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ORIGINAL PAPER

# More invasive than non-invasive Asteraceae plants can reproduce uniparentally

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**Abstract** A plant that is capable of uniparental reproduction should be a better coloniser than one without that capability, because one individual can establish a persisting population. This advantage, formulated as Baker's law, can bias which species become invasive. Further, within predominantly biparentally reproducing species, this advantage can also lead to selection of individuals with uniparental reproduction during invasion. While studies have shown that invasive species tend to have uniparental reproduction, the reproductive strategies of non-invasive species occupying the same, and often disturbed, regions are understudied. Hence, to better understand the relationship between reproductive strategies and invasion, we experimentally assessed and compared the mating systems of 11 invasive, eight alien non-invasive and nine native species in India. All these species belong to the predominantly self-incompatible family, Asteraceae. In addition, we assessed whether the mating systems of the extremely invasive *Ageratum conyzoides* and *Bidens pilosa* differ between Mexico, where they are native, and India, where they are invasive. All the invasive Asteraceae assessed experimentally were found to have a mode of uniparental reproduction, whereas most of the natives and alien non-invasive species were self-incompatible. The mating systems of *A. conyzoides* and *B. pilosa* were self-incompatible in their native range and self-compatible in India, consistent with evolution due to selection of self-compatible lineages during invasion. The study robustly supports Baker's Law, such that among Asteraceae in southern India, those that are invasive are uniparental, while those that are not invasive follow the family's tendency toward self incompatibility.

சுருக்கம் பாலிலா இனப்பெருக்கம் மற்றும் தன் மகரந்தச் சேர்க்கை செய்யக்கூடிய தாவரங்களில் இனப்பெருக்கத்திற்கு ஒரே தாவரம் போதுமானவை என்பதால், அவ்வகைத் தாவரங்கள் புதிய சூழல்களில் மற்ற தாவரங்களை விட சுலபமாக தன் தாவரத் தொகையை நிறுவக் கூடும். இந்த கோட்பாடு பேக்கரின் விதி (பேக்கர்ஸ் லா) என அழைக்கப்படுகிறது. இதன் அடிப்படையில் ஆக்கிரமிப்பு தாவரங்கள் பெரும்பாலும் பாலிலா இனப்பெருக்கம் அல்லது

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த ன் - இ ண க் க ம் ( செ ல் ஃ ப் கம்பாட்டிபிலிட்டி) கொண்டிருக்க வேண்டும். மேலும் இந்த விதியின் அடிப்படையில் அதிகப்பட்சமாக தன்-ஒவ்வாமை (செல்ஃப் இன்கம்பாட்டிபிலிட்டி) கொண்டிருக்கக் கூடியத் தாவரத் தொகை புதிய சூழல்களில் தன்-இணக்கம் மிகுந்த தாவரத்தொகையாக பரிணாமம் அடையக்கூடும். இவ்விதிக்கு சான்றாக பெரும்பான்மையான ஆக்கிரமிப்பு தாவரங்கள் பாலிலா இனப்பெருக்கம் அல்லது தன்-இணக்கத் தன்மையை கொண்டிருப்பதை பல ஆராய்ச்சிகள் கண்டறிந்துள்ளன. தாவரத்தின் ஆக்கிரமிப்பு தன்மைக்கும் பேக்கரின் விதிக்கும் உள்ள தொடர்பை மேலும் இந்தியாவில் ஆராய நாங்கள் 11 ஆக்கிரமிப்பு தாவர சிற்றினங்கள், எட்டு ஆக்கிரமிக்கா அயல் நாட்டு தாவர சிற்றினங்கள் மற்றும் ஒன்பது பூர்வீக தாவர சிற்றினங்களின் இனப்பெருக்க முறையை சோதித்தோம். கூடுதலாக ஆக்கிரமிப்பின் பொழுது இனப்பெருக்க முறை பரிணாமம் அடைகிறதா என்றறிய ஏஜெரேட்டம் கொனிஸோய்டஸ் (*Ageratum conyzoides*) மற்றும் பைடன்ஸ் பைலோஸா (*Bidens pilosa*) ஆகிய இரண்டு சிற்றினங்களின் இனப்பெருக்க முறையை அதன் பூர்வீகமான மெக்சிகோவிலும் ஆக்கிரமிப்பு சூழலான இந்தியாவிலும் சோதித்தோம். இத்தாவரங்கள் அனைத்தும் ஆஸ்டெரேசி குடும்பத்தை சேர்ந்தவை. இக்குடும்பம் பெரும்பாலும் தன்-ஒவ்வாமை கொண்டவை. ஆராயப்பட்ட 11 ஆக்கிரமிப்பு தாவரங்களும் பாலிலா இனப்பெருக்கம் அல்லது தன்-இணக்கம் கொண்டிருந்தன. ஆனால் மற்ற இரண்டு வகைகள் குடும்பத்தின் இனப்பெருக்க முறை விகிதத்தை தழுவி இருந்தன. ஏ.கொனிஸோய்டஸ் மற்றும் பை.பைலோஸா தன் பூர்வீகத்தில் பெரும்பாலும் தன்-ஒவ்வாமை கொண்டவையாகவும் இந்தியாவில் பெரும்பாலும் தன்-இணக்கம் கொண்டவையாகவும் இருந்தன. இந்த ஆராய்ச்சி முடிவுகள் பேக்கரின் விதியை ஆதரிக்கின்றன.

**Keywords** Baker's law · India · Invasion · Reproductive strategy · Self compatibility · Seed viability

## Introduction

The number of invasive plant species is growing at an alarming rate, with roughly 3,800 well-documented invasive plant species reported worldwide (Laginhas and Bradley 2022). The problem of plant invasion requires us to better understand what makes a plant likely to become invasive. Studies have shown that no single trait underlies invasiveness in plants; rather, multiple characteristics, such as plasticity and seed dispersal, may potentially portend a plant's invasiveness (Gioria et al.,2023; Grooves,2006; Moles, 2008; Rejmánek and Richardson,1996; van Kleunen et al. 2010). One such trait that should be advantageous during invasion is the ability to reproduce uniparentally, which allows individual plants or those growing at low density to reproduce, either by propagating from vegetative organs or through autonomous seed setting. Autonomous seed setting can occur either through mating with self (self compatibility) or through parthenogenesis (apomixis).

Colonisation is an essential part of the invasion process, both at initial establishment as well as during subsequent spread, as the invasion front may comprise low-density satellite populations (Theoharides and Dukes 2007). Botanist H.G. Baker postulated that self-compatible plants are more effective at colonisation because a single individual is sufficient to establish a sexually reproducing colony, whereas self-incompatible individuals would face difficulty finding mates, and might fail to reproduce and establish a colony (Baker 1955, 1967, 1974). This concept has become known as Baker's law (Baker 1955; Stebbins 1957), and has been further extended to accommodate other modes of uniparental reproduction, such as apomixis (Whitehead et al. 2018). Consistent with Baker's Law, several studies have shown that invasive plant species tend to reproduce uniparentally (Rambuda and Johnson 2004; van Kleunen et al. 2008; Hao et al. 2011). For instance, Ramduba and Johnson (2004) showed that all 17 invasive species they studied in South Africa were either self-compatible or apomictic. Additionally, Pannell and Barrett (1998) predicted that the effect of Baker's Law would be

reduced in perennial plants. This is because living for multiple mating seasons increases the chance of sexual reproduction. This is especially true where the arrival of propagules is a recurring event, bringing in new individuals periodically. In such a case, if a plant does not reproduce in the first flowering season, it could potentially reproduce later when mates are available. This is empirically supported by Petanidou et al. (2012), who observed the mating systems of perennial and annual invasives.

Most flowering plants can reproduce sexually, and their reproductive strategies, including self incompatibility and self compatibility, are heritable (Bala et al. 2023; Igic et al. 2008). While in some plant species all individuals possess the same reproduction strategy, Whitehead et al. (2018) estimated that 63% of flowering plant species are made up of individuals with different reproductive strategies. In such species with mixed mating systems, the proportion of individuals with each mating system often differs among populations. For instance, Warwick and Thompson (1989) reported that self compatibility of *Carduus nutans* (Asteraceae) ranges from 8 to 60% across populations in Canada. Because self compatibility or uniparental reproduction is favoured during colonisation, the self compatible individuals from mixed populations would have an advantage during the establishment and spreading stages of invasion. This can cause evolution of mating systems during invasion as a result of new populations being founded by predominantly self-compatible genetic lineages from an originally mixed population (Charlesworth 2006; Cheptou 2012; Pannell et al. 2015). Indeed, several studies have found plant species in which populations are predominantly outcrossing in their native regions, and are selfing or clonally reproducing where they are invasive (Barrett 1979; Ren et al., 2005; Hollingsworth and Bailey 2000; Li et al. 2006; White et al. 1993; Petanidou et al. 2012). An example is the shift from outcrossing to selfing during invasion from Brazil to Jamaica by the water hyacinth, *Eichhornia paniculata* (Barrett and Husband 1997). In spite of this overall pattern, several studies have also detected no shift in mating strategies after invasion. For example, Li et al. (2012) and Zhang et al. (2017) found *Ambrosia artemisiifolia* (Asteraceae) and *Solanum rostratum* (Solanaceae), which are self incompatible in their native range, to also be self incompatible where they were invasive in China.

Habitat disturbance disrupts plant communities, making resources available for colonisation by invasive plants. This leads to invasive plants being common in disturbed areas (Lozon et al. 1997), where native species also generally persist. Plants growing in human-disturbed landscapes have also been found to have higher rates of selfing than plants growing in undisturbed places. Eckert et al. (2010) found that human disturbance causes significant reduction in the proportion of seed set by outcrossing in 27 native and invasive species. While previous studies have shown that invasive species tend to have a mode of uniparental reproduction (Razanajatovo et al. 2016), native plants can also possess high levels of selfing or uniparental reproduction, especially in disturbed landscapes (Grossenbacher et al. 2015). There are relatively few studies comparing the reproductive strategies of sympatric native and invasive plants. Petanidou et al. (2012) found that populations of *Centaurea solstitialis* (Asteraceae), a predominantly self-incompatible plant, are self-compatible in disturbed areas within the native range. In a study at the genus level, Vervoort et al. (2011) found that invasive *Impatiens* (Balsaminaceae) species had more autonomous seed setting than native *Impatiens* in the areas of invasion. Studies such as these imply that both native and invasive species should be found to be predominantly uniparental in disturbed habitats. However, native species may have advantages, such as large nearby populations in undisturbed habitats, that reduce the disadvantages of self incompatibility, allowing self incompatibility to persist. No studies that we are aware of have compared multiple native and invasive species inhabiting disturbed habitats in the same region. Moreover, even though comparison of native and invasive plants provides immense insight into colonisation, to evaluate the importance of a trait concerning invasion, one must also consider alien non-invasive plants, which are those that are present, but are not, or not yet, invasive. This is because native and invasive plants could both possess traits that make them successful in a particular habitat, while alien non-invasive plants likely do not. (van Kleunen et al. 2015). Finally, even with multiple lines of support for Baker's Law and documentable shifts in the mating systems, there are self-incompatible invasive species (Hao et al. 2011).

To better understand the relationship between mating system and plant invasion, we investigated

**Table 1** The locations from which invasive and native plants were sampled in southern India

| Location of collection | State of India | Lat long |
|---|---|---|
| Ooty town* | Tamil Nadu | 11.4102° N, 76.6950° E |
| Biligirirangan hills* | Karnataka | 11.9988° N, 77.1398° E |
| Yercaud town* | Tamil Nadu | 11.7748° N, 78.2097° E |
| Honnavar | Karnataka | 14.2798° N, 74.4439° E |
| Bengaluru | Karnataka | 12.9629° N, 77.5775° E |
| Salem | Tamil Nadu | 11.6643° N, 78.1460° E |
| Challakere (Indian Institute of Science campus) | Karnataka | 14.3134° N, 76.6528° E |

*Species were identified on site, prior to collection, to avoid collecting protected plants, as these locations were in the vicinity of forest lands

Baker's Law empirically by systematically comparing the reproductive strategies of native, invasive, and non-invasive alien Asteraceae species found in southern India. Additionally, since perennial plants have more mating opportunities than annual plants (Pannell and Barrett, 1998) we also include life cycle (annual vs perennial) of the plants in the analyses.

Lastly, because natural selection on mating systems can occur during invasion, and Asteraceae as a family is predominantly self-incompatible, we tested if there is a difference in the predominant mating systems between populations in the native and invasive regions for two Asteraceae species, *Ageratum conyzoides* and *Bidens pilosa,* which are highly invasive in India. Both species are native to the neotropics and are invasive in multiple countries globally (Sankaran and Suresh 2013; POWO 2025). Asteraceae was chosen for this study because it is a large, predominantly self-incompatible family, with about one-third of the species being self-compatible or pseudo-self-incompatible (Ferrer and Good-Avila 2007). There are many invasive Asteraceae in India, including six of the 11 high-concern invasive plant species in the country (Mungi et al. 2023).

The specific questions we addressed are 1) Do more invasive Asteraceae species have uniparental reproduction compared to alien non-invasive and native species in southern India? and 2) Has there been shift in mating systems from self-incompatible to self-compatible within the invasive Asteraceae species *Ageratum conyzoides* and *Bidens pilosa* between native and invasive regions?

## Methods

### Study species, sites, and sampling

To assess the reproductive strategies of invasive, native and alien non-invasive Asteraceae species found in southern India, invasive and native plants were sampled from populations in disturbed areas, such as road sides and unoccupied open spaces in unprotected areas, at seven locations in the states of Karnataka and Tamil Nadu (Table 1, supplementary material). The study was conducted from May 2024 to March 2025.

At each site, the seeds or vegetative propagules of a minimum of five individuals per species present were collected, which was treated as a sample of a population. Each of the invasive and native species (Table 2) was identified using taxonomic keys from Gamble (1936) and Hajra et al. (1995a, 1995b), and were designated as native or invasive using Sankaran and Suresh (2013) and Khuroo et al. (2021). The native vs introduced status was verified with data from the Kew Garden's Plants of the World Online website (POWO 2025). Seeds of the alien non-invasive species, which were all ornamental, were purchased from the Indian seed companies Ugaoo and A1 and from the Indian Institute of Horticultural Research (Table 2 and supplementary material).

Depending on availability, five to thirty seeds were selected haphazardly and germinated per population per species and were grown until they flowered in pots in an enclosure at the Indian Institute of Science, Bengaluru campus. For the species that were propagated from vegetative organs, all plants that survived the transplantation and flowered were used in experiments. The enclosure was open to and visited by insect pollinators. The flowers were used to assess reproductive strategies (described below). Four native species could not be relocated or successfully grown in the enclosure. For these species, the experiments were conducted on 5 to 20

**Table 2** The life cycles, sample sizes (numbers of populations and numbers of individuals), and reproductive strategies determined experimentally and/or reported in the literature for each of the study species. The native and alien invasive species were collected from field sites in southern India in 2024 (Table 1), and the alien non-invasive species were purchased as seeds at the same time (see supplementary material for details)

| Species | Invasion status in India | Life cycle | No. populations sampled | No. individuals assessed | Reproductive strategy found experimentally | Reproductive strategy in literature |
|---|---|---|---|---|---|---|
| *Ageratum conyzoides* | Alien invasive | Annual | 3 | 90 | Self-compatible | Self-compatible[1], apomixis[1], self-incompatible[2], Male sterile[3] |
| *Bidens pilosa* | Alien invasive | Annual | 4 | 120 | Self-compatible | Self-compatible[1,] Mixed[4 *] |
| *Calyptocarpus vialis* | Alien invasive | Annual | 2 | 40 | Self-compatible, Vegetative propagation | Self-compatible[5*] |
| *Crassocephalum crepidioides* | Alien invasive | Annual | 2 | 32 | Self-compatible | Self-compatible[6] |
| *Chromolaena odorata* | Alien invasive | Perennial | 3 | 30 | Apomixis | Apomixis 7, Vegetative propagation [8] |
| *Eclipta prostrata* | Alien invasive | Annual | 2 | 10 | Self-compatible, Vegetative propagation | Vegetative propagation [9] |
| *Galinsoga parviflora* | Alien invasive | Annual | 2 | 60 | Self-compatible | Self-compatible[10], Vegetative propagation [11] |
| *Parthenium hysterophorus* | Alien invasive | Annual | 4 | 50 | Apomixis | Self-compatible[12] |
| *Synedrella nodiflora* | Alien invasive | Annual | 2 | 40 | Self-compatible | Self-pollinating [13, 14] |
| *Tridax procumbens* | Alien invasive | Annual | 2 | 50 | Self-compatible | Self-compatible[15] |
| *Sphagneticola trilobata* | Alien invasive | Perennial | 2 | 10 | Self-incompatible, Vegetative propagation | |
| *Callistephus chinensis* | Alien non-invasive | Annual | 1 | 30 | Self-compatible | Self-compatible [16] |
| *Calendula officinalis* | Alien non-invasive | Annual | 1 | 10 | Self-incompatible | Self-incompatible[17] |
| *Chrysanthemum morifolium* | Alien non-invasive | Annual | 2 | 20 | Self-incompatible | Self-incompatible[18] |
| *Coreopsis tinctoria* | Alien non-invasive | Annual | 1 | 30 | Self-incompatible | Self-incompatible[19] |
| *Cosmos bipinnatus* | Alien non-invasive | Annual | 2 | 35 | Self-incompatible | Self-incompatible [20] |
| *Gaillardia pulchella* | Alien non-invasive | Annual | 1 | 30 | Self-incompatible | Self-incompatible [21] |
| *Tagetes erecta* | Alien non-invasive | Annual | 2 | 46 | Self-compatible | Self-compatible [16] |
| *Zinnia peruviana* | Alien non-invasive | Annual | 1 | 30 | Self-compatible | |
| *Artemesia nilagirica* | Native | Perennial | 1 | 10 | Self-incompatible, Vegetative propagation | Self-incompatible, vegetative propagation [22] |
| *Blumea mollis* | Native | Annual | 2 | 20 | Self-incompatible | |
| *Cyanthillium cinereum* | Native | Annual | 3 | 25 | Self-compatible | Mixed [23] |
| *Dicoma tomentosa* | Native | Annual | 1 | 17 | Self-incompatible | |
| *Echinops echinatus* | Native | Annual | 1 | 8 | Self-incompatible | |
| *Glossocardia bosvallia* | Native | Annual | 2 | 35 | Self-incompatible | |

**Table 2** (continued)

| Species | Invasion status in India | Life cycle | No. populations sampled | No. individuals assessed | Reproductive strategy found experimentally | Reproductive strategy in literature |
|---|---|---|---|---|---|---|
| *Pulicaria wightiana* | Native | Annual | 1 | 15 | Self-incompatible | |
| *Psuedoconyza viscosa* | Native | Annual | 2 | 10 | Self-compatible | |
| *Youngia japonica* | Native | Annual | 1 | 15 | Self-compatible | |

*Reproductive strategy reported in native region for invasive species. References: [1]Hao et al. (2011); [2]Ming (1999), [3]Kaul and Neelangini (1989), [4]Grombone-Guaratini et al. (2004), [5]Estes (2018), [6]Cui et al., (2025), [7] Tripathi et al (2012), [8]Zachariades et al. (2009), [9]Lee and Moody (1988), [10]Warwick and Sweet (1983), [11]Damalas (2008), [12]Usharani and Raju (2018a), [13]Usharani and Raju (2018b), [14]Shabbir et al. (2024), [15]Shivanna (2014), [16]North (1979), [17]Heyn and Joel (1983), [18]Wang et al. (2014), [19]Zeng et al. (2021), [20]Little et al. (1940), [21]Heywood (1993), [22]Jabeen et al. (2012), [23]Rao et al. (2017)

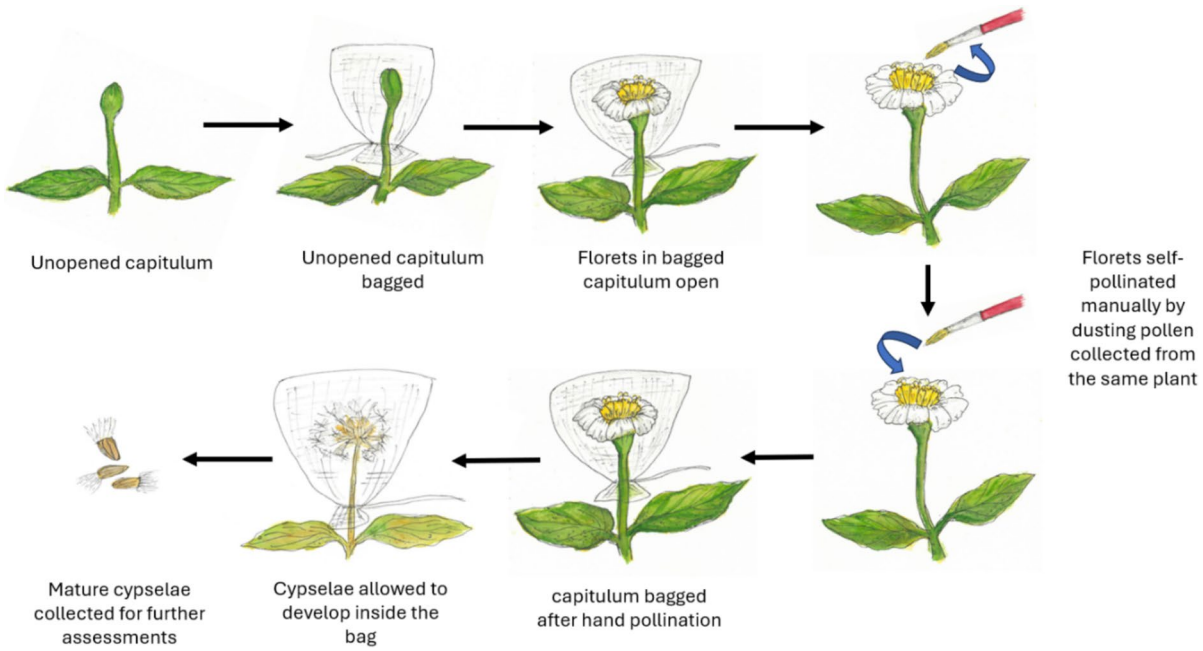


**Fig. 1** Diagrammatic representation of the methodology followed to assess uniparental seed setting in this study

individuals (depending on species) in the wild at the Indian Institute of Science, Challakere campus (Table 2 and supplementary material).

The comparison of mating systems between the native region and invasive region was done in Mexico (native) and India (invasive). *Ageratum conyzoides* and *Bidens pilosa* were the two species studied. In India, the samples from the previous assessment were used. In Mexico, 31 individuals of each species were used for experimentation; these were collected from naturally growing plants in a home yard at Xalapa, Veracruz, Mexico.

Assessment of reproductive strategies

To assess the reproductive strategies of the sampled populations of each species, the reproductive strategies of individuals were determined and extrapolated to the population. If an individual was observed to propagate vegetatively or found to be apomictic, it was considered capable of vegetative reproduction or apomixis, respectively. A species was considered self-compatible if all or nearly all individuals (greater than 95%) were self-compatible, and self-incompatible if nearly all individuals were self-incompatible

(greater than 95%). No species fell between these two, so there were none designated as having mixed mating systems (see supplementary material for individual-level data).

The morphology and phenology of the plants were observed to assess vegetative propagation, especially from the stem/ rhizome. For each species found to be capable of vegetative reproduction, we also checked reproductive strategies published in the literature (see Table 2 for specific references).

To assess uniparental seed setting, for every individual, a capitulum (flower head containing multiple small flowers or florets found in Asteraceae) bud was selected and bagged. After blooming, the capitulum was hand-pollinated using pollen from the same capitulum, and then bagged and left to develop into cypselae (dry fruits with a single seed found in Asteraceae) (Fig. 1). Another capitulum was left unbagged for open pollination to occur. The enclosure was visited by naturally occurring pollinators common on the Indian Institute of Science campus, Bangalore, including honey bees (mostly *Apis dorsata*), solitary bees, and blue pansy (*Junonia orithya)*, chocolate pansy (*J. iphita)* and common tiger (*Danaus chrysippus*) butterflies. To ensure pollination had occurred, the stigmas were observed using a magnifying lens for the presence of pollen on the receptive surface. Only a few individuals of *Tagetes erecta* were not found to be naturally pollinated and were hand pollinated using pollen from other individuals of the same species. All the treatments were left to develop into cypselae.

The morphology of the mature cypselae from the treatment (bagged) were compared to the control (open pollinated) or to the parent cypselae to assess if they appeared fully developed. Plants that produced fully developed cypselae from bagged capitula were considered to be capable of uniparental seed setting (Hao et al. 2011). This assessment was done in both India and Mexico. However, since fully developed cypselae do not guarantee viability (Turner 1933), the cypselae were further subjected to seed viability tests.

Seed viability was tested using triphenyl tetrazolium chloride (TTZ) to detect dehydrogenase enzymatic activity, diagnostic of live cells. Several bagged cypselae (about 10 to 30, based on size) from each individual were soaked in distilled water for 24 h. For bigger cypselae, the seeds and the seed coats were removed. Small cypselae were gently pressed to expose the seed or cotyledons. The seeds were soaked in 0.1% TTZ solution for 48 h in the dark at room temperature and then observed. The seeds showing red staining were considered viable, while those that did not show a colour change were considered inviable, and the plant that produced the seeds was considered self-incompatible (Verma and Majee 2013). Cypselae from the individuals that showed viability in the TTZ test were then subjected to germination. For this, the cypselae were soaked in 500 mg/L gibberellic acid (GA3) solution for 24 h to break dormancy, and were then placed in damp cotton in the dark at room temperature.(Bunker 1994) The cotton was sprayed with water to maintain moisture and observed for 15 days. If the seeds germinated, the species was considered capable of reproducing uniparentally; otherwise, the plant was considered not capable of uniparental reproduction.

Further, to understand the requirement of pollination in uniparental reproduction, species capable of reproducing uniparentally through seeds were subjected to aniline blue staining (adapted from Herburger and Holzinger 2016; Zavaliev and Epel 2014). This was done to detect pollen germination on the stigma to verify if the mode of autonomous seed setting was through self pollination in self-compatible plants, or through autogamous apomixis in self-incompatible plants. Since the florets in our experiment aborted after emasculation, determining combinations such as autogamous apomixis in self-compatible plants is difficult. We could not separate apomictic events from self-fertilisation in self-compatible plants without using molecular markers, which was beyond the scope of this study. The possibility of pseudogamous apomixis in self-incompatible plants was also not explored, as the plants would require unrelated mates to reproduce, hence functioning as self-incompatible plants in the context of Baker's law.

For the aniline blue staining pollen germination assay, three individuals were selected from each species that produced viable cypselae in the self-pollinated treatment. New capitula were bagged before anthesis. Upon maturation of the stigma in each floret, they were hand pollinated with pollen from the same individual and then bagged. This was performed in all florets of the capitulum. Twenty-four hours after pollination of the last floret, the capitula were plucked and fixed in FAA (Formalin, Acetic acid, Ethanol

**Table 3** Reproductive strategies of *Ageratum conyzoides* and *Bidens pilosa* tested in their native (Xalapa, Veracruz, Mexico) and invasive (India) ranges. The numbers represent the number of plants assessed from each origin found in our study to be self-compatible or incompatible

| Species | Population | Nativity | No. self compatible individuals | | No. self incompatible individuals | |
|---|---|---|---|---|---|---|
| | | | Per population | Total | Per population | Total |
| *Ageratum conyzoides* | Xalapa, Mexico | Native | 2 | 2 | 29 | 29 |
| | Bengaluru, India | Invasive | 30 | 88 | 0 | 2 |
| | Biligirirangan hills, India | | 28 | | 2 | |
| | Yercaud, India | | 30 | | 0 | |
| *Bidens pilosa* | Xalapa, Mexico | Native | 0 | 0 | 31 | 31 |
| | Bengaluru, India | Invasive | 30 | 116 | 0 | 4 |
| | Biligirirangan hills, India | | 30 | | 0 | |
| | Ooty, India | | 30 | | 0 | |
| | Yercaud, India | | 26 | | 4 | |

and Distilled water at ratios of 10:5:50:35). After a minimum of four hours the capitula were rehydrated in distilled water for an hour and dissected to extract the stigmas and styles. Stigmas and styles of florets from different positions of the capitula were used to assess the different stages. The extracted samples were treated with 4N NaOH solution for six hours to soften the tissue. Then, each sample was washed in distilled water for 10 min and stained for four hours using 0.1% Aniline blue solution in Sorenson's buffer. After staining, the sample was mounted on a microslide in Sorenson's buffer and visualised under UV light filtered through a fluorescence filter cube in a Leica DM 3000 microscope (Kho and Baer 1968; Herburger and Holzinger 2016). If the pollen was found to have germinated on the surface of the stigma or if the pollen had penetrated into the stigma without being surrounded by a callose layer, then the plant was considered self-compatible. If not, the plant was considered an autogamous apomictic (Hiscock 2000; Hao et al. 2011). The pollen germination on the stigma occurred within 24 h for all species. Additionally, to verify that the reproductive barrier was due to self incompatibility, the species not capable of uniparental reproduction were also subjected to aniline blue staining to observe if pollen from the same individual germinated on the stigma. If there was no pollen germination on the stigma, the plant was considered self-incompatible. If the pollen germinated on the stigma, then there are potentially post-fertilisation barriers in the species.

### Analysis

The reproductive strategy of each plant individual was recorded. Because there were nearly no populations showing mixed mating systems (for the two slight exceptions, see Table 3 and supplementary material), each species was categorized as capable of uniparental reproduction or not, and the numbers of species in each category were compared using a contingency table. The association of uniparental reproduction and invasiveness was tested using Fisher's Exact Test. The Holm-Bonferroni method for correction was used for pairwise comparison between multiple groups. To assess the potential shift in mating system from the native to the invasive region, the number of plant individuals of each species from Mexico and from India exhibiting each mating system was tabulated and compared using Fisher's Exact Test. All tests were done using $\alpha < 0.0\,5$.

## Results

The reproduction strategies of a total of 918 plants from 28 species were assessed. Out of these, 11 species were alien invasive, eight were alien non-invasive, and nine were native to southern India (Table 2). All alien invasive species had at least one mode of uniparental reproduction, including the two perennial species. This was in accordance with the mating systems reported in the literature for these species. The mating systems of all the invasive species have

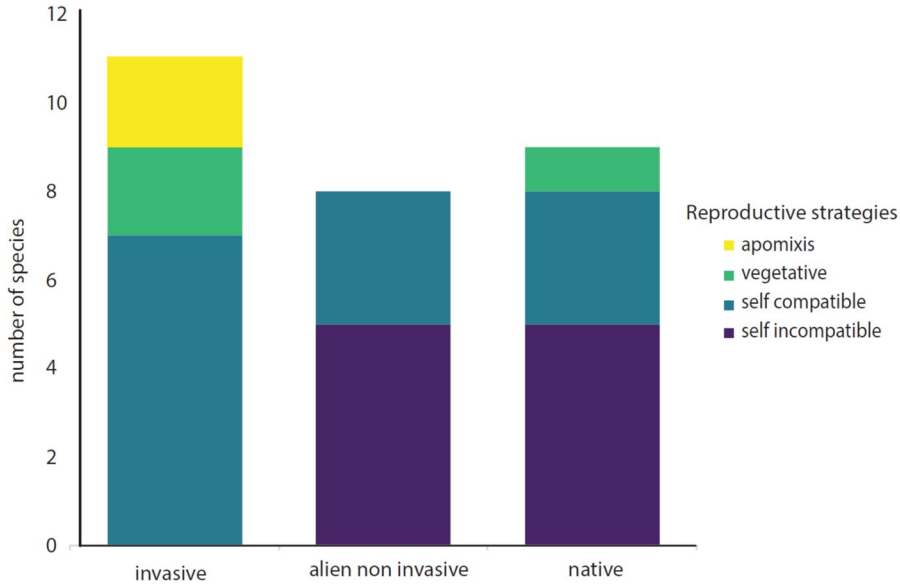


**Fig. 2** The number of species with each reproductive strategy (apomixis, vegetative, self compatible, self incompatible) found in the categories: invasive, alien non invasive and native. See Table 2 for the numbers of individuals and populations tested for each species

been published from their invasive ranges, except for *B. pilosa* and *Calyptocarpus vialis* (Table 2). Out of eight alien non-invasives, three were found to be self-compatible, and five were found to be self-incompatible (Table 2). Four of the nine native species were found to have a mode of uniparental reproduction.

Only four out of the 28 species showed vegetative propagation, *Calyptocarpus vialis*, *Eclipta prostrata*, *Sphagneticola trilobata* and *Artemisia nilagirica*. All of these possessed stolons or stems that grow prostrate with roots at nodes. The first three are alien invasive species, while *A. nilagirica* is native (Table 2). Notably, the invasive *S. trilobata* propagated vegetatively, did not have autonomous seed setting, and was verified to be self-incompatible. In the alien non-invasive group, *Calendula officianalis*, *Callistephus chinensis, Tagetes erecta* and *Zinnia peruviana* showed uniparental seed setting, and the other species did not. Out of these four species, the seeds of *C. officianalis* failed both the TTZ test and the germination test. In the native group, *Cyanthillium cinereum* and *Psuedoconyza viscosa* showed full uniparental seed setting, whereas the other species did not. However, *Dicoma tomentosa*, *Glossocordia boslavalia* and *Echinops echinatus* set a few fully developed and partially developed cypselae, but failed the TTZ and germination tests. Out of all the species with autonomous seed setting, *Chromolaena odorata* and *Parthenium hysterophorus* were the only two species in which all the individuals showed no pollen germination under aniline blue epifluorescence, suggesting these two species are apomictic. Literature supports *C. odorata* being apomictic (Zachariades et al. 2009), but there is no literature exploring the apomictic nature of *P. hysterophorus*. Both the species we observed to be apomictic are invasive in India.

Out of the 28 species studied, three were perennial. Of these, *C. odorata* and *S. trilobata* are invasive and *A. nilagirica* is native. All three species were incapable of self fertilisation but had a mechanism of uniparental reproduction. *Chromolaena odorata* reproduced through apomixis, and *S. triobata* and *Anilagirica* both reproduced through vegetative propagation.

Uniparental reproduction was strongly associated with species invasiveness (Fig. 2; Fisher's Exact Test, $p = 0.0036$ ). A significant difference was observed both between invasive and natives ($p = 0.005$) and between invasive and alien non-invasive ($p = 0.008$). Native and alien non-invasive species did not differ significantly (Fig. 2).

The mating systems of *Ageratum conyzoides* and *Bidens pilosa* were each assessed in several populations in India where they are invasive, and in one population in Mexico where they are native. Both species were found to be predominantly self-compatible in India and self-incompatible in Mexico (Table 3). In India, out of 120 *B. Pilosa* individuals, four individuals from Yercaud were self-incompatible (4%), and out of 90 *A. conyzoides* individuals, two individuals

from BRT hills were self-incompatible (2%). All other individuals were self-compatible. In Mexico, of 31 individuals per species, all *B. pilosa* were self-incompatible (100%). Two *A. conyzoides* individuals were self-compatible and 29 were self-incompatible (93%).

## Discussion

The invasive Asteraceae we tested all possessed at least one mode of uniparental reproduction, whereas just three out of eight of the alien non-invasive species, and four of nine native species were capable of uniparental reproduction. This pattern supports Baker's Law, in that "one plant with uniparental reproduction is more likely to establish a reproducing population than two plants without uniparental reproduction" (Baker 1955; Stebbins 1957), as an explanation for the high representation of uniparental reproduction among invasive plant species.

Other research has shown similar results based on the proportion of seed set in invasive plant species. Rambuda and Johnson (2004) studied 17 species from 11 families invasive in South Africa and reported that all 17 species were either self-compatible or apomictic. van Kluenen and Johnson (2007) compiled the mating system of 361 species invasive to United States and found that species with autonomous seed setting have larger invasive ranges than species lacking autonomous seed setting. And Hao et al. (2011) studied 12 Asteraceae species invasive in China and found that ten were capable of autonomous seed setting.

In addition to the proportion of autonomous seed setting in invasive species, our study assessed the proportions of uniparental reproduction in local native and alien non-invasives, as a baseline against which to evaluate the invasive species. While all the invasive Asteraceae were able to reproduce uniparentally, only some of the native and alien non-invasive Asteraceae were able to reproduce uniparentally. Since some seeds may be non-viable (Turner 1933), We also checked for the viability of the seed produced by plants uniparentally. All fully developed cypselae of invasive species showed germination, while fully developed cypselae of the non-invasive species, *C. offcianalis, D. tomentosa, G. bosvalia* and *E. echinatus,* which were produced uniparentally, failed to germinate. We also collected the previously published reports that we could find on the reproductive strategies of species in our study (Table 2). Out of these, *B. pilosa* and *C. vialis* were the only invasives with published observations of self-compatible individuals in the native region. Our study is the first record of mating systems of seven species native to India (Table 2).

During invasion, the founding populations are generally small. In such small populations, self-incompatible individuals would face difficulty finding suitable mates, and might eventually fail to reproduce and establish a colony. However, plants with uniparental modes of reproduction do not face such mate limitations and could potentially establish a persisting colony (Cheptou 2012; Pannell et al. 2015; Petanidou et al. 2012). This includes self compatible as well as clonal populations produced by vegetative propagation or apomixis. Although uniparentally reproducing populations face the risk of low genetic diversity and inbreeding depression, in small populations, the reduction in fitness due to inbreeding is likely to be lower than the reduction in fitness due to mate limitation (Barrett 2015). This is consistent with uniparentally reproducing plants having an advantage in a new habitat, making them more likely to become invasive.

Although in this study we did not find self-incompatible invasive species, other studies have(Hao et al. 2011; Li et al. 2012). While self-compatible plants have reproductive assurance, this advantage should be less in perennial than annual plants (Pannell and Barrett 1998; Petanidou et al. 2012). This is because perennial plants have multiple mating seasons, increasing the opportunities of finding a mate, especially if recurrent arrival of propagules brings potential mates (Pannell and Barrett 1998; Petanidou et al. 2012). Thus we expect perennial invasive plants to be unlikely to have a uniparental mode of reproduction. While we did not study this extensively, it is notable that this was not the case in our study, as the two perennial invasives, *Chromolaena odorata* and *Sphagneticola trilobata,* were found to have uniparental modes of reproduction.

Arriving propagules need open spaces and resources to colonise. Thus, disturbed habitats are often dominated by invasive species (Lozon et al. 1997). But native species are present as well. The majority of native Asteraceae members used in the

experiment were self-incompatible, yet they occupied the same disturbed habitats as the invasive species. The native plants may have dispersed short distances from less disturbed habitats such that the number of propagules arriving were enough to overcome mate limitation. Alternatively the native species may be particularly well adapted to the site, or be remnant populations on their way to local extinction (Gilbert and Levine 2013). Similarly, the majority of alien non-invasives in this study were self-incompatible. While the non-invasiveness of self-incompatible alien species can be explained by mate limitation, other limitations such as climatic conditions, edaphic conditions, and competitors and herbivores, might play roles as barriers to invasiveness in self-compatible alien species (Jeschke 2014; Mathakutha et al. 2019; van Kleunen et al., 2015; Williamson and Fitter 1996). Furthermore, alien non-invasive plants that were found to be self-compatible in our experiments are known to be invasive elsewhere in the world. For example, *Z. peruviana* is invasive in South Africa (Datiles, 2022) and *T. erecta* is invasive in China (Zhang et al. 2021). Thus, considering these results and that Asteraceae as a whole is predominantly self incompatible, the pattern we observed provides strong support for plant mating system being related to invasiveness.

Since a shift in mating systems during invasion is possible, and there were no previous records of shifts in mating systems in plant species invasive in India, we assessed the mating systems of *A. conyzoides* and *B. pilosa* in India and in Mexico. We found that both species were predominantly self-incompatible in the native region in Mexico but predominantly self-compatible in the invasive regions in India. This shift in mating system could explain the high levels of invasiveness of these species worldwide. In such species with mixed mating systems, the selection for uniparental reproduction can occur within populations. In native ranges, species with mixed mating systems have suitable pollinators and adequate population density so mate limitation is low or non-existent (Barrett 2015). In these areas, a reduction in fitness due to inbreeding that results from self compatibility would be higher than the low reduction in fitness caused by mate limitation. In such cases, self-incompatible plants are favoured, and the population would be predominantly outcrossing with a few self-compatible individuals (Barrett 2015). When a few individuals from such a population disperse into a new location, self-compatible individuals would be at an advantage over self-incompatible individuals, and their increasing frequency would result in new populations that were predominantly self-compatible (Barrett 2015; Cheptou 2012; Pannell et al. 2015).

Such evolution (change in frequency of a trait under selection in a population) in mating system has been previously observed in invasive plant species (Barrett 1979; Barrett and Husband, 1990; Ren et al., 2005; Hollingsworth and Bailey 2000, Li et al. 2006; White et al. 1993). There have been few studies of evolution of mating systems in Asteraceae. Li et al. (2012) found no shift in the mating system of *A. artemmisiifolia,* an Asteraceae native to North America that is invasive in China. They found the plant to be self-incompatible in both places. In contrast, we found a shift from predominantly self-incompatible to self-compatible in *A. conyzoides* and *B. pilosa*. While our study reports the species to have a strongly biased but mixed mating system (Table 3), the outcome might depend on the native and invasive populations used. Kaul and Neelangini (1989) found that the population of *A. conyzoides* they studied in India was self incompatible, whereas Hao et al. (2011) reported the same species as self-compatible in China; both of the studies are from invasive regions. We found the native population of *B. pilosa*, from Xalapa, Mexico to be completely self-incompatible. However, Grombone-Guaratini et.al. (2004) found native populations of the same species in Brazil to be self-compatible. This suggests a shift in mating system is not necessarily caused only by long-distance dispersal. Additionally, many species known to be widely invasive are also abundant and widespread in their native region (Paudel et al. 2025). This could be due in part to the presence of uniparental reproduction (Grossenbacher et al. 2015).

Overall, the association of mating system with invasiveness is due to the optimal mating system being related to population density. If the density of the population is low, there is mate limitation, and uniparental reproduction is advantageous even given the costs of inbreeding (Barrett 2015). When the density of the population is high, there is no mate limitation and self incompatibility and dioecy are favoured, reducing inbreeding.

While a self-compatible mating system by itself might not be the sole trait that supports invasiveness, our study and several others suggest it is important.

The number of invasive species is growing at an unprecedented rate, and many have not been documented (Laginhas and Bradley 2023; IPBES, 2023). Current global policies against invasive species have limited effectiveness (IPBES, 2023). Therefore, it is crucial to assess and document the mating system of as many plant species as possible, including testing the viability of autonomously produced seeds, to predict the risk of a species becoming invasive. The Weed Risk assessment model described in Pheloung et al. (1999) includes assessment of the mating system of a species in calculating the risk of a plant becoming invasive. This model is officially used by the Australian Government Department of Agriculture, Fisheries and Forestry. We strongly emphasise that reproductive strategy should be included in other risk assessment protocols involving invasive plants.

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**Declarations**

**Competing interests** The authors have no competing interests.

## References

Baker HG (1955) Self-compatibility and establishment after "long distance" dispersal. Evolution 9:347–349. https://doi.org/10.1111/j.1558-5646.1955.tb01544.x

Baker HG (1967) Support for Baker's law as a rule. Evolution 21:853–856. https://doi.org/10.1111/j.1558-5646.1967.tb03440.x

Baker HG (1974) The evolution of weeds. Annu Rev Ecol Evol Syst 5:1–24

Bala M, Rehana S, Singh MP (2023) Self-incompatibility: a targeted, unexplored pre-fertilization barrier in flower crops of Asteraceae. J Plant Res 136:587–612. https://doi.org/10.1007/s10265-023-01480-6

Barrett SCH (1979) The evolutionary breakdown of tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth). Evolution 33:499–510. https://doi.org/10.1111/j.1558-5646.1979.tb04702.x. (**7**)

Barrett SCH (2015) Foundations of invasion genetics: the Baker and Stebbins legacy. Mol Ecol 24:1927–1941. https://doi.org/10.1111/mec.13014

Barrett SCH, Husband BC (1997) Ecology and genetics of ephemeral plant populations: *Eichhornia paniculata* (Pontederiaceae) in Northeast Brazil. J Hered 88:277–284

Barrett SCH (2011) Why reproductive systems matter for the invasion biology of plants. In: Richardson, D. M. (Ed.) Fifty years of invasion ecology: the legacy of Charles Elton, Wiley - Blackwell, pp 195–210.

Bunker KV (1994) Overcoming poor germination in Australian daisies (Asteraceae) by combinations of gibberellin, scarification, light and dark. Sci Hortic 59:243–252

Charlesworth D (2006) Evolution of plant breeding systems. Curr Biol 16:726–735. https://doi.org/10.1016/j.cub.2006.07.068

Cheptou PO (2012) Clarifying Baker's law. Ann Bot 109:633–641. https://doi.org/10.1093/aob/mcr127

Cui X, Luo Y, Luo Y (2025) A study on the reproductive characteristics and invasiveness of *Crassocephalum rubens* and *Crassocephalum crepidioides*. Front Ecol Evol 13:1571992. https://doi.org/10.3389/fevo.2025.1571992

Damalas CA (2008) Distribution, biology, and agricultural importance of *Galinsoga parviflora* (Asteraceae). Weed Biol Manag 8:147–153

Datiles MJ, Puttock C (2022) Zinnia peruviana (Peruvian zinnia). CABI Compendium. https://doi.org/10.1079/cabicompendium.120142

de Jv L, de S JRF, Aca A, da Sl CA, Vds F (2015) Use of aniline blue stain to observing pollen tubes development in different *Manihot* Mill. species. Afr J Agric Res 10:1805–1809. https://doi.org/10.5897/ajar2014.8976

Eckert CG, Kalisz S, Geber MA, Sargent R, Elle E, Cheptou PO, Goodwillie C, Johnston MO, Kelly JK, Moeller DA, Porcher E, Ree RH, Vallejo-Marín M, Winn AA (2010) Plant mating systems in a changing world. Trends Ecol Evol 25:35–43. https://doi.org/10.1016/j.tree.2009.06.013

Estes J (2018) Anther number, anther apical appendages, and pollination biology of Calyptocarpus vialis Lessing (Heliantheae; Asteraceae). Okla Native Plant Rec. https://doi.org/10.22488/okstate.19.100005

Ferrer MM, Good-Avila SV (2007) Macrophylogenetic analyses of the gain and loss of self-incompatibility in the Asteraceae. New Phytol 173:401–414. https://doi.org/10.1111/j.1469-8137.2006.01905.x

Gamble JS (1915–1936) Flora of the Presidency of Madras, Vol 2 (Reprinted). Botanical Survey of India, Kolkata.

Gilbert B, Levine JM (2013) Plant invasions and extinction debts. Proc Natl Acad Sci U S A 110:1744–1749. https://doi.org/10.1073/pnas.1212375110

Gioria M, Hulme PE, Richardson DM, Pyšek P (2023) Why are invasive plants successful? Annu Rev Plant Biol 74:49. https://doi.org/10.1146/annurev-arplant-070522-071021

Grombone-Guaratini MT, Solferini VN, Semir J (2004) Reproductive biology in species of *Bidens* L. (Asteraceae). Sci Agric 61:185–189

Grossenbacher D, Briscoe Runquist R, Goldberg EE, Brandvain Y (2015) Geographic range size is predicted by plant mating system. Ecol Lett 18(7):706–713

Groves RH (2006) Are some weeds sleeping? Some concepts and reasons. Euphytica 148(1):111–120

Hajra PK, Rao RR, Singh DK, Uniyal BP (eds.) (1995a) Flora of India. Volume 12: Asteraceae (Anthemideae - Heliantheae). Botanical Survey of India, Kolkata.

Hajra PK, Rao RR, Singh DK, Uniyal BP (eds.) (1995b). Flora of India, Volume 13: Asteraceae (Inuleae–Vernonieae). Botanical Survey of India, Kolkata.

Hao JH, Qiang S, Chrobock T, van Kleunen M, Liu QQ (2011) A test of Baker's law: breeding systems of invasive species of Asteraceae in China. Biol Invasions 13:571–580. https://doi.org/10.1007/s10530-010-9850-4

Herburger K, Holzinger A (2016) Aniline blue and Calcofluor white staining of callose and cellulose in the streptophyte green algae *Zygnema* and *Klebsormidium*. Bio-Protoc 6(20):e1969. https://doi.org/10.21769/BioProtoc.1969

Heyn CC, Joel A (1983) Reproductive relationships between annual species of *Calendula* (Compositae). Plant Syst Evol 143:311–329

Heywood JS (1993) Biparental inbreeding depression in the self-incompatible annual plant *Gaillardia pulchella* (Asteraceae). Am J Bot 80:545–550. https://doi.org/10.1002/j.1537-2197.1993.tb13838.x

Hiscock SJ (2000) Self-incompatibility in *Senecio squalidus* L. (Asteraceae). Ann Bot 85:181–190. https://doi.org/10.1006/anbo.1999.1058

Hollingsworth ML, Bailey JP (2000) Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knot weed). Bot J Linn Soc 133:463–472

Igic B, Lande R, Kohn JR (2008) Loss of self-incompatibility and its evolutionary consequences. Int J Plant Sci 169:93–104. https://doi.org/10.1086/523362

IPBES (2023) Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Roy HE, Pauchard A, Stoett P, Renard Truong T, Bacher S, Galil BS, Hulme PE, Ikeda T, Sankaran KV, McGeoch MA, Meyerson LA, Nuñez MA, Ordonez A, Rahlao SJ, Schwindt, E, Seebens H, Sheppard AW, Vandvik V (eds.). IPBES secretariat, Bonn, Germany

Jabeen N, Bharti U, Sharma N (2012) Inter-population chromosome variation in *Artemisia nilagirica* L. The Nucleus 55:67–71. https://doi.org/10.1007/s13237-012-0055-3

Jeschke JM (2014) General hypotheses in invasion ecology. Divers Distrib 20:1229–1234. https://doi.org/10.1111/ddi.12258

Kaulo MLH (1989) Male sterility in diploid *Ageratum conyzoides* L. Cytologia 54(3):445–448

Kho YO, Baer J (1968) Observing pollen tubes by means of fluorescence. Euphytica 17:298–302

Khuroo AA, Ahmad R, Hamid M, Rather ZA, Malik AH, Rashid I (2021) An annotated inventory of invasive alien flora of India. In T. Pullaiah & M. R. Lelmini (ed) Invasive alien species: observations and issues from around the world, 2, John Wiley & Sons Ltd. pp 16–37.

Laginhas BB, Bradley BA (2022) Global plant invaders: a compendium of invasive plant taxa documented by the peer-reviewed literature. Ecology. https://doi.org/10.1002/ecy.3569

Laginhas BB, Fertakos ME, Bradley BA (2023) We don't know what we're missing: evidence of a vastly undersampled invasive plant pool. Ecol Appl 33(2):e2776

Lee HK, Moody K (1988) Seed viability and growth characteristics of *Eclipta prostrata* (L.) L. Korean J Weed Sci 8:309–316

Li W, Wang B, Wang J (2006) Lack of genetic variation of an invasive clonal plant *Eichhornia crassipes* in China revealed by RAPD and ISSR markers. Aquat Bot 84:176–180

Li XM, Liao WJ, Wolfe LM, Zhang DY (2012) No evolutionary shift in the mating system of North American *Ambrosia artemisiifolia* (Asteraceae) following its introduction to China. PLoS ONE 7:e31935

Little TM, Kantor JH, Robinson BA (1940) Incompatibility studies in *Cosmos bipinnatus*. Genetics 25(2):150–156. https://doi.org/10.1093/genetics/25.2.150

Lozon JD, Macisaac HJ, Lozon JD, Macisaac HJ (1997) Biological invasions: are they dependent on disturbance? Environ Rev 5(2):131–144

Mathakutha R, Steyn C, le Roux PC, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M (2019) Invasive species differ in key functional traits from native and non-invasive alien plant species. J Veg Sci 30:994–1006. https://doi.org/10.1111/jvs.12772

Ming LC (1999) *Ageratum conyzoides*: A tropical source of medicinal and agricultural products. In: Janick J (ed) Perspectives on new crops and new uses. ASHS Press, Alexandria, pp 469–473

Moles AT, Gruber MA, Bonser SP (2008) A new framework for predicting invasive plant species. J Ecol 96(1):13–17

Mungi NA, Qureshi Q, Jhala YV (2023) Distribution, drivers and restoration priorities of plant invasions in India. J Appl Ecol 60:2400–2412. https://doi.org/10.1111/1365-2664.14506

North C (1979) Plant breeding and genetics in horticulture. Mac Millan press Ltd. London, 107

Pannell JR, Barrett SCH (1998) Baker's law revisited: reproductive assurance in a metapopulation. Evolution 52(3):657–668

Pannell JR, Auld JR, Brandvain Y, Burd M, Busch JW, Cheptou PO, Conner JK, Goldberg EE, Grant AG, Grossenbacher DL, Hovick SM, Igic B, Kalisz S, Petanidou T, Randle AM, de Casas RR, Pauw A, Vamosi JC, Winn AA (2015) The scope of Baker's law. New Phytol 208(3):656–667. https://doi.org/10.1111/nph.13539

Paudel R, Fristoe TS, Kinlock NL, Davis AJS, Zhao W, van Calster H, Chytrý M, Danihelka J, Decocq G,

Ehrendorfer-Schratt L, Guo K, Guo WY, Kaplan Z, Pierce S, Wild J, Dawson W, Essl F, Kreft H, Pergl J, Pyšek P, Winter M, van Kleunen M (2025) Many plants naturalized as aliens abroad have also become more common within their native regions. Nat Commun. https://doi.org/10.1038/s41467-025-63293-6

Petanidou T, Godfree RC, Song DS, Kantsa A, Dupont YL, Waser NM (2012) Self-compatibility and plant invasiveness: comparing species in native and invasive ranges. PPEES 14:3–12. https://doi.org/10.1016/j.ppees.2011.08.003

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. J Environ Manage 57:239–251

Pierson JC, Swain SM, Young AG (2013) Incest versus abstinence: reproductive trade-offs between mate limitation and progeny fitness in a self-incompatible invasive plant. Ecol Evol 3:5066–5075. https://doi.org/10.1002/ece3.875

POWO (2025). "Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; https://powo.science.kew.org/ Retrieved 06 May 2025

Rambuda TD, Johnson SD (2004) Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? Divers Distrib 10:409–416. https://doi.org/10.1111/j.1366-9516.2004.00100.x

Rao MM, Raju AS, Ramana KV (2017) Secondary pollen presentation and psychophily in *Vernonia albicans* and *V. cinerea* (Asteraceae). Phytol Balcan 23:171–186

Razanajatovo M, Maurel N, Dawson W, Essl F, Kreft H, Pergl J, Pyšek P, Weigelt P, Winter M, van Kleunen M (2016) Plants capable of selfing are more likely to become naturalized. Nat Commun. https://doi.org/10.1038/ncomms13313

Rejmanek M, Richardson DM (1996) What attributes ma0ke some plant species more invasive? Ecology 77:1655–1661

Ren MX, Zhang QG, Zhang DY (2005) Random amplified polymorphic DNA markers reveal low genetic variation and a single dominant genotype in *Eichhornia crassipes* populations throughout China. Weed Res 45:236–244. https://doi.org/10.1111/j.1365-3180.2005.00445.x

Sankaran KV, Suresh TA (2013) Invasive alien plants in the forests of Asia and the Pacific. Food and Agriculture Organization of United Nations, Bangkok, Thailand

Shabbir A, Bajwa AA, Mao R, Kezar S, Dorji S, Adkins SW (2024) Biology of invasive plants 6. *Parthenium hysterophorus* L. Invasive Plant Sci Manag 17:129–156. https://doi.org/10.1017/inp.2024.23

Shivanna K (2014) Reproductive assurance through autogamy in some annual weed species. Proc Natl Acad Sci India Sect B Biol Sci 84:681–687

Stebbins GL (1957) Self fertilization and population variability in the higher plants. Am Nat 91:337–354

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273. https://doi.org/10.1111/j.1469-8137.2007.02207.x

Tripathi RS, Yadav AS, Kushwaha SPS (2012) Biology of *Chromolaena odorata, Ageratina adenophora* and *Ageratina riparia*: a review. In: Bhatt JR et.al. (eds) Invasive alien plants: an Ecological Appraisal for the Indian Subcontinent, CABI 32:43–56.

Turner JH (1933) The viability of seeds. Kew Bull 1933:257–269

Usharani B, Raju AJS (2018a) Reproductive ecology of the globally invasive Whitetop Weed, *Parthenium hysterophorus* (Asteraceae). Phytol Balcan

Usharani B, Raju AJS (2018b) Pollination ecology of *Synedrella nodiflora* (L.) Gaertn. (Asteraceae). J Threat Taxa 10:12538–12551

van Kleunen M, Johnson SD (2007) Effects of self-compatibility on the distribution range of invasive European plants in North America. Conserv Biol 21:1537–1544. https://doi.org/10.1111/j.1523-1739.2007.00765.x

van Kleunen M, Manning JC, Pasqualetto V, Johnson SD (2008) Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. Am Nat 171:195–201. https://doi.org/10.1086/525057

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

van Kleunen M, Dawson W, Maurel N (2015) Characteristics of successful alien plants. Mol Ecol 24:1954–1968. https://doi.org/10.1111/mec.13013

Verma P, Majee M (2013) Seed germination and viability test in tetrazolium (TZ) assay. Bio-Protoc 3(17):e884. https://doi.org/10.21769/BioProtoc.884

Vervoort A, Cawoy V, Jacquemart AL (2011) Comparative reproductive biology in co-occurring invasive and native *Impatiens* species. Int J Plant Sci 172:366–377. https://doi.org/10.1086/658152

Wang F, Zhang FJ, Chen FD, Fang WM, Teng NJ (2014) Identification of *Chrysanthemum* (*Chrysanthemum morifolium*) self-incompatibility. Sci World J 2014(1):625658

Warwick SI, Sweet RD (1983) The biology of Canadian weeds.: 58. *Galinsoga parviflora* and *G. quadriradiata* (= *G. ciliata*). Can J Plant Sci 63:695–709

Warwick SI, Thompson BK (1989) The mating system in sympatric populations of *Carduus nutans, C. acanthoides* and their hybrid swarms. Heredity 63(3):329–337

White DJ, Haber E, Keddy C (1993) Invasive plants of natural habitats in Canada. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada

Whitehead MR, Lanfear R, Mitchell RJ, Karron JD (2018) Plant mating systems often vary widely among populations. Front Ecol Evol 6:38. https://doi.org/10.3389/fevo.2018.00038

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77(6):1661–1666

Zachariades C, Day M, Muniappan R, Reddy GV (2009) *Chromolaena odorata* (L.) king and robinson (Asteraceae). In: Muniappan R, Reddy GV, Raman A (eds) Biological control of tropical weeds using arthropods. Cambridge University Press, Cambridge, pp 130–162

Zavaliev R, Epel BL (2014) Imaging callose at plasmodesmata using Aniline Blue: Quantitative Confocal Microscopy. Methods Mol Biol Plasmodesmata. https://doi.org/10.1007/978-1-4939-1523-1_7

Zeng JJ, Zhou B, Wang N (2021) Comparing the reproductive biological characteristics of the alien invasive *Coreopsis lanceolata* to those of the non-invasive alien congener *Coreopsis tinctoria*. Plant Species Biol 36(3):379–389. https://doi.org/10.1111/1442-1984.12323

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

Zhang A, Hu X, Yao S, Yu M, Ying Z (2021) Alien, naturalized and invasive plants in China. Plants. https://doi.org/10.3390/plants10112241