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Non-naturalized alien plants receive fewer flower visits than naturalized and native plants in a Swiss botanical garden

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ABSTRACT

Many animal-pollinated plant species have been introduced to non-native regions without their usual pollinators. Nevertheless, some of these alien species managed to establish reproducing naturalized populations, which might negatively affect native plants. Recent studies have shown that many naturalized alien species can readily attract native pollinators. However, it is not known whether alien species that have not established naturalized populations are less successful in attracting pollinators. Therefore, we tested whether flower-visitation rates are lower for non-naturalized aliens than for naturalized alien and native species. We conducted a comparative study on flower visitation of 185 native, 37 naturalized alien and 224 non-naturalized alien plant species in the Botanical Garden of Bern, Switzerland. Our phylogenetically corrected analyses showed that non-naturalized alien species received fewer flower visitors than both naturalized alien and native species. Native, naturalized alien and non-naturalized alien species were visited by similar flower-visitor communities. Furthermore, among the naturalized alien species, the ones with a broader distribution range in Switzerland received a more diverse set of flower visitors. Although it has been suggested that most alien plants can readily integrate into native plant–pollinator networks, we show evidence that the capacity to attract flower visitors in non-native regions is different for naturalized and non-naturalized alien plants. Therefore, we conclude that successful naturalization of alien plants may be related to flower visitation.

1. Introduction

Many plant species have been introduced, for example as garden plants, to new regions where they encounter novel abiotic and biotic conditions. Some of these alien plant species managed to establish reproducing naturalized populations and some of those species have become invasive and constitute a threat to native communities by displacing native organisms and altering ecosystem functioning (Pimentel et al., 2000; Vilà et al., 2011; Vitousek et al., 1997). In order to predict and prevent invasions, and therefore to allow natural resource managers and policy makers to set priorities in management policies, it is of both basic and applied interest to understand the invasion process. Consequently, a major question in ecology and conservation biology is what determines successful naturalization of alien species.

The establishment of alien species obviously depends, at least partly, on successful reproduction. Globally, an estimated 87.5% of flowering plant species rely fully or partly on animals for pollination (Ollerton et al., 2011). Baker (1955) posed that the ability to attract pollinators in a new range is an important constraint for establishment, particularly if the species does not have the means of uniparental reproduction. Nevertheless, many alien plant species have managed to reproduce and establish naturalized populations in new ranges without their usual pollinators, and some have become invasive. Recent studies showed that many naturalized and invasive alien plant species are capable of autonomous self-fertilization (Harmon-Threatt et al., 2009; van Kleunen et al., 2008), which makes them less reliant on pollinators. Other recent studies showed that many naturalized and invasive alien plant species have managed to integrate into native plant pollinators webs, can use a range of different pollinators (Memmott and Waser, 2002; Vilà et al., 2009), and might negatively affect the pollination of co-occurring native plants (Morales and Traveset, 2009). In other words, naturalized alien species are able to attract pollinators in their new ranges, and this might have allowed them to establish and maintain wild populations. However, none of these studies looked at flower visitation of alien species that have

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not become naturalized. Therefore, it remains unclear whether the capacity of attracting pollinators distinguishes naturalized alien from non-naturalized alien species, that is, whether it could drive naturalization of alien species (van Kleunen et al., 2010).

The capacity of a plant to attract flower visitors is influenced by many factors, such as flower size and color, plant size, and area covered by and density of the plant population (Faegri and Van der Pijl, 1966; Schemske and Bradshaw, 1999; van Kleunen et al., 2007b). Many alien plants have showy and attractive flowers due to a biased introduction of such species (van Kleunen et al., 2007a). This means that species traits that are associated with naturalization and invasiveness might actually be related to human preference and selection for introduction on ornamental or cultivation purposes (Chrobock et al., 2011). Thus, it is important to account for these factors when comparing flower visitation among groups of species.

To test the importance of flower visitation for naturalization of alien plant species, we used a powerful multi-species comparative approach (van Kleunen et al., 2014) by assessing visitation rates on 446 alien and native plant species in the Botanical Garden of Bern, Switzerland. Botanical gardens offer unique opportunities for hosting comparative studies because species from a broad taxonomic range and from a wide geographic area are growing under similar and thus comparable conditions (Primack and Miller-Rushing, 2009). Flower visitation might differ between garden habitats and (semi-)natural habitats (Chrobock et al., 2013b). However, as many naturalized alien species often escaped from botanical gardens (Hulme, 2011), it is highly relevant to study the potential drivers of naturalization of alien species in such garden habitats.

Species that are alien to Switzerland but native to other parts of Europe might be more likely to encounter suitable flower visitors as it is likely that many of the flower visitors in their native range also occur in Switzerland. Therefore, we also tested whether flower visitation differed between alien species of European origin and the ones of non-European origins. It has been shown that flower visitation may change along the different stages of the invasion process as a newly introduced species may receive fewer visits at an early stage (King and Sargent, 2012). Therefore, we also tested among our naturalized alien species, whether the ones that occur more frequently in Switzerland attract more flower visitors. Because effective pollen transfer is most likely determined by the number of insect visits, the duration of each visit and the diversity of flower visitors (Herrera, 1989; Ollerton et al., 2007; Vázquez et al., 2005), we assessed these different parameters.

Our specific questions were: (1) Is flower visitation (number of visits, duration of visits, flower-visitor diversity) lower for non-naturalized species than for naturalized alien and native species? (2) Are native, naturalized alien and non-naturalized alien plant species visited by different insect communities? (3) Do alien species from other parts of Europe attract more flower-visitors than alien species from other continents? (4) Is flower visitation higher for more widespread than for less widespread naturalized aliens in Switzerland?

2. Methods

2.1. Study site and flower-visitor observations

To test whether native, naturalized alien and non-naturalized alien plant species differ in number of insect visits, duration of visits, diversity of flower visitors and composition of flower-visitor community, we conducted observations of flower visitors to 185 native, 37 naturalized alien, and 224 non-naturalized alien plant species (Table S1) in the Botanical Garden of Bern, Switzerland (46.57° N, 7.26° E). The botanical garden contains about 4500 plant species growing outdoors, mostly in mixed garden beds, in a total area of 24470 m^2 under similar climatic conditions (altitude: 501–537 m, rainfall: 1028 mm/year, annual mean temperature: 8.1 °C). The garden is situated near the city center of Bern, along the River Aare, which provides a green corridor connecting it to surrounding (semi-)natural habitats. We recorded all native, naturalized alien and non-naturalized alien entomophilous plant species that were flowering in the botanical garden during the observation periods, and from each of these three groups we randomly selected species for observations.

To cover the complete plant flowering season, we did seven observation censuses: 24 March, 19 April, 24 May, 27 June, 29 July, 29 August and 23 September 2011. At each census, we did observations on natives, naturalized and non-naturalized aliens (Table S2), and each species was used in one census only (Table S1). A few days prior to each observation census, we prepared a list of the flowering entomophilous species in the botanical garden at that time. To account for potential confounding factors that could influence flower visitation, we measured species' characteristics that are likely to determine how conspicuous and attractive they are to flower visitors. For each species, we recorded maximum plant height, total area occupied in the botanical garden (i.e. abundance of the species in the garden), the number of flower units per m^2 (i.e. flower-unit density), size of flower units, flower color categories (blue, green, red, white, yellow), flower symmetry (bilaterally or radially symmetric) and exposure to the sun at the moment of observation (yes/no). A flower unit was defined as a unit of one or more flowers that an insect has to fly to in order to reach the next unit (Dicks et al., 2002). So, one capitulum with multiple flowers of an Asteraceae species was considered to be one flower unit. Our flower-color categories might not capture all the optical cues that are relevant for pollinators. We documented the origin and the status of each species, i.e. whether it is native to Europe or not (Tutin et al., 1980), and whether it is a native, naturalized alien or non-naturalized alien species in Switzerland (Lauber and Wagner, 2007).

Because flower-visitor activity depends strongly on the weather, each census was carried out on a sunny day. Furthermore, to reduce variation in flower visitation due to diurnal changes in weather conditions, we did all observations within the short time frame of approximately two hours. We chose the time frame c. 1300–1500 h because most flower visitors in the botanical garden were then active. Therefore, for each census, a team of 7–15 volunteers (a total of 34 persons for the whole study), which consisted of students, lab members and colleagues from other research labs, did the observations simultaneously. For each flowering species, ten flower units, if available, were observed simultaneously for 15 min. All flower units were in close proximity but were not necessarily on the same individual. If there were fewer than 10 flower units available, we recorded the number of observed flower units.

All flower visitors that made contact with reproductive organs of the focal flower units were assumed to be pollinators. Since the observations were performed by volunteers without specific taxonomic knowledge on insects, and we could not catch all flower visitors, it was not possible to identify flower visitors to the species level. We recorded the number of visits, the duration of visits, using a watch, and the flower-visitor taxonomic groups (ants, bee flies, bees, beetles, bumblebees, butterflies, flies, hover flies, moths and wasps). We recorded duration of visits because long visitation periods may increase the likelihood of the flower visitor to function as pollinators (Ollerton et al., 2007). In total, we observed flower visitors for 111.5 h. Although 15 min of observation per species will not have given a complete picture of flower visitation to each of the individual species, the objective of our study was to compare the groups of native, naturalized alien and non-naturalized rather than the individual species. Therefore, we chose to maximize the number of species (i.e. the most relevant unit of replication) over the time per species as this increases the