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Outcrossing breeding system does not compromise invasiveness in *Buddleja davidii*

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ABSTRACT

Introductions of alien plant species are often likely to consist of a few individuals. Thus, invasion success may strongly depend on their reproductive biology. A high number of self-compatible plants species are known to be successful colonizers of new habitats, even able to establish populations from single propagules. However, many other invasive species require pollen vectors. Here, we investigated the mating system of *Buddleja davidii*, a fast growing shrub native to China that colonizes quickly in disturbed habitats such as quarries, river banks, along railways and roads, both in its native and invasive regions. It was intentionally introduced to Europe as an ornamental plant because of its fragrant and showy flowers. We additionally studied its vulnerability to biparental inbreeding depression by performing a controlled crossing experiment using pollen from the same population or from geographically close and distant populations, respectively. As a measure for pollination success, we used capsule weight, seed number per capsule and seed weight for each treatment.

The self-incompatibility index for *B. davidii* was found to be 96% suggesting that successful reproduction strongly depends on cross-pollination and the presence of appropriate pollen vectors. Since cross-pollination did not reveal significant differences in measured traits, it is assumed that invasive *B. davidii*-populations do not suffer from biparental inbreeding depression. *B. davidii* has fragrant and rewarding flowers that mainly attract butterflies. We conclude that the long distance pollen transfer performed by these insects may have prevented inbreeding so far and thus contributes to the invasive spread of *B. davidii* in Europe.

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Introduction

Small population size and isolation of a population cause a particular vulnerability to genetic drift and inbreeding which may negatively affect mean population fitness (e.g., Reed and Frankham, 2003). The breeding system can therefore be considered to be of major importance for the survival of small or isolated populations. This relationship has usually been studied using rare plant species as a model system (Fischer et al., 2003; Paschke et al., 2002; Rathke and Jules, 1993), but may also apply for non-native species introduced to a new environment: They usually reach their new habitat with only few individuals, often isolated and not optimally adapted to the environmental conditions. Consequently, invasion success may be tightly linked to their reproductive biology (Küster et al., 2008). For instance, self-compatible plants are usually thought to be particularly successful colonizers of new habitats as they have the ability to establish populations from single propagules after being dispersed over long distances (Baker, 1967). But, paradoxically, this will limit (at least initially) their ability to better adapt to their new conditions and ineffective pollination may stop or substantially retard the invasion of a flowering plant. However, autogamy is more common in invasive plant species than allogamy (van Kleunen and Johnson, 2007). Apart from natural processes, human activities such as multiple introductions, cultivation and breeding may further contribute to the success of non-native plants (Ellstrand and Schierenbeck, 2000; Kitajima et al., 2006).

Despite the higher frequency of autogamy among invasive species, many others still require pollen vectors (Bartomeus et al., 2008a; Brown and Mitchell, 2001; Campbell, 1989; Chittka and Schurkens, 2001). For those species, the success in colonization and spread not only depends on the ability to attract the services of resident pollinators but also on the quantity and quality of pollen transfer. Pollinators may stay away when the reward is not abundant enough. Thus, a high number of flowers with attractive colors and nectar guides or far-reaching fragrance facilitate pollinator attraction.

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The fragrant and showy flowers of *Buddleja davidii* are the cause of its introduction for ornamental purposes from China to Europe around 1890. Since 1920, *B. davidii* has been subject to different breeding programs focusing on flower color, size and shape of inflorescences resulting in more than 90 different cultivars (Stuart, 2006). However, *B. davidii* populations can now be found commonly outside human care along railways and riverbanks, streets and in quarries. After escaping from gardens the species has become naturalized (Csurshes and Edwards, 1998; Leeuwenberg, 1979; Tutin, 1972; Webb et al., 1988). Due to its high growth rates, early maturity, high reproductive output of easily distributed seeds and its tolerance to a broad range of environmental conditions (Kreh, 1952; Webb et al., 1988), *B. davidii* is considered to have a high invasive potential (Ebeling et al., 2008; Kriticos et al., 2011) that may cause serious problems in invaded areas (Anisko and Im, 2001; Smale, 1990). Despite evidence for outbreeding in the native range of *B. davidii* (Chen et al., 2011) we lack a deeper understanding of the pollination system and its vulnerability to inbreeding in its invasive area of occurrence. Unraveling these factors will be important for designing control programs. Within the genus there are both self-compatible and self-incompatible species (Norman, 2000). Based on their conspicuous flower coloration and morphology, the species is especially known to attract butterflies (Guédot et al., 2008; Owen and Whiteway, 1980) which might indicate the necessity of allogamy. Although some basic work has been done on its reproductive biology, mainly addressing the flower morphology, seed production and pollinator attractiveness (Brown, 1990; Brown, 2008; Guédot et al., 2008; Pfitzner, 1983), little is known about the mating system of *B. davidii*.

Here we investigate the mating system of *Buddleja davidii* to reveal whether the species is self-pollinating within its invasive range. Due to the large floral display, ample floral reward and frequent insect visitors, we hypothesize that (1) the invasive *B. davidii* does not self-pollinate. Since *B. davidii* is typically visited by butterflies which fly over long distances, we further hypothesize that the species (2) does not suffer from biparental inbreeding depression.

Materials and methods

Study species

Butterfly Bush (*Buddleja davidii* Franch., Scrophulariaceae) is a 3–5 m tall multi-stemmed shrub, native to China (Wu and Raven, 1996) and with a life span of approximately 40 years. It flowers from July to September, usually 1 year after germination (Esler, 1988), but sometimes in its first year (Ebeling et al., 2011). The terminal inflorescences are thyrsoid panicles appearing on current-year stems or branches and are up to 30 cm in length (Leeuwenberg, 1979; Wu and Raven, 1996). The flowering is asynchronous: the individual flowers at each panicle mature acropetally from the base to the top of the inflorescence (Findley et al., 1997). The flower shape is a typical butterfly flower: The corolla is made up of four petals that are fused into a corolla-tube (Tallent-Halsell and Watt, 2009), which is about 5–8 mm long. While the flower itself is commonly purple and lilac (white and red can be found in cultivars), the interior of the flower is orange with a series of yellow nectar guides leading to the interior of the tube (Tallent-Halsell and Watt, 2009). To attract insects, *Buddleja davidii* produces fragrance and nectar (Guédot et al., 2008).

While individual flowers last for 1–3 days, a panicle may persist for more than two weeks (Findley et al., 1997). Each panicle may produce between 100 and more than 1700 capsules, with 28–75 seeds per capsule (Brown, 1990; Kreh, 1952). A single mature individual of *B. davidii* may produce 100,000 to 3 million seeds per year (Miller, 1984). The seeds are about 3 mm long with linear wings at both ends (Wu and Raven, 1996) facilitating the dispersal by wind or water (Campbell, 1984).

Test for mating system and inbreeding depression

For our study we used plants derived from seeds sampled in 20 invasive populations across western and central Europe (Table 1). The spatial distance among them ranged from 17 to 1442 km, with a median of 599 km. In 2005, seeds from five individuals per population were germinated in potting soil in a greenhouse and, when having attained a height of 10 cm, two progenies of each of the five seed families per population (200 plant individuals in total) were planted randomly in a common garden in Halle, Germany (51°29′N, 11°58′O). This common garden experiment was originally designed to investigate population differentiation in plant growth and reproduction, and to test whether local adaptation to climatic conditions has contributed to the invasive spread of the species across Europe (Ebeling et al., 2011). In addition, we made use of individuals planted in the common garden to carry out the present study on *B. davidii*'s breeding system.

Our first pollination experiment was designed to investigate the mating system of invasive *B. davidii*. For this purpose, we used one individual each out of 13 of the 20 populations planted in the common garden (Table 1). Before anthesis, four inflorescences of each individual were bagged with Crispac®-bags allowing ventilation and growth of flowers but preventing pollen vectors from visiting the flowers. From mid to end of August 2006, the following treatments for testing the mating system were applied to each of these individuals:

1. test for spontaneous autogamy: complete pollinator exclosure by keeping flowers bagged;
2. test for self-incompatibility: hand pollination with pollen of the same individual (geitonogamy);
3. cross pollination: hand pollination with pollen of another individual of the same population;
4. control: open pollination.

Assuming that individuals within the same population are more closely related than among populations, pollination between plants within populations may lead to biparental inbreeding and biparental inbreeding depression (Nason and Ellstrand, 1995). To test for biparental inbreeding depression, we did a second pollination experiment with four populations in the common garden (Table 1). We defined two populations as geographically close, if the distance between their places of origin was shorter than the 25% quantile (314 km) of all pairwise spatial distances among the sampled 20 populations. Accordingly, we considered them as geographically distant, if their places of origin were farther away from each other than the 25% quantile. While individuals from Duisburg (Germany), Cologne (Germany) and Reading (Great Britain) acted as both, pollen donor and pollen receptor, individuals from Manchester (Great Britain) were only used as a pollen donor. We applied the following treatments to eight individuals (Duisburg, Reading) or ten individuals (Cologne) of each populations, respectively:

1. effect of biparental inbreeding: hand pollination with pollen of the same population;
2. effect of outcrossing between geographically close populations: hand pollination with pollen from a population at a distance shorter than the 25% quantile (63 km or 242 km respectively);
3. effect of outcrossing between two geographically distant populations: hand pollination with pollen from a population of a distance larger than the 25% quantile (556 km or 537 km respectively);
4. control: open pollination.

Table 1
List of the 20 European populations of *Buddleja davidii* provenances of which were planted in the common garden in Halle (Saale), and their respective use for experimentally studying (1) the mating system and/or (2) inbreeding depression.

Population	Geographic coordinates		Altitude a.s.l. [m]	Experiment for which the plants were used
	Latitude	Longitude		
France/St. Malo	48.6122N	2.0525W	40	Mating system
Germany/Cologne	50.9627N	6.9730E	46	Inbreeding depression
Germany/Darmstadt	49.8894N	8.6380E	127	Mating system
Germany/Duisburg	51.4827N	6.7856E	30	Inbreeding depression
Germany/Essen	51.4652N	7.0266E	37	Mating system
Germany/Halle	51.4869N	11.9683E	99	Mating system
Germany/Oldenburg	53.1438N	8.2138E	68	Mating system
Germany/Seligenstadt	50.0402N	8.9681E	114	Mating system
Germany/Sulzbach	48.8630N	8.3711E	470	Mating system
Germany/Tettnang	47.6300N	9.5847E	447	Not used
Italy/Merano	46.6667N	11.1666E	402	Mating system
Spain/Leioa	43.3277N	2.9869W	37	Not used
Switzerland/Basel	47.5472N	7.5892E	280	Mating system
Switzerland/Geneve	46.2083N	6.1428E	387	Not used
UK/Eastleigh	50.9666N	1.3506W	15	Mating system
UK/Egham	51.4305N	0.5467W	17	Mating system
UK/Manchester	53.4777N	2.2456W	50	Mating system, inbreeding depression
UK/Reading	51.4527N	0.9631W	42	Inbreeding depression
UK/Wallingford	51.6000N	1.1258W	48	Not used
UK/Yarmouth	50.7027N	1.4967W	1	Mating system

In both experiments, hand pollination was carried out by rubbing ripe anthers of the pollen donor against the stigma of the receptor flower using forceps thoroughly cleaned with alcohol after each pollination treatment. For each treatment, four flowers out of one inflorescence per individual were randomly chosen and labelled using straps of different colors according to treatment. In January 2007, matured capsules were collected and stored at room temperatures. As a measure for pollination success, we weighed the whole capsule, counted seeds per capsule and determined dry mass of individual seeds. Assuming that all apparently well-developed seeds were viable, we calculated the self-incompatibility index according to Pound et al. (2002) as ISI = $[(V_C - V_S)/V_C] \times 100$, with V_C = viable seed per flower cross-pollinated and V_S = viable seed per flower self-pollinated by geitonogamy.

Statistical analysis

For statistical analyses, data of the four flowers per individual and treatment were averaged ('plant' was the experimental unit). The mating system experiment (experiment 1) was analyzed using ANOVA, considering pollination treatment as a fixed factor and plant individual as block (procedure GLM of the software package SAS, version 9.1). Orthogonal contrasts were used to test the following a priori hypotheses for the mating system: (1) "bagged vs. pollinated flowers": dry mass of individual capsules and seeds, as well as seed set per capsule, would be lower in permanently bagged flowers than in hand- or open-pollinated flowers; (2) "hand- vs. open-pollinated flowers": hand pollination would be as effective as open pollination. (3) "selfing vs. outcrossing treatment": flowers which were hand-pollinated with pollen from another flower of the same plant would have lower capsule and seed mass as well as seeds mass than in flowers which were cross-pollinated by hand.

For the analysis of biparental inbreeding depression (experiment 2), we considered treatment as a fixed effect, and population, individual within population, and population × treatment interaction as random effects. Since the data were unbalanced, we used type III sum of squares (Shaw and Mitchell-Olds, 1993). We used orthogonal contrasts to test following a priori hypotheses: (1) "hand vs. open pollination": hand pollination would be as effective as open pollination; (2) "own population vs. foreign population": if pollination by the same population leads to biparental inbreeding depression, seed set would be lower than in flowers pollinated with foreign pollen; (3) "close population vs. distant population": assuming that geographically close populations are closer related to each other than geographically distant populations, seed set should be lower if pollen donors were from a close population compared to a far-off population.

Results

In our first experiment, investigating the mating system, permanently bagged flowers produced only a very few well-developed capsules and seeds (Fig. 1). Accordingly, capsule mass and seed set were strongly reduced compared to flowers which were hand- or open-pollinated (Table 2), indicating that spontaneous autogamy is rather uncommon in *B. davidii*, also in its invasive range. Average dry mass of the few seeds produced by spontaneous autogamy, however, did not differ from the other treatments. The comparison between hand- and open-pollinated flowers revealed a higher capsule mass, seed set and average seed mass of the latter. Note that the lower capsule mass and seed set of hand-pollinated flowers were caused by the selfing treatment only. These values were nearly identical for outcrossed and open-pollinated flowers, indicating that hand pollination was as effective as open pollination. The slightly lower seed mass of outcrossed compared to open-pollinated flowers may indicate a side effect of hand-pollination, perhaps due to the bagging of flowers. Capsule mass and seed set resulting from geitonogamy were significantly lower compared to cross-pollinated flowers (Fig. 1; Table 2). Selfing did not completely prevent seed production, but reduced it to a very low level, resulting in a self-incompatibility index of 95.8%.

In our second experiment, testing for biparental inbreeding depression, we could not detect any significant effect of pollination treatments on capsule mass, number of seeds and seed mass (Table 3). The population × treatment interaction was only significant for the number of seeds. None of the a priori hypotheses could be confirmed by the contrasts. There was no significant difference between hand and open pollination. Moreover, there was neither a difference between pollination by the same population versus pollination by foreign populations, nor between pollination by a geographically close population and pollination by a geographically distant population (Table 3).

Table 2
Results of analyses of variance (ANOVA) for three reproductive traits of *Buddleja davidii* after different pollination treatments in a common garden (pollination experiment 1): spontaneous autogamy (exclusion of pollinators from permanently bagged flowers), self-incompatibility (hand-pollination with pollen from the same plant), outcrossing (hand-pollination with pollen from another plant), and natural open-pollination.

Source of variation	Mean capsule mass			Mean seed number per capsule			Mean seed mass		
	d.f.	Sum of squares	*F* value	d.f.	Sum of squares	*F* value	d.f.	Sum of squares	*F* value
Individual	12	50.4	1.21	12	3988	1.36	12	1413	0.66
Pollination treatment	3	253.4	24.35***	3	16,820	22.91***	3	908	2.02
Bagged vs. pollinated flowers	1	95.6	27.54***	1	5763	23.55***	1	131	0.87
Hand vs. open pollination	1	44.6	12.85**	1	2702	11.04**	1	732	4.88*
Selfing vs. outcrossing	1	113.3	32.65***	1	8355	34.14***	1	184	1.23
Residuals	36	124.9		36	8811		18	2700	

[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

Discussion

In our study, we found that selfing in *Buddleja davidii* (either by spontaneous autogamy or by geitonogamy) produced only a few capsules and very few viable seeds compared to open pollination or cross-pollination by hand, indicating self-incompatibility. This suggests the presence of a gametophytic self-incompatibility system preventing fertilization as frequently found in Scrophulariaceae (de Nettancourt, 1997). Alternatively, very strong (uniparental) inbreeding depression in the ovule stage would be necessary if fertilization was successful. We therefore conclude that successful reproduction of invasive *B. davidii*, and hence the local population increase as well as the large-scale spread, critically depend on cross-pollination and appropriate pollen vectors.

Due to flower morphology and abundant nectar, butterflies may be the most efficient pollinators of *B. davidii* although bees and other insects are frequent visitors of the flowers (Houghton et al., 2003; Miller, 1984; Owen and Whiteway, 1980; Chen et al., 2011). Several studies have shown that most pollinators on invasive plants are generalists (e.g. Brown et al., 2002; Olesen et al., 2002; Richardson et al., 2000). In fact, most of the butterfly species found on *B. davidii* are generalist pollinators belonging to the families of Nymphalidae, Satyridae and Pieridae (Owen and Whiteway, 1980). However, the ability to attract pollinators does not guarantee sufficient quantity and quality of pollen transfer (Aizen and Harder, 2007; Fishbein and Venable, 1996). To produce a high amount of viable seeds, it is important for *B. davidii*, that the foraging distance of pollinating butterflies exceeds 1000 m (Cant et al., 2005) guiding them to visit different individuals within a population. Pollinator visitation rates of the alien plant must be equal to or greater than those of native plant species visited by the same pollinators in order to prevent pollen limitation. Consequently, the presence of an invasive species like *B. davidii* may affect interactions among native plant species and their pollinators either negatively, by decreasing visitation rates and therefore the pollen transport in native species (e.g. Brown et al., 2002; Larson et al., 2006; Lopezaraiza-Mikel et al., 2007), or positively, by additionally attracting pollinators to shared sites, increasing by this way the visitation rate (Bartomeus et al., 2008b; Moragues and Traveset, 2005). However, there are also studies that showed no effect of invasive plants on visitation rates and reproduction of native species (Bartomeus et al., 2010; Moragues and Traveset, 2005). The few data available for invasive *B. davidii* populations are inconsistent (Pfitzner, 1983; Giuliano et al., 2004) and neither those observations nor our study directly investigated the competition for pollinators within the study areas. We thus cannot conclude that the establishment of *B. davidii* and its distribution in the invasive area depends on its attractiveness to and competition for pollinators. Butterflies may facilitate high gene flow within and between *B. davidii* populations as they forage over large distances (Cant et al., 2005). High gene flow by seed or pollen dispersal can counteract effects of genetic drift in outcrossing species (Kloss et al., 2011). This aspect may also explain why there are no hints for biparental inbreeding depression in invasive *B. davidii* populations in Europe. Although pollination with pollen from the same individual led to some seed set, cross pollination clearly showed a much higher pollination success. This success did not correlate to the distance of the pollen source population. In a molecular study using microsatellite markers, Schreiter et al. (2011) revealed a multilocus outcrossing rate of 93% in a local *B. davidii* population in Central Germany which supports the findings of our pollination experiment. In addition, the fact that *B. davidii* is a tetraploid species ($2n = 76$, ($4\times$); Chen et al., 2007, 2011) may be advantageous to compensate for deleterious mutations (Barrett and Richardson, 1986).

In our study we showed that the invasive species *Buddleja davidii* is largely outcrossing and does not suffer from inbreeding

Table 3
Results of analyses of variance (ANOVA) for three reproductive traits of *Buddleja davidii* after different pollination treatments in a common garden (pollination experiment 2): biparental inbreeding (hand pollination with pollen from another plant of the same population), short-distance outcrossing (hand pollination with pollen from a population of small geographic distance), and long-distance outcrossing (hand pollination with pollen from a population of large geographic distance).

Source of variation	d.f.	Error d.f.	Mean capsule mass		Mean seed number per capsule		Mean seed mass	
			Sum of squares	*F* value	Sum of squares	*F* value	Sum of squares	*F* value
Population	2	23	32.1	0.81	414	0.13	497	1.31
Individuals (population)	23	45 (46)	457.2	3.04***	37,694	6.01***	4349	8.83***
Pollination treatment	3	6	40.3	1.75	615	0.32	150	1.43
Hand vs. open pollination	1	6	36.9	4.81	439	0.68	131	3.77
Own vs. foreign population	1	6	2.8	0.36	165	0.26	17	0.48
Close vs. distant population	1	6	0.4	0.05	2	0.00	2	0.05
Population × pollination	6	45 (46)	46.0	1.17	3892	0.04*	208	1.62
Residuals	45 (46)		293.8		12,266		985	

[*] $P < 0.05$.
[***] $P < 0.001$.

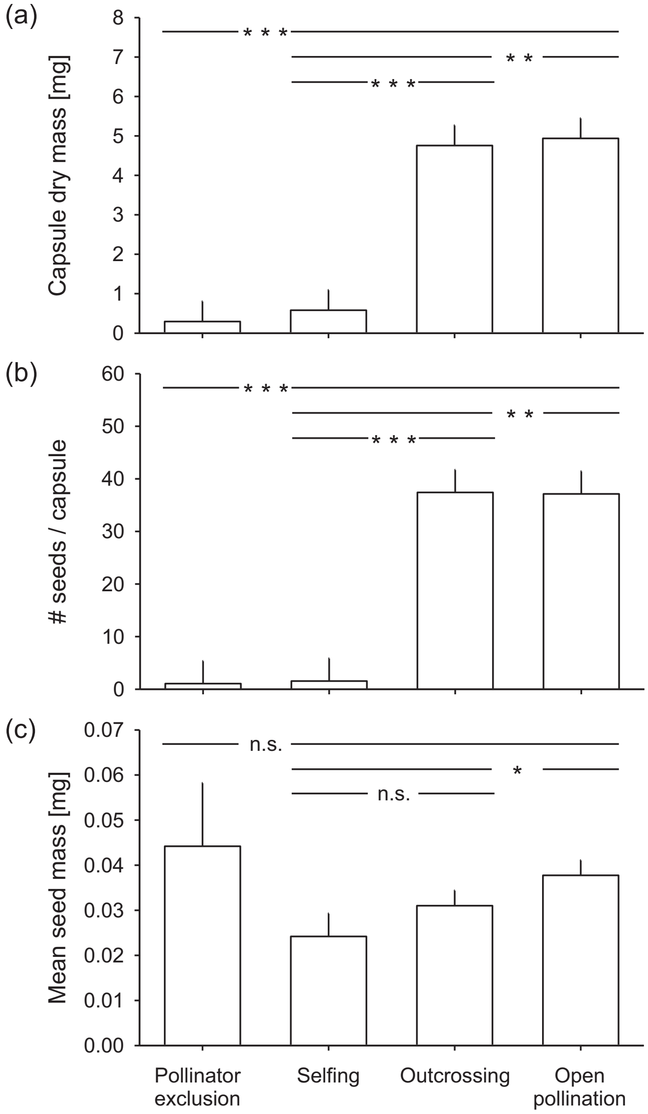

Fig. 1. Capsule dry mass (a), number of seeds per capsule (b), and average seed mass (c) of *Buddleja davidii* (means + S.E.) after different pollination treatments in a common garden (pollination experiment 1). Horizontal lines above bars refer to orthogonal contrasts among the pollination treatments: (1) bagged vs. pollinated flowers, (2) hand- vs. open-pollinated flowers, and (3) selfing vs. outcrossing treatment. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

depression in its invasive range. These results suggest that fragrance and nectar production successfully attract native pollinators and thus, contribute to its invasiveness. Breeding of sterile cultivars or cultivars with altered flower and fruit morphology (Lindstrom et al., 2004; Podaras, 2005) should be encouraged as well as their marketing. Nevertheless, further studies are needed to evaluate whether there is pollinator competition between *B. davidii* and native species sharing the same habitat, or whether the presence of the butterfly bush might be beneficial for either pollinators or native plants or both.

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