiosperms. In C. E. Jones & R. J. Little (Eds.), *Handbook of experimental pollination biology* (pp. 73–113). Van Nostrand Reinhold.

Buchmann, S. L., Jones, C. E., & Colin, L. J. (1978). Vibratile pollination of *Solanum douglassii* Dunal and *S. xanti* Gray (Solanaceae) in southern California. *The Wasmann Journal of Biology*, *35*(1), 1.

CABI. (2018). *Invasive species data*. CAB International. https://www.cabi.org/projects/invasive-species-data/

CABI. (2022). *Invasive species compendium*. CAB International. www.cabi.org/isc

Cane, J. H. (2014). The oligolectic bee *Osmia brevis* sonicates *Penstemon* flowers for pollen: A newly documented behavior for the Megachilidae. *Apidologie*, *45*(6), 678–684. https://doi.org/10.1007/s13592-014-0286-1

Cane, J. H., Eickwort, G. C., Wesley, F. R., & Spielholz, J. (1983). Foraging, grooming and mate-seeking behaviors of *Macropis nuda* (Hymenoptera, melittidae) and use of *Lysimachia ciliata* (Primulaceae) oils in larval provisions and cell linings. *The American Midland Naturalist*, *110*, 257–264. https://doi.org/10.2307/2425267

Cane, J. H., Eickwort, G. C., Wesley, F. R., & Spielholz, J. (1985). Pollination ecology of *Vaccinium stamineum* (Ericaceae: Vaccinioideae). *American Journal of Botany*, *72*, 135–142.

Cardoso, J. C. F., de Deus, F. F., Silva, S. C. S., & Oliveira, P. E. (2018). Bow to the middle: Reproductive system and style behaviour of *Tococa guianensis*, a widespread Melastomataceae from the neotropics. *Plant Systematics and Evolution*, *304*, 259–267. https://doi.org/10.1007/s00606-017-1473-0

Cassey, P., Delean, S., Lockwood, J. L., Sadowski, J. S., & Blackburn, T. M. (2018). Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. *PLoS Biology*, *16*, e2005987. https://doi.org/10.1371/journal.pbio.2005987

Cheon, C. P., Chung, M., & Chung, M. G. (2000). Allozyme and clonal diversity in Korean populations of *Ardisia japonica* and *Ardisia crenata* (Myrsinaceae). *Israel Journal of Plant Sciences*, *48*, 239–245. https://doi.org/10.1560/V7M9-RWQM-H0NF-L14V

Cooley, H., & Vallejo-Marin, M. (2021). Buzz-pollinated crops: A global review and meta-analysis of the effects of supplemental bee pollination in tomato. *Journal of Economic Entomology*, *114*(2), 505–519. https://doi.org/10.1093/jee/toab009

Cortés-Rivas, B., Smith-Ramirez, C., Monzón, V. H., & Mesquita-Neto, J. N. (2022). Native bees with floral sonication behaviour can achieve high-performance pollination of highbush blueberry in Chile. *Agricultural and Forest Entomology*, *25*(1), 91–102. https://doi.org/10.1111/afe.12533

Darwin, C. R. (1876). *The effects of cross and self fertilisation in the vegetable kingdom*. John Murray.

De Araujo Campos, G. P., Barros, C. T., Carneiro, L. T., Santa-Martinez, E., de Oliveira Milfont, M., & Castro, C. C. (2022). Pollinator efficiency in openly grown eggplants: Can non-vibrating bees produce high-quality fruits? *Arthropod-Plant Interactions*, *16*, 159–170. https://doi.org/10.1007/s11829-022-09885-1

De Luca, P. A., & Vallejo-Marín, M. (2013). What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology*, *16*, 429–435. https://doi.org/10.1016/j.pbi.2013.05.002

Dellinger, A. S. (2020). Pollination syndromes in the 21st century: Where do we stand and where may we go? *New Phytologist*, *228*, 1193–1213. https://doi.org/10.1111/nph.16793

Dieringer, G., & Cabrera, R. L. (2022). Stamen dimorphism, bee visitation, and pollen removal in three species of *Agalinis* (Orobanchaceae). *Botany*, *100*, 377–386. https://doi.org/10.1139/cjb-2021-0110

Eeraerts, M., DeVetter, L. W., Batáry, P., Ternest, J. J., Mallinger, R., Arrington, M., Benjamin, F. E., Blaauw, B. R., Campbell, J. W., Cavigliasso, P., Daniels, J. C., de Groot, G. A., Ellis, J. D., Gibbs, J., Goldstein, L., Hoffman, G. D., Kleijn, D., Melathopoulos, A., Miller, S. Z., … Isaacs, R. (2023). Synthesis of highbush blueberry pollination research reveals region-specific differences in the contributions of honeybees and wild bees. *Journal of Applied Ecology*, *60*(12), 2528–2539. https://doi.org/10.1111/1365-2664.14516

Erfmeier, A., & Bruelheide, H. (2004). Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora—Morphology, Distribution, Functional Ecology of Plants*, *199*(2), 120–133. https://doi.org/10.1078/0367-2530-00141

Estravis-Barcala, M. C., Palottini, F., Macri, I., Nery, D., & Farina, W. M. (2021). Managed honeybees and South American bumblebees exhibit complementary foraging patterns in highbush blueberry. *Scientific Reports*, *11*, 8187. https://doi.org/10.1038/s41598-021-87729-3

Gao, J.-Y., Ren, P.-Y., Yang, Z.-H., & Li, Q.-J. (2006). The pollination ecology of *Paraboea rufescens* (Gesneriaceae): A buzz-pollinated tropical herb with mirror-image flowers. *Annals of Botany*, *97*, 371–376. https://doi.org/10.1093/aob/mcj044

Global Invasive Species Database. (2024). Species profile: *Clidemia hirta*. http://www.iucngisd.org/gisd/species.php?sc=53

Goodman, R., & Clayton-Greene, K. (1988). Honeybee pollination of highbush blueberries (*Vaccinium corymbosum*). *Australian Journal of Experimental Agriculture*, *28*(2), 287–290. https://doi.org/10.1071/EA9880287

Gross, C. L. (1993). The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a Pioneer shrub in tropical Australia. *Biotropica*, *25*, 468–474. https://doi.org/10.2307/2388870

Harter, B., Leistikow, C., Wilms, W., Truylio, B., & Engels, W. (2002). Bees collecting pollen from flowers with poricidal anthers in a south Brazilian *Araucaria* forest: A community study. *Journal of Apicultural Research*, *41*, 9–16. https://doi.org/10.1080/00218839.2002.11101063

Hingston, A. (2002). *Pollination ecology of Eucalyptus globulus subsp. globulus and Eucalyptus nitens (Myrtaceae)* (PhD thesis). Centre for Environmental Studies, University of Tasmania.

Holsinger, K. E. (2000). Reproductive systems and evolution in vascular plants. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(13), 7037–7042. https://doi.org/10.1073/pnas.97.13.7037

IPNI. (2023). *International plant names index*. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium. http://www.ipni.org

Kosiński, I. (2015). Ontogenetic development and maturity of individuals of *Polygonatum multiflorum*. *Flora—Morphology, Distribution, Functional Ecology of Plants*, *216*, 1–5.

Larson, B. M., & Barrett, S. C. (1999). The pollination ecology of buzz-pollinated *Rhexia virginica* (Melastomataceae). *American Journal of Botany*, *86*, 502–511.

Liu, H., & Pemberton, R. W. (2009). Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive Solanum. *Oecologia*, *159*, 515–525. https://doi.org/10.1007/s00442-008-1232-6

Lopresti, L., Lach, L., & Montesinos, D. (2024). *The specialised buzz-pollination syndrome poses a partial barrier to plant invasions*. James Cook University. https://doi.org/10.25903/hvd5-v603

Luo, Z., & Zhang, R. (2008). Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. *Functional Ecology*, *22*, 794–800. https://doi.org/10.1111/j.1365-2435.2008.01444.x

Luque, G. M., Bellard, C., Bertelsmeier, C., Bonnaud, E., Genovesi, P., Simberloff, D., & Courchamp, F. (2014). The 100th of the world's worst invasive alien species. *Biological Invasions*, *16*, 981–985. https://doi.org/10.1007/s10530-013-0561-5

Macfarlane, R. P. (1992). An initial assessment of blueberry pollinators in New Zealand. *New Zealand Journal of Crop and Horticultural Science*, *20*(1), 91–95. https://doi.org/10.1080/01140671.1992.10422331

Mackin, C. R., Peña, J. F., Blanco, M. A., Balfour, N. J., & Castellanos, M. C. (2021). Rapid evolution of a floral trait following acquisition of novel pollinators. *Journal of Ecology*, *109*, 2234–2246. https://doi.org/10.1111/1365-2745.13636

Melo, G. F., Machado, I. C., & Luceño, M. (1999). Reprodución de tres especies de *Clidemia* (Melastomataceae) en Brasil. *Revista de Biología Tropical*, *47*, 359–363.

Mesquita-Neto, J. N., Blüthgen, N., & Schlindwein, C. (2018). Flowers with poricidal anthers and their complex interaction networks—Disentangling legitimate pollinators and illegitimate visitors. *Functional Ecology*, *32*, 2321–2332. https://doi.org/10.1111/1365-2435.13204

Moquet, L., Bruyère, L., Pirard, B., & Jacquemart, A. L. (2017). Nectar foragers contribute to the pollination of buzz-pollinated plant species. *American Journal of Botany*, *104*(10), 1451–1463. https://doi.org/10.3732/ajb.1700090

Nesom, G. L. (2010). Overview of *Liriope* and *Ophiopogon* (Ruscaceae) naturalized and commonly cultivated in the USA. *Phyton*, *56*, 1–31.

Nogueira, A., Valadão-Mendes, L. B., El Ottra, J. H. L., Guimarães, E., Cardoso-Gustavson, P., Quinalha, M. M., Paulino, J. V., & Rando, J. G. (2018). Relationship of floral morphology and development with the pattern of bee visitation in a species with pollen-flowers, *Chamaecrista desvauxii* (Fabaceae). *Botanical Journal of the Linnean Society*, *187*, 137–156. https://doi.org/10.1093/botlinnean/boy008

Olesen, J., & Dupont, Y. (2006). Andromonoecy and buzz-pollination in *Solanum* species (Solanaceae) endemic to the Canary Islands. *Anales del Jardin Botánico de Madrid*, *63*, 63–66. https://doi.org/10.3989/ajbm.2006.v63.i1.35

Oliveira, F. D. S., Ribeiro, M. H. M., Nunez, C. V., & Albuquerque, P. M. C. (2016). Flowering phenology of *Mouriri guianensis* (Melastomataceae) and its interaction with the crepuscular bee *Megalopta amoena* (Halictidae) in the restinga of Lençóis Maranhenses National Park, Brazil. *Acta Amazonica*, *46*(3), 281–290. https://doi.org/10.1590/1809-4392201504853

Ollerton, J., Killick, A., Lamborn, E., Watts, S., & Whiston, M. (2007). Multiple meanings and modes: On the many ways to be a generalist flower. *Taxon*, *56*, 717–728. https://doi.org/10.2307/25065855

Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C.-D., & Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Current Biology*, *31*, 451–458. https://doi.org/10.1016/j.cub.2020.10.053

Palchetti, M. V., Cantero, J. J., & Barboza, G. E. (2020). Solanaceae diversity in South America and its distribution in Argentina. *Annals of the*

Brazilian Academy of Sciences, *92*(2), e20190017. https://doi.org/10.1590/0001-3765202020190017

Pannell, J. R., Auld, J. R., Brandvain, Y., Burd, M., Busch, J. W., Cheptou, P.-O., Conner, J. K., Goldberg, E. E., Grant, A.-G., Grossenbacher, D. L., Hovick, S. M., Igic, B., Kalisz, S., Petanidou, T., Randle, A. M., de Casas, R. R., Pauw, A., Vamosi, J. C., & Winn, A. A. (2015). The scope of Baker's law. *New Phytollogist*, *208*, 656–667. https://doi.org/10.1111/nph.13539

Pascarella, J. B. (1997). Breeding systems of *Ardisia* Sw. (Myrsinaceae). *Brittonia*, *49*, 45–53. https://doi.org/10.2307/2807693

Paschapur, A. M., Baht, S., Subhanna, A. R. N. S., Hedau, N. K., Mishra, K. K., & Kant, L. (2022). Insect pollinators of eggplant (*Solanum melongena* L.) in the Indian Himalayas and their role in enhancement of fruit quality and yield. *Arthropod-Plant Interactions*, *16*(3–4), 349–360. https://doi.org/10.1007/s11829-022-09902-3

Petanidou, T., Godfree, R. C., Song, D. S., Kantsa, A., Dupont, Y. L., & Waser, N. M. (2012). Self-compatibility and plant invasiveness: Comparing species in native and invasive ranges. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*, 3–12. https://doi.org/10.1016/j.ppees.2011.08.003

Pigot, A. L., Cassey, P., & Blackburn, T. M. (2017). How to incorporate information on propagule pressure in the analysis of alien establishment success. *Methods in Ecology and Evolution*, *9*, 1097–1108. https://doi.org/10.1111/2041-210X.12930

Pritchard, D. J., & Vallejo-Marín, M. (2020). Buzz-pollination. *Current Biology*, *30*, R858–R860. https://doi.org/10.1016/j.cub.2020.05.087

Ranieri, B. D., Silveira, F. A. O., & Franceschinelli, E. V. (2013). Biologia floral e comportamento de polinizadores de *Tococa guianensis* Aubl. (Melastomataceae). *Lundiana: International Journal of Biodiversity*, *11*, 3–8. https://doi.org/10.35699/2675-5327.2013.23831

Richardson, D. M., Allsopp, N., D'antonio, C. M., Milton, S. J., & Rejmánek, M. (2000). Plant invasions—The role of mutualisms. *Biological Reviews*, *75*, 65–93. https://doi.org/10.1017/S0006323199005435

Rodger, J. G., van Kleunen, M., & Johnson, S. D. (2010). Does specialised pollination impede plant invasions? *International Journal of Plant Sciences*, *171*, 382–391. https://doi.org/10.1086/651226

Roh, M. S., Lee, A.-K., & Suh, J.-K. (2005). Production of high quality *Ardisia* plants by stem tip cuttings. *Scientia Horticulturae*, *104*, 293–303. https://doi.org/10.1016/j.scienta.2004.09.001

Roubik, D. W., Ackerman, J. D., Copenhaver, C., & Smith, B. H. (1982). Stratum, tree, and flower selection by tropical bees: Implications for the reproductive biology of outcrossing *Cochlospermum vitifolium* in Panama. *Ecology*, *63*, 712–720. https://doi.org/10.2307/1936792

Russell, A. L., Buchmann, S. L., Ascher, J. S., Wang, Z., Kriebel, R., Jolles, D. D., Orr, M. C., & Hughes, A. C. (2024). Buzz-world: Global patterns and drivers of buzzing bees and poricidal plants. *bioRxiv*, 2024.03.06.583730. https://doi.org/10.1101/2024.03.06.583730

Russell, A. L., Zenil-Ferguson, R., Buchmann, S. L., Jolles, D. D., Kriebel, R., & Vallejo-Marin, M. (2024). Widespread evolution of poricidal flowers: A striking example of morphological convergence across flowering plants. *bioRxiv*, 2024.02.28.582636. https://doi.org/10.1101/2024.02.28.582636

Santos, A. O. R., Bartelli, B. F., & Nogueira-Ferreira, F. H. (2014). Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. *Journal of Economic Entomology*, *107*, 987–994. https://doi.org/10.1603/EC13378

Solis-Montero, L., & Vallejo-Marin, M. (2017). Does the morphological fit between flowers and pollinators affect pollen deposition? An experimental test in a buzz-pollinated species with anther dimorphism. *Ecology and Evolution*, *7*(8), 2706–2715. https://doi.org/10.1002/ece3.2897

Solis-Montero, L., Vega-Polanco, M., Vázquez-Sánchez, M., & Suárez-Mota, M. E. (2022). Ecological niche modelling of interactions in a buzz-pollinated invasive weed. *Global Ecology and Conservation*, *39*, e02279. https://doi.org/10.1016/j.gecco.2022.e02279

Solís-Montero, L., Vergara, C. H., & Vallejo-Marin, M. (2015). High incidence of pollen theft in natural populations of a buzz-pollinated plant. *Arthropod-Plant Interactions*, *9*(6), 599–611. https://doi.org/10.1007/s11829-015-9397-5

Staines, M., Vo, C., Puiu, N., Hayes, S., Tuiwawa, M., Stevens, M. I., & Schwarz, M. P. (2017). Pollen larceny of the tropical weed *Solanum torvum* by a Fijian endemic halictine bee with implications for the spread of plants with specialised pollinator requirements. *Journal of Tropical Ecology*, *33*, 183–187. https://doi.org/10.1017/S0266467417000098

Standley, L. A., Kim, S. S.-H., & Hjersted, I. M. (1988). Reproductive biology of two sympatric species of *Chimaphila*. *New England Botanical Club, Inc*, *90*(863), 233–244.

Stebbins, G. L. (1957). Self fertilization and population variability in the higher plants. *The American Naturalist*, *91*, 337–354. https://doi.org/10.1086/281999

Stubbs, C. S., & Drummond, F. A. (1997). Pollination of wild lowbush blueberry, *Vaccinium angustifolium* by the alfalfa leafcutting bee, *Megachile rotundata*. *Acta Horticulturae*, *446*(446), 189–196. https://doi.org/10.17660/ActaHortic.1997.446.28

Sun, Q., Zhao, X., Wu, L., Zhao, J., Yang, Y., & Zhang, Y. (2021). Differences in pollination efficiency among three bee species in a greenhouse and their effects on yield and fruit quality of northern highbush 'bluecrop' blueberry. *HortScience*, *56*, 603–607. https://doi.org/10.21273/HORTSCI15714-21

Switzer, C. M., Hogendoorn, K., Ravi, S., & Combes, S. A. (2016). Shakers and head bangers: Differences in sonication behavior between Australian *Amegilla murrayensis* (blue-banded bees) and North American *Bombus impatiens* (bumblebees). *Arthropod-Plant Interactions*, *10*, 1–8. https://doi.org/10.1007/s11829-015-9407-7

Switzer, C. M., Russell, A. L., Papaj, D. R., Combes, S. A., & Hopkins, R. (2019). Sonicating bees demonstrate flexible pollen extraction without instrumental learning. *Current Zoology*, *65*, 425–436. https://doi.org/10.1093/cz/zoz013

Tavares, P. R. A., Alves, V. V., Morais, G. A., Polatto, L. P., & Dutra, J. C. S. (2018). Pollen availability and behavior of visiting bees of *Solanum lycocarpum* A. St. Hill (Solanaceae). *Entomological News*, *127*, 375–385. https://doi.org/10.3157/021.127.0410

Tayal, M., & Kariyat, R. (2021). Examining the role of buzzing time and acoustics on pollen extraction of *Solanum elaeagnifolium*. *Plants*, *10*, 2592. https://doi.org/10.3390/plants10122592

Thorp, R. W. (1979). Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Annals of the Missouri Botanical Garden*, *66*, 788–812.

Thorp, R. W. (2000). The collection of pollen by bees. *Plant Systematics and Evolution*, *222*, 211–223.

Tong, Y.-U., Wu, L.-Y., Feng, H. H., Zhang, M. W., Armbruster, S., Renner, S. S., & Huang, S. H. (2023). New calculations indicate that 90% of flowering plant species are animal-pollinated. *National Science Review*, *10*(10), nwad219. https://doi.org/10.1093/nsr/nwad219

Traveset, A., Cavieres, L. A., Richardson, D. M., Adhikari, A., Aizen, M. A., Allen, W. J., Baltzinger, C., Caldwell, I. R., Callaway, R. M., & Catford, J. A. (2020). *Plant invasions: The role of biotic interactions*. CAB International.

Udayakumar, A., Chaubey, B. K., & Shivalingaswamy, T. M. (2021). *Amegilla violacea* (Lepeletier, 1841) (Anthophorini: Apidae)—A native bee, an effective pollinator of eggplant (*Solanum melongena*). *Journal of Apicultural Research*, *62*, 411–417. https://doi.org/10.1080/00218839.2020.1862393

Upadhyaya, M. K., Tilsner, H. R., & Pitt, M. D. (1988). The biology of Canadian weeds 87. *Cynoglossum officinale* L. *Candadian Journal of Plant Science*, *68*, 763–774. https://doi.org/10.4141/cjps88-089

Vallejo-Marín, M. (2019). Buzz-pollination: Studying bee vibrations on flowers. *New Phytologist*, *224*, 1068–1074. https://doi.org/10.1111/nph.15666

Vallejo-Marin, M., & Russell, A. L. (2023). Harvesting pollen with vibrations: Towards an integrative understanding of the proximate and ultimate reasons for buzz pollination. *Annals of Botany*, *133*, 379–398. https://doi.org/10.1093/aob/mcad189

Vallejo-Marín, M., Solís-Montero, L., Souto Vilaros, D., & Lee, M. Y. Q. (2013). Mating system in Mexican populations of the annual herb *Solanum rostratum* Dunal (Solanaceae). *Plant Biology*, *15*(6), 948–954. https://doi.org/10.1111/j.1438-8677.2012.00715.x

Vallejo-Marín, M., & Vallejo, G. C. (2021). Comparison of defence buzzes in hoverflies and buzz-pollinating bees. *Journal of Zoology*, *313*, 237–249. https://doi.org/10.1111/jzo.12857

Wille, A. (1963). Behavioral adaptations of bees for pollen collecting from *Cassia* flowers. *Revista de Biología Tropical*, *11*, 205–210.

Williams, N., Minckley, R., & Silveira, F. (2001). Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*, *5*. https://doi.org/10.5751/ES-00259-050107

Zhang, L., Yu, L., & Lou, A. (2017). No evolutionary change in the mating system of *Solanum rostratum* (Solanaceae) during its invasion in China. *Scientific Reports*, *7*, 17698. https://doi.org/10.1038/s41598-017-17881-2

Zilko, J. P., Hoebee, S. E., Edwards, T. J., Zilko, J. P., Hoebee, S. E., & Edwards, T. J. (2017). Floral morphology of *Eucalyptus leucoxylon* (Myrtaceae) facilitates pollination by lorikeet (Aves: Psittacidae) tongues. *Australian Journal of Botany*, *65*, 368–374. https://doi.org/10.1071/BT16242

SUPPORTING INFORMATION

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

Table S1: Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium Open Data Repository report of invasive angiosperms (downloaded 30 May 2022). We added additional columns (poricidal anthers or solanoid morphology) which detail whether each species had traits consistent with the buzz-pollination syndrome. We conducted visual assessments from available online imagery to individually examine whether the species had these traits. We reviewed the literature for species for which we could not assess the floral morphology from available online imagery to determine whether these species had poricidal anthers, exhibited a solanoid floral morphology, or had other evidence of buzz-pollination recorded. We provide the reference(s) for species for which we obtained information on floral morphology from published records.

Table S2: Synonymous species names included in the literature search to assess the mechanisms for overcoming specialist plant-pollinator barriers in invasive buzz-pollinated plants (Table S3).

Table S3: The reproductive biology and ecology of invasive angiosperms that exhibit traits consistent with the buzz pollination syndrome (poricidal anthers or solanoid morphology) listed on the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium Open Data Repository. For each species, in each of the native and invasive ranges, we reviewed the literature and provide details on the breeding system, whether the species requires a pollinator for seed set, whether each species has evidence of vegetative asexual reproduction, the method(s) used to assess the reproductive biology, and location of the study.

How to cite this article: Lopresti, L. C., Lach, L., & Montesinos, D. (2024). The specialised buzz pollination syndrome poses a partial barrier to plant invasions. *Journal of Ecology*, *00*, 1–15. https://doi.org/10.1111/1365-2745.14338