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The cobblers stick to their lasts: pollinators prefer native over alien plant species in a multi-species experiment

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Abstract The majority of plant species rely, at least partly, on animals for pollination. Our knowledge on whether pollinator visitation differs between native and alien plant species, and between invasive and non-invasive alien species is still limited. Additionally, because numerous invasive plant species are escapees from horticulture, the transition from human-assisted occurrence in urbanized habitats to unassisted persistence and spread in (semi-)natural habitats requires study. To address whether pollinator visitation differs between native, invasive alien and non-invasive alien species, we did pollinator observations for a total of 17 plant species representing five plant families. To test whether pollinator visitation to the three groups of species during the initial stage of invasion depends on habitat type, we did the study in three urbanized habitats and three semi-natural grasslands, using single potted plants. Native plants had more but smaller flower units than alien plants, and invasive alien plants had more but smaller flowers than non-invasive alien plants. After accounting for these differences in floral display, pollinator visitation was higher for native than for alien plant species, but did not differ between invasive and non-invasive alien plant species. Pollinator visitation was on average higher in semi-natural than in urbanized habitats, irrespective of origin or status of the plant species. This might suggest that once an alien species has managed to escape from urbanized into more natural habitats, pollinator limitation will not be a major barrier to establishment and invasion.

Keywords Habitat transition · Introduced plant species · Invasive plant species · Plant invasion · Pollination · Pollinator visitation

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Introduction

Biotic interactions have been suggested to play key roles in establishment and spread of alien plant species (Richardson et al. 2000a; Mitchell et al. 2006). More than 80 % of the plant species rely partly or completely on animals for pollination (Ollerton et al. 2011). This implies that many alien plant species can reproduce—and become invasive—only if potential pollinators also occur in the introduced region (Parker and Haubensak 2002; Vanparys et al. 2008). Whether an alien plant species will attract pollinators in the new range likely depends on its level of generalization towards pollinators (Baker 1974), and also on its residence time in the area of introduction (Pyšek et al. 2011). However, so far, only few studies explicitly compared pollinator visitation of native and alien species.

In studies that compared pollinator visitation between invasive alien species and non-related native species ambiguous results were found. In some cases invasive alien species had higher pollinator visitation than native species (Chittka and Schürkens 2001; Bartomeus et al. 2008; Morales and Traveset 2009), but the opposite has been found too (Moragues and Traveset 2005; Bartomeus et al. 2008). Studies comparing pollinator visitation of related native and alien species that overlap in flowering phenology are scarce but have increased during the last decade (Brown et al. 2002; Muñoz and Cavieres 2008; Vanparys et al. 2008; Harmon-Threatt et al. 2009; Kandori et al. 2009; Powell et al. 2011; Pyšek et al. 2011; Woods et al. *in press*). Comparing related species helps to overcome difficulties in interpreting differences (or the lack thereof) between groups of species (e.g. native vs. alien species) by minimizing potential confounding effects of phylogeny. Accordingly, closely related species often share floral and/or ecological traits (Vanparys et al. 2008; Woods et al. *in press*) making them ideal study objects for comparative studies. However, most of these studies compared native to invasive or naturalized species, and, thus, it is not known yet whether pollinator visitation of alien species in general differs from that of related native species, and whether it differs between invasive and non-invasive alien species. Furthermore, comparisons between alien and native species are most informative when invasive as well as non-invasive alien species are included in such comparisons (van Kleunen et al. 2010). Therefore, one should explicitly compare related native, invasive alien and non-invasive alien species to advance the knowledge on the importance of pollinator visitation for plant invasiveness.

Many alien plant species have been introduced to new regions for ornamental (i.e. garden or horticultural) purposes (Forman 2003; Weber 2003; Lambdon et al. 2008), and numerous invasive species likely started as garden escapees (Reichard and White 2001; Dehnen-Schmutz et al. 2007a, b; Dawson et al. 2008; Marco et al. 2010; Hulme 2011). The transitions from human-assisted occurrence in urbanized habitats to unassisted establishment, persistence and spread into (semi-)natural habitats are crucial steps in plant invasions (Richardson et al. 2000b; Blackburn et al. 2011). Moreover, attraction of pollinators by alien plants in the introduced ranges likely depends also on properties of the recipient plant community and the environment (Williams et al. 2011). Therefore, it is important to know whether ecological interactions of alien plants with pollinators differ between urbanized and (semi-)natural habitats.

We simultaneously exposed individually potted plants of native, invasive alien and non-invasive alien species to pollinators in different locations of two habitat types to test whether pollinator visitation depends on origin (i.e. native vs. alien) and status (i.e. invasive vs. non-invasive) of species, and whether this differs between urbanized and semi-natural environments. To avoid biased results due to phylogenetic non-independence of species, we used congeneric or confamilial groups. We assessed for each plant species the numbers of individuals, morphospecies and taxonomic groups of pollinators per plant and the time a pollinator spent on a plant. We asked the following specific questions: (1) Does pollinator visitation differ (a) between native and alien species, and (b) between invasive and non-invasive alien species? (2) Is pollinator visitation higher in semi-natural habitats than in urbanized ones, and, if there is a habitat-effect, does it differ among native, invasive alien and non-invasive alien species?

Materials and methods

Selection of species and locations

From a list of species that were introduced to Central Europe and Switzerland, compiled from several sources (DAISIE-database: http://www.europe-aliens.org; Moser et al. 2002; Wittenberg et al. 2006; Lauber and Wagner 2007) and from a list of Swiss native species (Lauber and Wagner 2007), we chose invasive alien ($n = 5$), and related (i.e. congeneric or confamilial) non-invasive alien ($n = 6$) and native ($n = 6$) species (Table 1) that do or could potentially co-occur due to their habitat affinities. For three families (Balsaminaceae, Campanulaceae and Malvaceae), we included one species from each category. For the Asteraceae, we included two species from each category, because it is the largest dicot family, and is known to have many invasive species (e.g. Hao et al. 2011). For the Caryophyllaceae, an invasive alien species was not available. Although not all of the alien species that we classified as invasive are currently considered invasive in Switzerland, they are so in other countries of Central Europe. Although some of the study species are known to be self-fertile, all of them are also pollinated by insects (Online Resource Table 1).

To test whether pollinator visitation differs between habitat types (i.e. urbanized and semi-natural), we selected three locations of each of these two different habitat types in Switzerland. As representatives of non-natural urbanized habitats, we used the Botanical Garden of the University of Bern (46°57’10’’N; 7°26′41′’E, DMS), the Municipal Nursery of the City of Bern (46°56′0′’N; 7°28′03′’E) and the research garden of the University of Bern in Muri near Bern (46°55′16′’N; 7°30′08′’E). These locations are characterized by a mosaic of different plant species intermingled with buildings, roads and tracks, as typical for urban habitats. The minimum distance between these locations was 2.8 km (Botanical Garden–Municipal Nursery). As representatives of semi-natural habitats of the Swiss agricultural landscape, we used extensively managed grasslands (i.e. non-fertilized meadows with one or two cuttings per year; personal communication with land-owners) with adjacent forest (approx. 50 m distance) near Rüderswil (46°59′32″N; 7°42′49″E), Heimiswil (47°03′34″N; 7°38′44″E) and Walliswil (47°15′12″N; 7°49′53″E). The minimum distance between these locations was 9.1 km (Heimiswil–Rüderswil). Selected urbanized and semi-natural habitats were at least 17.8 km from each other (Rüderswil—research garden in Muri). Although minimum distances between urbanized habitats are within the potential foraging distances of some pollinators (e.g. honey bees), we think that it is unlikely that individual pollinators visit more than one of these locations.

Plant material and data collection

Twenty-five plants of each species were pre-grown from seeds ordered from commercial seed suppliers, and were individually potted. Exceptions were *Osteospermum sp.*, for which we bought plants in a supermarket (Migros-Genossenschafts-Bund, Switzerland), *Impatiens noli-tangere* and *I. glandulifera*, for which we dug out plants in a semi-natural site in Wabern near Bern, Switzerland, and in the Botanical Garden of the University of Bern, respectively. All plants were kept in a glasshouse in Muri near Bern to ensure that at the time of the pollinator observations, we had flowering individuals that were not previously pollinated. Simultaneously flowering individuals of all species within a family were randomly selected for the observations on each census day.

We recorded pollinator visitation from June 23rd to July 25th 2010 for Asteraceae, Campanulaceae and Caryophyllaceae, and from August 19th to 22nd 2010 for Malvaceae and Balsaminaceae. Pollinator observations were done during the daily major period of pollinator activity (i.e. approx. from 10 am to 5 pm). Each plant species was tested twice a day (i.e. once am, once pm) on two non-consecutive days because we were constrained by logistics and weather. All species but those of Balsaminaceae and Malvaceae, of which we accidentally lost most of the plants, were tested in both habitat types (Online Resource Table 2). The latter families were tested in the Botanical Garden and the research garden of the University of Bern only. The weather was sunny and calm during the observations periods. For each observation session, three potted plants of one family (i.e. one native, one invasive alien and one non-invasive alien species) were placed 1 m apart from each other. For Caryophyllaceae, we had only two plants, one of a native and one of a non-invasive alien species, per observation session. For each observation session, we used new plant individuals that had not been used before. To allow the insects to find the plants, we waited for 15 min, and then observed the plants for 30 min. This waiting period before observations was evaluated to be long enough for insects to recognize the

Table 1 Species used in this study on pollinator visitation of native, invasive and non-invasive alien species in Switzerland

Species	Family	Origin and status[c]	Mean flower unit diameter ± 1SE (cm)	Mean number of flower units ± 1SE
Achillea millefolium[a]	Asteraceae	Native	5.2 ± 0.6	13.91 ± 0.90
Leucanthemum vulgare[b]	Asteraceae	Native	4.2 ± 0.3	13.42 ± 1.07
Achillea filipendulina[a]	Asteraceae	Non invasive	5.6 ± 0.6	5.55 ± 0.47
Osteospermum sp.[b]	Asteraceae	Non invasive	5.5 ± 0.5	6.13 ± 0.77
Helianthus annuus[b]	Asteraceae	Invasive	7.1 ± 0.4	4.14 ± 0.32
Rudbeckia hirta[a]	Asteraceae	Invasive	6.3 ± 0.6	15.25 ± 0.88
Campanula rotundifolia	Campanulaceae	Native	2.0 ± 0.2	31.86 ± 2.87
Platycodon grandiflorum	Campanulaceae	Non invasive	5.9 ± 0.6	6.07 ± 0.68
Lobelia erinus	Campanulaceae	Invasive	1.4 ± 0.2	85.5 ± 12.27
Dianthus armeria	Caryophyllaceae	Native	1.0 ± 0,2	51.38 ± 2.80
Dianthus caryophyllus	Caryophyllaceae	Non invasive	4.4 ± 0.2	21.38 ± 2.00
Malva moschata	Malvaceae	Native	6.7 ± 0.4	17.50 ± 2.72
Alcea rosea	Malvaceae	Non invasive	6.8 ± 0.7	3.00 ± 1.16
Hibiscus trionum	Malvaceae	Invasive	2.7 ± 0.3	3.50 ± 1.44
Impatiens noli-tangere	Balsaminaceae	Native	2.1 ± 0.1	13.75 ± 3.61
Impatiens balfourii	Balsaminaceae	Non invasive	3.6 ± 0.3	22.75 ± 1.32
Impatiens glandulifera	Balsaminaceae	Invasive	2.8 ± 0.2	16.25 ± 2.96

[a, b] Species were observed simultaneously

[c] Compiled from: Moser et al. 2002; Wittenberg et al. 2006; Lauber and Wagner 2007, DAISIE-database (www.europe-aliens.org)

plants, and longer waiting periods did not appear to affect visitation. Every flower visitor that touched the reproductive parts of a flower unit was considered to be a pollinator. Although pollinators differ in their effectiveness and efficiency of pollination (Ne'eman et al. 2010), visitation rate is considered a good predictor of pollination (Vázquez et al. 2005). One 'flower unit' was defined as a unit of one (e.g. Campanulaceae) or more flowers (Asteraceae) requiring an insect to fly in order to reach the next unit (Dicks et al. 2002). We counted the number of pollinator individuals and morpho-species and grouped them taxonomically as honeybees, bumblebees, other bees, hover flies, flies, wasps, other dipterans, butterflies, beetles, and other pollinators, and measured the time an individual pollinator spent on a plant. In total, we recorded 1,459 plant-pollinator interactions. Flower unit diameter of a species was calculated as the mean of five randomly chosen flower units, each on a different plant. For each of the non-radial flowers of the Balsaminaceae species, we took the mean of horizontal and vertical flower dimensions.

Data analysis

We tested whether the diameter and number of flower units differed between native and alien species, and between invasive and non-invasive alien species, by applying Welch two sample t-tests. We analyzed each of the response variables (i.e. numbers of pollinator individuals, morpho-species and taxonomic groups per plant and the time a pollinator spent on a plant) with generalized linear models (GLMs) using the free statistical software package R (version 2.10.0, R Development Core Team 2009). To account for differences in floral display size (see results section), we included $\log_{10}$(number of flower units per plant) and mean diameter of a species' floral unit as covariables. The number of flower units was $\log_{10}$-transformed to linearize the relationship between response variables and number of flower units. Both covariables were scaled to a mean of zero and a standard deviation of one to reduce possible collinearity, and to facilitate comparisons among estimates (Schielzeth 2010). As main factors, we included 'family', 'origin' (i.e. native or alien), 'non-native status' (i.e. invasive or non-invasive alien; fitted sequentially after 'origin'), 'species' nested in the preceding three factors, 'habitat type' (i.e. urbanized or semi-natural), 'location' nested within 'habitat type' and 'observation session' (to account for differences between observation sessions; i.e. date, daytime, weather). We also included all possible two-way interactions. To avoid overfitting, we did not include higher order interactions. In the models for count data (i.e. the numbers of pollinator individuals, morpho-species and taxonomic groups per plant), we used a Poisson error distribution. For the numbers of pollinator individuals and morpho-species, we used quasi-GLM models to account for overdispersion (Zuur et al. 2009). In the model evaluating the effect on time a pollinator spent on a plant, the response variable was $\log_{10}$-transformed to meet assumptions of a Gaussian error distribution. Observations where plants had no flower visitors were excluded from the latter analysis.

We tested whether the main factors or their interactions had significant effects on the response variables by removing all model terms sequentially (Zuur et al. 2009). Here, we first removed the last factor (or interaction) from the model and compared the result to the model including this factor. When these two models significantly differed from each other, then the factor (or interaction) was assumed to be significant. Then, we removed the next factor (or interaction) and proceeded as mentioned before. As fixed factors, we considered 'origin','non-native status' and'habitat type'. Because (quasi-)GLMs do not explicitly distinguish between fixed and random factors, we first, for the models using a Poisson-error distribution, calculated for each model term the mean deviance by dividing the change of deviance by the degrees of freedom. Then we calculated the ratio of the mean deviance of the model term of interest by the mean deviance of the corresponding error term. These ratios of mean deviances are approximately F-distributed (Payne et al. 2008). Similarly, for the models using a Gaussian distribution, we calculated for each model term the F-values as the ratio of the mean squares divided by the mean squares of the corresponding error term.

Results

On average, the native species had smaller but more flower units than alien species (mean flower unit diameter ± SE; native species: 3.53 ± 0.39 cm; alien species: 4.74 ± 0.27 cm; $t = -2.55$, $df = 57.74$, $p = 0.014$; mean number of flower units ± SE; native species: 26.44 ± 1.92; alien species: 16.89 ± 2.08; $t = 3.37$, $df = 240.19$, $p < 0.001$). Among alien plant species, invasive species had smaller but more flower units than non-invasive ones (mean flower unit diameter ± SE: invasive species: 4.06 ± 0.48 cm; non-invasive species: 5.30 ± 0.27 cm; $t = -2.25$, $df = 38.46$, $p = 0.030$; mean number of flower units ± SE; invasive species: 25.49 ± 4.52; non-invasive species: 10.54 ± 0.96; $t = 3.23$, $df = 73.04$, $p = 0.002$).

The number of flower units per plant had a significant positive effect on the different measures of pollinator visitation (Tables 2, 3). The diameter of flower units also had a positive effect on visitation, but this was statistically not significant (Tables 2, 3). There was significant variation in visitation among plant species (Tables 2, 3; Fig. 1, Online Resource Fig. 1). The numbers of pollinator individuals and morpho-species, but not groups, per plant were significantly higher on native than on alien species (mean ± SE: pollinator individuals: 8.70 ± 0.79 on native and 4.12 ± 0.36 on alien species; pollinator morpho-species: 3.69 ± 0.30 on native and 2.11 ± 0.14 on alien species; pollinator groups: 2.64 ± 0.18 on native and 1.88 ± 0.12 on alien species; Table 2; Fig. 1). They did not differ significantly between invasive and non-invasive alien species (mean ± SE; pollinator individuals: 3.93 ± 0.50 on invasive and 4.26 ± 0.51 on non-invasive species; pollinator morpho-species: 2.25 ± 0.19 on invasive and 2.00 ± 0.20 on non-invasive species; pollinator groups: 2.07 ± 0.17 on invasive and 1.73 ± 0.16 on non-invasive species; Table 2; Fig. 1). The time a pollinator spent on a plant did not differ significantly between native and alien species (mean ± SE; 84.78 ± 7.11 s on native and 97.05 ± 13.32 s on alien species), and also not between invasive and non-invasive alien species (mean ± SE; 114.83 ± 24.69 s on invasive and 81.81 ± 12.73 s on non-invasive species; Table 3, Online Resource Fig. 1).

In the semi-natural sites, plants received significantly more pollinator individuals, morpho-species and taxonomic groups than in the urbanized sites (mean ± SE; pollinator individuals: 7.87 ± 0.71 in semi-natural and 4.15 ± 0.37 in urbanized sites;

pollinator morpho-species: 3.51 ± 0.26 in semi-natural and 2.04 ± 0.16 in urbanized sites; pollinator groups: 2.74 ± 0.17 in semi-natural and 1.70 ± 0.11 in urbanized sites; Table 2; Fig. 1), but there were no differences in time a pollinator spent on a plant (mean ± SE; 90.10 ± 13.39 s in semi-natural and 94.02 ± 10.94 s in urbanized sites). These effects of habitat type were the same for native, invasive alien and non-invasive alien species (no significant 'origin' × 'habitat type' and 'non-native status' × 'habitat type' interactions; Table 2).

The significances of the effects of species origin (native vs alien), status (invasive vs non-invasive alien) and habitat type (semi-natural vs urbanized) remained qualitatively similar when we excluded the two plant families that were not tested at all locations (i.e. Balsaminaceae and Malvaceae; Online Resource Tables 3 and 4) or the family for which we did not have an invasive species (i.e. Caryophyllaceae; see Online Resource Tables 5 and 6).

Discussion

In this study, we compared pollinator visitation between native and alien plant species, and between invasive and non-invasive alien plant species in urbanized and semi-natural habitats. As expected, plants with more flower units attracted significantly more pollinators. The size of flower units also had a positive effect on pollinator visitation, but this was not significant. Native plants had more but smaller flower units than alien plants, which probably reflects an introduction bias (Chrobock et al. 2011). Invasive plants had more but smaller flowers than non-invasive alien plants. Due to the negative correlation between size and number of flower units, the overall floral display was most likely not very different for the three categories of species. After accounting for variation in floral display, we found that numbers of pollinator individuals and morpho-species were higher on native than on alien plant species. This indicates that pollinators did distinguish between native and alien species, but not between invasive and non-invasive alien species. Additionally, numbers of pollinator individuals, morpho-species and taxonomic groups per plant were generally higher in semi-natural sites than in urbanized sites indicating that pollinator limitation of native and alien species is less likely to occur in semi-natural habitats than in urbanized ones.

In contrast to our study, most previous studies that compared pollinator visitation of related native and alien species found that the alien species received more pollinator visits or that there were no consistent differences. This may partly reflect an effect of taxonomy, as in our study the difference in visitation between native and introduced plants was most pronounced in the Asteraceae, while in the Balsaminaceae an opposite trend was found (see Fig. 1). The invasive alien *Cirsium vulgare* had higher pollinator visitation rates than five native congeneric species in Northern California (Powell et al. 2011). The invasive alien *Lespedeza cuneata* had higher pollinator visitation rates than three native congeners (Woods et al. *in press*) in a North American tallgrass prairie. The invasive alien *Taraxacum officinale* had higher pollinator visitation rates than the native *T. japonica* in Japan (Kandori et al. 2009). The invasive alien *Senecio inaequidens* had higher pollinator visitation rates than the native *S. jacobea* in semi-natural and garden habitats in Belgium (Vanparys et al. 2008). Furthermore, the presence of the invasive *Lythrum salicaria* reduced pollinator visitation to the native *L. alatum* in the Northeast of the USA (Brown et al. 2002). In a recent study, Williams et al. (2011) found that with increasing anthropogenic disturbance of habitats bee species interacted more frequently with naturalized alien than with native plants. However, this pattern reflected the dominance of the alien species in these habitats and not a preference of bees for alien plants (Williams et al. 2011). Furthermore, a study on ten pairs of native and alien (naturalized or invasive) species in a semi-natural site in the USA did not find consistent differences in pollinator visitation between the two groups (Harmon-Threatt et al. 2009). The discrepancy between the findings of these studies and our finding that native species were visited more frequently than the alien species could have several reasons. First, not all of the previous studies did choice experiments by comparing native and alien plants that were in close proximity. Second, the other studies used natural stands consisting of multiple plants of the native and alien species, while we used single potted plants. Third, in contrast to our study, the studies above compared the native species to established alien species (i.e. naturalized or invasive alien species), while we also included non-invasive alien species that have not established in the wild. However, although we had expected that the lower pollinator visitation of alien species would be mainly due to a lower pollinator visitation of the non-invasive alien species, we did not find a difference between the invasive and non-invasive alien species. Possibly, we did not find such a difference because some of the invasive species in our study are not invasive in the direct surroundings of the study sites, and thus could be considered as locally non-invasive. Clearly, to test whether the absence of a difference in pollinator visitation between invasive and non-invasive alien species is a general pattern, more studies including both categories of alien species, as well as native species, are required.

We used single plants per species in our study to simulate the initial stage of a colonization event (Baker 1955). However, one of the native species we tested (*Achillea millefolium*) was also naturally present at one of the sites (Rüderswil), and this may have affected visitation to our experimental plants of that species at this particular site. It could be that differences in pollinator visitation between native, invasive and non-invasive alien species will become even more apparent or even change when their populations become larger and attract more pollinators. Several studies in heavily invaded sites have reported negative effects of alien plant species on pollinator visitation of related (e.g. Brown et al. 2002; Kandori et al. 2009) and non-related (e.g. Chittka and Schürkens 2001; Thijs et al. 2012)

Table 2 Results of the statistical analyses of pollinator visitation per plant of native and related alien plant species in urbanized and semi-natural habitats in Switzerland

		Number of pollinator individuals		Number of pollinator morpho-species		Number of taxonomic pollinator groups	
	df	Mean deviance[b]	*quasi*-F	Mean deviance[b]	*quasi*-F	Mean deviance[b]	*quasi*-F
Scaled $\log_{10}$(Number of flower units)$_6$	1	49.593	18.223***[a]	21.078	18.250***[a]	11.380	12.607***[a]
Scaled flower unit diameter$_1$	1	25.060	1.073[a]	17.871	2.355[a]	15.856	3.140[a]
Family$_1$	4	29.665	1.270	10.945	1.442	5.772	1.143
Origin$_1$	1	208.230	8.912*	42.409	5.589*	12.184	2.413
Non-native status$_1$	1	24.220	1.037	2.274	0.300	0.221	0.044
Species$_6$	9	23.365	8.586***	7.588	6.570***	5.049	5.593***
Habitat type$_2$	1	112.214	15.072*	32.792	31.683**	20.306	14.343*
Location$_5$	4	7.445	2.547*	1.035	0.917	1.416	2.036
Family × Habitat type$_3$	2	3.201	1.230	1.453	0.963	1.124	1.079
Origin × Habitat type$_3$	1	0.254	0.098	1.028	0.681	2.116	2.030
Non-native status × Habitat type$_3$	1	0.312	0.120	1.198	0.794	0.595	0.571
Species × Habitat type$_6$	6	2.603	0.956	1.509	1.306	1.042	1.155
Family × Location$_4$	8	8.097	2.076	2.669	2.331	1.293	1.171
Origin × Location$_4$	4	5.493	1.408	1.848	1.614	0.730	0.661
Non-native status × Location$_4$	4	5.593	1.434	2.005	1.751	1.127	1.020
Species × Location$_6$	24	3.901	1.433	1.145	0.991	1.104	1.223
Observation session$_6$	66	2.924	1.074	1.129	0.978	0.695	0.77
Residuals	113	2.721		1.155		0.903	

Subscript numbers denote error term used for calculating *quasi*-F- and *p*-values

Error terms: 1: Species; 2: Location; 3: Species × Habitat type; 4: Species × Location; 5: Observation session; 6: Residuals

df degrees of freedom

*** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$

[a] Covariables had a positive effect on response variables

[b] The proportion of variation explained by each factor can be estimated using the change in deviance (i.e. the mean deviance multiplied by the *df*) relative to the total deviance

Table 3 Results of the statistical analysis of the time a pollinator spent on native and related alien plant species in urbanized and semi-natural habitats in Switzerland, per plant

	$\log_{10}$(Time a pollinator spent on a plant)		
	df	Mean squares	F
Scaled($\log_{10}$(Number of flower units))$_6$	1	0.294	1.183[a]
Scaled flower unit diameter$_1$	1	1.078	1.562[a]
Family$_1$	4	1.098	1.590
Origin$_1$	1	1.474	2.135
Non-native status$_1$	1	0.465	0.674
Species$_6$	9	0.690	2.784**
Habitat type$_2$	1	0.498	0.607
Location$_5$	4	0.820	2.625*
Family × Habitat type$_3$	2	0.317	2.801
Origin × Habitat type$_3$	1	0.418	3.697
Non-native status × Habitat type$_3$	1	0.014	0.123
Species × Habitat type$_6$	6	0.113	0.456
Family × Location$_4$	8	0.195	0.756
Origin × Location$_4$	4	0.302	1.175
Non-native status × Location$_4$	4	0.123	0.476
Species × Location$_6$	21	0.257	1.038
Observation session$_6$	66	0.313	1.260
Residuals	79	0.248	

Subscript numbers denote error term used for calculating F- and *p*-values

Species without flower visitors were excluded from these analyses

Error terms: 1: Species; 2: Location; 3: Species × Habitat type; 4: Species × Location; 5: Observation session; 6: Residuals

df degrees of freedom

** $0.001 < p < 0.01$, * $0.01 < p < 0.05$

[a] Covariables had a positive effect on response variable

native species. These effects may depend on the spatial scale over which the species co-occur (Jacobsson et al. 2009), and increase with density or abundance of the alien invasive species (Grabas and Laverty 1999; Muñoz and Cavieres 2008; Kandori et al. 2009) indicating that larger populations of alien species have a stronger effect. Furthermore, the results of a recent data base study on pollinator visitation of alien species (Pyšek et al. 2011) suggest that alien species may accumulate more pollinator species with increasing residence time. Thus, it would be interesting to test, in large multi-species studies, whether and how pollinator visitation of native, related invasive and non-invasive alien species differs in larger populations, between populations differing in size and between populations differing in age.

In our study, pollinator visitation in semi-natural habitats was higher than in urbanized habitats. This result is in line with a recent meta-analysis showing that richness and abundance of wild, unmanaged bee species declines with increasing anthropogenic disturbance (Winfree et al. 2009). Similarly, Trant et al. (2010) detected lower pollinator visitation to *Sabatia kennedyana* in disturbed than in undisturbed sites. The availability of nesting sites, which determines pollinator community composition (Kremen et al. 2007), may be higher in semi-natural than in urbanized habitats resulting in higher pollinator diversity and abundance, and thus in higher pollinator visitation in semi-natural sites. This higher pollinator visitation likely benefits reproduction of both native and alien species, and potentially increases the likelihood for an escaped plant species to establish and become invasive.

Increased pollinator visitation is likely to increase cross-pollination, and to result in increased seed set,

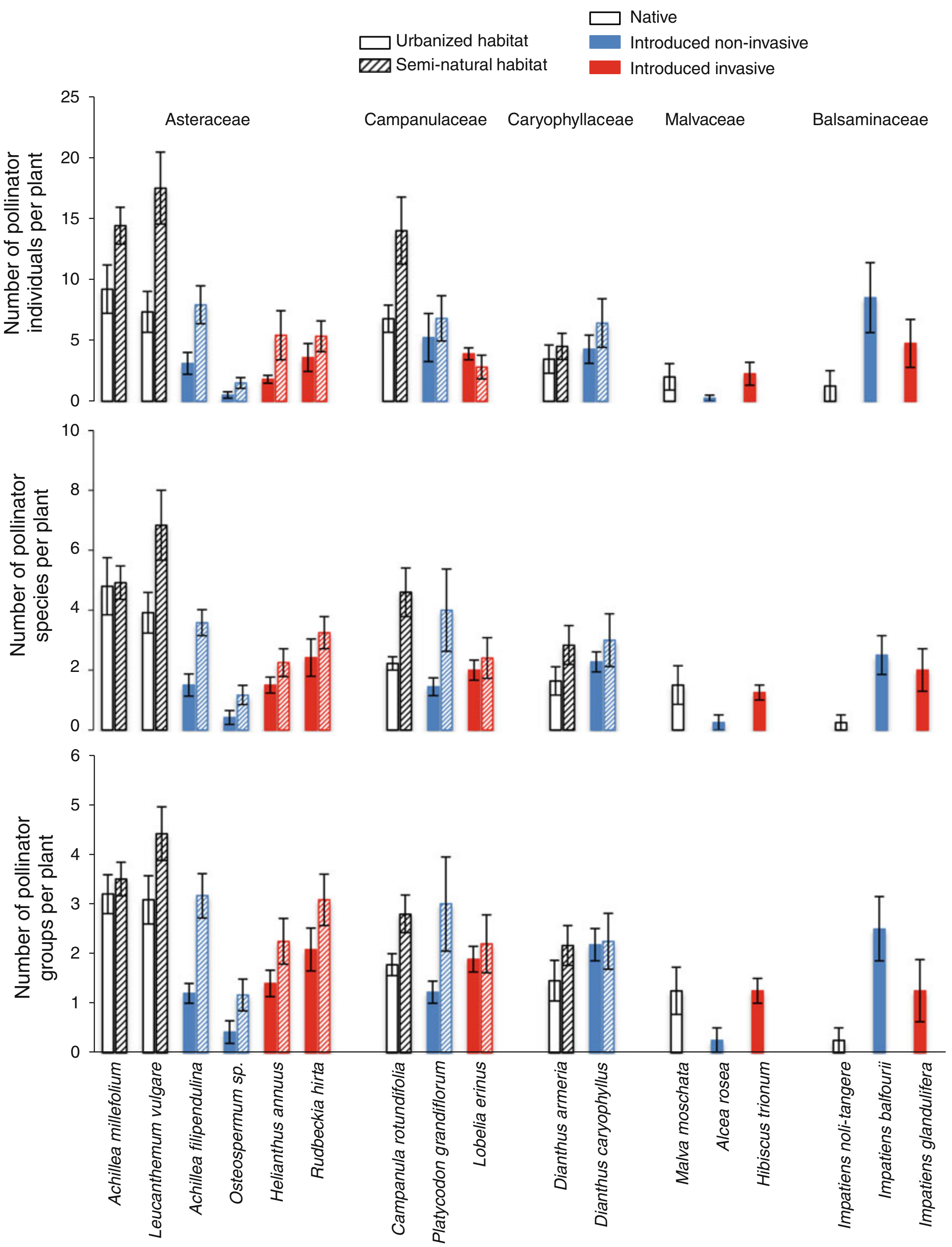

Fig. 1 Numbers of pollinator individuals (*top*), morpho-species (*middle*) and taxonomic groups (*bottom*) per plant species observed within 30 min in urbanized and semi-natural habitats in Switzerland, shown are means ± 1SE

higher seed viability, and more vigorous and genetically diverse offspring (Jacobi et al. 2005; Kremen et al. 2007; Bartomeus and Vilà 2009; Geerts and Pauw 2009; Rodger et al. 2010; Woods et al. 2012). Thereby, it avoids potential negative effects of inbreeding more likely to occur when pollinator visitation is limited. For alien species this may be even more important than for native species because it helps them to overcome reproductive disadvantages resulting from small population sizes and limited pollinator visitation in urbanized habitats compared to native species that are already present in semi-natural habitats. Moreover, increased pollinator visitation may help alien species to establish and maintain self-sustainable populations, which are both prerequisites for invasion (Richardson et al. 2000b; Blackburn et al. 2011). Although pollinator visitation of invasive and non-invasive alien species did not differ in our study, effectiveness and efficiency of pollinators (Ne'eman et al. 2010) might differ for the two groups of alien species. Therefore, studies comparing pollinator visitation, but also seed set, of native, non-invasive alien and invasive alien species in different habitat types that represent different stages of the invasion process (i.e. human-assisted occurrence in artificial habitats, and unassisted occurrence in man-made/disturbed, semi-natural and natural habitats; sensu Richardson et al. 2000b) would greatly enhance the understanding of the role of plant reproductive characteristics in plant invasions.

It is likely that pollinator communities differed between our study sites. Because we do not have full information about the actual pollinator species that visited our experimental plants, we could not do detailed analyses of differences in pollinator-community composition. However, multi-variate analyses based on pollinator groups (e.g. honey bees, bumble bees, other bees) indicates that the pollinator-group composition differed between native and alien plant species, irrespective of whether the latter are invasive or non-invasive, and between urbanized and semi-natural habitats (see Online Resource). These differences most likely reflect higher frequencies of hover flies, flies, beetles and bees other than honey bees and bumble bees on native than on alien species and in semi-natural than in urbanized habitats. Future studies, however, should do more detailed assessment of the pollinator communities on native and alien plant species. Moreover, such studies should, as suggested by Bjerknes et al. (2007), also take into account the whole flowering period of plant species instead of testing them during limited time periods only. Furthermore, it would also be informative to test whether alien species differ in their pollination visitation when comparing populations already established for a longer time with populations established recently, and to do this for different habitat types repeatedly at multiple locations.

Conclusions

The results of our study suggest that pollinator visitation is higher for native than for alien plant species, and that there are no differences between invasive and non-invasive alien plant species. We showed, however, that pollinator visitation was higher in semi-natural than in urbanized habitats, and that this was true for species of different origin and status. The latter might suggest that once an alien species has managed to escape from urbanized sites and establishes in (semi-)natural habitats, a subsequent invasion may be likely due to a lack of pollinator limitation.

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