

Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time

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Abstract. Pollination mode is an important reproductive characteristic, often assumed to play a considerable role in plant species invasiveness. We asked (1) whether alien and native species differed in the frequency of pollination modes (insect pollination, self-pollination, wind pollination, water pollination), (2) whether the pollination modes affected the invasion success of two groups of aliens, differing in their residence time in Central Europe: archaeophytes (introduced before 1500) and neophytes (introduced more recently), and (3) whether there were differences in the diversity of insect pollinators of native species, and of alien species at different stages of invasion and with different residence time. The analysis was carried out using 2817 species occurring in the Czech Republic (1596 native and 1221 alien, the latter comprising 331 archaeophytes and 890 neophytes). Data were analyzed using generalized linear models. The alien flora introduced to Central Europe contained a higher proportion of insect-pollinated species than did the Central European native flora and linked to a higher diversity of pollinators per species. However, the frequency of pollination modes in the introduced alien flora gradually changed during the process of naturalization, becoming more similar to that of native species, and eventually, the naturalized species that became invasive did not differ in their frequency of pollination modes from native species. The frequency of self-pollination increased from casual through naturalized to invasive alien species. This suggests a remarkable role for pollination mode in successful invasions; indeed, self-pollination tends to support spread of neophytes more than any other mode of pollination. The range of habitats occupied by plants of different invasion status affected the diversity of insect pollinator species. In contrast, regional commonness of plant species only affected the number of pollinator functional groups. In native species and archaeophytes, there was a steeper accumulation of pollinator species with increasing habitat range than in neophytes. This indicates that groups of plants that have been provided with longer time to sample a wider range of habitats than recently arriving alien species have formed more associations with native pollinator species occurring in those habitats.

Key words: alien plant species; Central Europe; habitat range; insect pollination; plant invasion; residence time; selfing; stage of invasion.

INTRODUCTION

With the increasing public and scientific concern in recent years about invasive alien plant species, there has been growing interest in studying the traits and processes allowing successful invasion (e.g., Cadotte et al. 2006, Richardson and Pyšek 2006, Nentwig 2007, Pyšek et al. 2009a, b). The role of pollination mode in plant invasion is among the traits that have achieved much attention. Most attempts to assess the role of pollination in invasion have used multispecies studies

that compare large species sets or complete regional floras. However, these studies have mostly failed to demonstrate differences in the frequency of pollination modes between native and alien species or provided contradicting results (see Pyšek and Richardson 2007 for review). Although aliens in Great Britain were found to be more likely insect-pollinated than native plant species (Crawley et al. 1996, Williamson and Fitter 1996), studies from North America (Cadotte and Lovett-Doust 2001, Sutherland 2004) concluded that they were not, and analysis of German flora revealed the opposite pattern, with 62% of natives but only 51% of aliens being insect-pollinated (data from Klotz et al. 2002). Pollination by animals and self-pollination were report-

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ed to decrease the probability of becoming invasive among alien plants of seminatural habitats in Ireland where invasive plants were assumed to rely more often on abiotic modes of pollination such as wind and water (Milbau and Stout 2008). Generally, pollen vector had little value in explaining invasion success in comparisons among different invasion stages of alien plants (Lloret et al. 2005, Pyšek and Richardson 2007, Küster et al. 2008). However, European invaders in North America capable of autonomous seed production were more widely distributed (van Kleunen and Johnson 2007), and species of *Iridaceae* that possessed this trait were more likely to be invasive than those that did not (van Kleunen et al. 2008). In summary, the results are rather ambiguous, and our general understanding of how the mode of pollination and local pollinator community influences plant species establishment is still rather poor.

Arguably, some of the mixed messages coming from the literature could result from the fact that different processes affect different stages of the invasion. The failure to discriminate among alien species that are in different stages of their invasion can obscure the results (Pyšek et al. 2008, 2009a). For example, as garden escapes are a major source of alien plants (Pyšek et al. 2002, Hanspach et al. 2008, Lambdon et al. 2008), species with showy flowers (and thus animal pollination) might be expected to be more likely introduced than those without showy flowers. Conversely, Baker's law (1955) suggests that, once introduced, establishment and spread should be more rapid in self-pollinating plants. Therefore, the role of pollination mode might be expected to shift between the early stage of invasion following introduction, when species occur as casuals and do not form self-sustaining populations (Richardson et al. 2000b), and in more advanced stages of the invasion process when rates of population spread become important.

The importance of mutualistic relationships for plant invasions has been recognized only recently (Richardson et al. 2000a, Morales and Aizen 2002, 2006, Traveset and Richardson 2006, Padrón et al. 2009), and it is becoming widely accepted that introduced alien species influence many ecosystem services, including pollination of plants by animals. Pollination systems face major anthropogenic impacts resulting from changing land use and habitat fragmentation (Steffan-Dewenter et al. 2001), changes in flower production and longevity due to elevated atmospheric carbon dioxide (Rusterholz and Erhardt 1998), disruption of seasonal timing of flowering and insect activity (Price and Waser 1998) as well as spatial mismatches due to climate change (Schweiger et al. 2008b), and introductions of alien species (Memmot and Waser 2002, Schweiger et al. 2010). Many newly introduced plant species need to forge mutualistic relationships in their new habitats before they can become successfully naturalized or invasive (Richardson et al. 2000a, Traveset and Richardson 2006). The relationship between alien plants invading a new region

and local pollinators is among the most important mutualistic interactions; for most flowering plants, sufficient pollen availability through animal pollination is an essential process for the long-term persistence of populations because it affects seed production and genetic variability (Stanton et al. 1986, Larson and Barrett 2000, Ashman et al. 2004, Bjerknes et al. 2007). Nevertheless, invasive plants are often visited by different pollinators in invaded areas than the pollinators in their native range (Forster 1994, Stout et al. 2006), and these new pollinator interactions may differ in efficiency compared to those in the plant's native range (Bartomeus and Vilà 2009). Yet, pollen limitation in invasive plants seems to be rather rare and context-specific (Parker 1997, Parker and Haubensak 2002, Liu et al. 2006). Recent reviews suggest that availability of pollinators in general does not represent an important constraint to successful invasion of alien plants because they are able to use services of local generalist pollinators (Richardson et al. 2000a, Traveset and Richardson 2006).

Examples from the literature indeed support the idea that successful invaders are able to co-opt the services of existing pollinators and successfully integrate into local pollination webs (Olesen et al. 2002, Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Morales and Traveset 2008, Vilà et al. 2009). Many well-studied invasive species are reported to receive high numbers of flower visits by a diverse array of generalist pollinators (Bartomeus et al. 2008, Bartomeus and Vilà 2009). In principle, positive, negative, and neutral effects of alien plants on native plant-pollinator interactions and thus native plant pollination can be found (Bjerknes et al. 2007), and the direction of these effects can be density dependent. Morales and Traveset (2009) conducted a meta-analysis on 40 studies and showed that alien plant species can alter pollinator visitation and, in turn, the sexual reproduction of natives. They found an overall significantly negative effect of aliens on visitation to and reproduction of native co-flowering plant species; this effect was stronger at high relative abundances of alien plants. In particular studies, alien plant species were reported to attract native generalist pollinators and hence facilitate pollination of native plant species (Lopezaraiza-Mikel et al. 2007, Molina-Montenegro et al. 2008), but in some alien species such effect was only observed at low but not high densities (Muñoz and Cavieres 2008). However, more often alien plant species attract pollinators to the detriment of native plants and compete for pollinators with members of native floras either by reducing visitation rates to native plants (Brown and Mitchell 2001, Chittka and Schürkens 2001, Brown et al. 2002, Traveset and Richardson 2006, Sargent and Ackerly 2008, Morales and Traveset 2009) or by deposition of heterospecific pollen on native stigmas (Grabas and Laverty 1999, Bjerknes et al. 2007). In a study comparing plant-pollination networks in noninvaded plant communities with those invaded by

five highly successful plant invaders in Europe, Vilà et al. (2009) found that some of the highly attractive invaders had higher visitation rates than had the native species in the same community, but the dominant role of these alien species over natives did not translate into overall changes in network properties. Therefore, although super-generalist alien plants can play a central role in the networks, the structure of the networks appeared to be very robust to the introduction of invasive plant species (Vilà et al. 2009).

The available knowledge on relationships between alien plants and native pollinators exclusively comes from case studies of individual invasive species and their interactions with co-occurring and/or congeneric native species (see Traveset and Richardson 2006, Sargent and Ackerly 2008 for reviews). This approach is fundamental because it allows experimental manipulation; but to obtain insights into the complex relationship between alien plants and pollinators, it is necessary to broaden the focus to include entire communities. This need is further enhanced by the fact that the impact of a single alien plant species may be less disruptive than that of alien species complexes acting synergistically (Simberloff 2006, Vilà et al. 2009). Few studies extended the scope of recent “single-species” studies by analyzing how assemblages of alien plant species integrate themselves into native flower visitation webs. Memmot and Waser (2002) used historical and recent records for 56 alien species in a plant community in the central United States to analyze the integration of alien plants into a native flower-pollination visitation web and found that flowers of alien species were visited by significantly fewer species of pollinating insects than those of native plants. Consequently, the web of interactions between flowers and visitors was less richly connected for alien than for native plants but aliens were well integrated into the native web. This integration implies both competitive and facilitative interactions between native and alien plants, mediated through insect visitors to flowers (Mommot and Waser 2002, Jakobsson et al. 2009). The seemingly contradictory result of this study and that of Vilà et al. (2009) on visitation rates to alien species points to the necessity of taking the invasion status of the species studied into account; highly invasive species occurring in high densities are likely to attract more pollinator visits than an “average” alien member of the local flora. This was clearly demonstrated by Aizen et al. (2008) who proposed a conceptual model portraying the invasion dynamics of a pollination web that accommodates these seemingly contradictory results. These authors showed that alien mutualists, especially when forming “super-generalist” complexes, can erode the structure of native webs, with consequences for species persistence. In their system, highly invaded webs exhibited weaker mutualism than less-invaded webs, as a result of a disproportionate increase in the importance and participation of alien species in the most asymmetric interactions. The integration of alien mutualists did not

alter overall network connectivity, but links were transferred from generalist native species to super-generalist alien species during invasion (Aizen et al. 2008).

An alternative approach is represented by multispecies studies that do not rely on primary data collected for a given purpose but compare complete alien and native floras of large regions (Pyšek and Richardson 2007). These studies have the potential for broader generalization but are, for obvious reasons, limited by the level of detail of the information available. As a consequence, such studies typically cannot assess the diversity of pollinator species associated with complete assemblages of native and alien plants in large regions, and the questions they raise are restricted to the comparison of pollination modes of alien and native plants, or of invasive and noninvasive aliens.

In this paper, we test for associations between pollination mode and alien population performance at a range of stages of invasion, using the well-documented flora of Central Europe as a testing ground. We further examine whether and to what extent alien plants successfully invading Central Europe co-opt the services of native pollinators by comparing frequencies of different pollination modes of alien plants with those of the temperate native flora. To get an insight into the temporal dynamics of this phenomenon, we also compared pollination mode frequencies of alien plant species occurring at different stages of the invasion process. The comparison of pollination modes of alien species with different invasion status can not only shed light on which pollination modes allow species to become invasive but also reflects the temporal phases of the invasion process, the progression from casual to naturalized to invasive stage as the species moves along the naturalization–invasion continuum (Richardson and Pyšek 2006). Typically, an alien species, after the introduction to a new region, occurs as a casual before it adapts to long-term climatic extremes and overcomes reproductive barriers; this is necessary for entering the naturalization stage, which precedes the stage of invasion (Richardson et al. 2000b). This has been illustrated in detail, for example, by the history of naturalization and invasion of *Ambrosia artemisiifolia* in Central Europe where, depending on local conditions, some populations are still in casual stage while others are naturalized or have started to invade (Essl et al. 2009). Woody plant species in Germany imported for cultivation displayed considerable time lags since introduction (Kowarik 1995). This is the time needed for a species to establish in the wild and provides additional support for the transition of particular alien species from one stage of invasion to the next. Therefore, although each invasion status group analyzed in this paper consists of different species, their sequence can be interpreted as a temporal one. In other words, invasive species in our data set were once naturalized species and they occurred in the naturalization stage

under the same conditions of the Central-European landscape, with probably the same pool of native pollinators available. Hence there is a good reason to assume that they were utilizing comparable pollinator spectra to those used by species that are newly naturalized.

We asked whether (1) alien and native floras differ in the frequency of pollination modes, and (2) whether the pollination modes affect the invasion success of two groups of aliens, differing in their residence time in Central Europe: archaeophytes (historical invaders) and neophytes (modern invaders). Finally, by acquiring data on pollinating insects associated with both alien and native plant species of the Central-European flora, we aim at contributing toward bridging the gap between detailed single-species studies addressing issues of pollinator diversity, and multispecies studies restricted to evaluating the role of pollination modes. To provide an insight into this issue, we explore the group of insect-pollinated plant species in our data set in detail, asking (3) whether there are differences in the diversity of pollinators of native species, and of alien species at different stages of invasion and with different residence time.

METHODS

Plant species analyzed

The flora of the Czech Republic was analyzed, based on the working database CzechFlor held at the Institute of Botany, Průhonice, which was compiled using national floral works (Hejný and Slavík 1988–1992, Slavík 1995–2000, Kubát et al. 2002, Slavík and Štěpánková 2004) and literature with original data. This database contains information on over 4000 native and alien plant species, their distribution, habitats, biological traits, and for aliens, invasion status and history (see Pyšek et al. 2002 for details); additional data on species biological traits were taken from the German database BiolFlor (Klotz et al. 2002, Kühn et al. 2004). The data sources are representative not only for the Czech Republic but for wider Central Europe (Pyšek et al. 2009a).

From the database, 2817 species (1596 native and 1221 alien) with known modes of pollination were included in the analyses (Supplement). Aliens were classified, based on their residence time, as archaeophytes (introduced to the region studied from the beginning of Neolithic agriculture up to the year AD 1500; 331 species) and neophytes (introduced after AD 1500; 890 species), following Pyšek et al. (2002). Based on their invasion status, species in each group were classified as casuals (species that reproduce only occasionally in the wild, but do not form self-sustaining populations and persist for a longer time only due to repeated introductions), naturalized (species that reproduce consistently and form self-sustaining populations without direct intervention by humans), and invasive (species that produce reproductive offspring in very

large numbers and at considerable distances from parent plants; see Richardson et al. 2000b, Pyšek et al. 2004a for definitions). Invasive plants are a subset of naturalized species, but in this paper the two groups are dealt with separately; hence the term “naturalized” here refers to naturalized but not invasive.

The analyses were thus performed on seven groups of plant species (hereafter referred to as “plant status”) defined on the basis of origin, residence time, and invasion status: native; casual, naturalized, and invasive archaeophytes; and casual, naturalized, and invasive neophytes.

Pollination and distributional data

For each species, the information on pollination mode was obtained from the CzechFlor database: insect pollination; self-pollination including geitonogamy, cleistogamy, and pseudocleistogamy; wind pollination; and water pollination (see Klotz et al. 2002 for definitions). These categories are not mutually exclusive and one species can have more than one pollination mode (Supplement).

In addition, details on pollinating insect species were found in the CrypTra database of biotic association of invertebrate fauna and vascular plants of northwestern Europe. This database includes ~39 000 records of visitation of plants by insects, extracted from ~1350 publications, and provides data on the association of ~2600 insect species and ~1300 plant species (see Ellis and Ellis-Adam 1993 for details). The information on the identity of their pollinators was available for 1051 plant species from our data set (644 native, 149 archaeophytes, and 258 neophytes) and included: (1) number of pollinator species as recorded on the given plant species in the CrypTra database; (2) number of functional groups of pollinators ($n = 13$: honey bees, bumble bees, short-tongued solitary bees, long-tongued solitary bees, hoverflies, bombylids, other flies, wasps including parasitic ones, beetles, butterflies, hawk moths, other moths, other insects) (Supplement).

Although the information on pollinators associated with plant species analyzed in our study was not derived directly from the focal region, its use is justified for two reasons. First, for floras most findings from Central Europe are also valid in more northerly and westerly located parts of the continent, e.g., the neighboring Germany and more distant UK; plant species widely distributed in the Czech Republic are also common in these countries (Pyšek et al. 2009a). Furthermore the ecological niches of plant species in Central and northwestern Europe are similar (Prinzing et al. 2001) and pollination types respond to similar environmental correlates (S. M. Bierman, G. Marion, R. Ohlemüller, and I. Kühn, *unpublished data*). Second, in this study we do not address species-specific relationships, but analyze the numbers of pollinators associated with plant species. In this regard, the use of the two data sets is justified by the assumption that a plant species pollinated by many

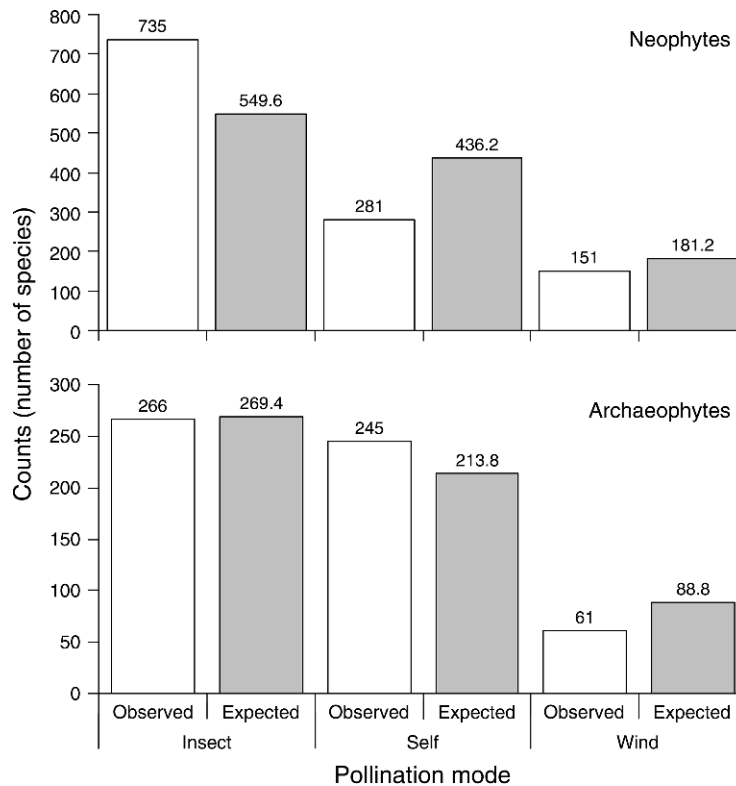


FIG. 1. Observed and expected frequencies of pollination modes for neophytes and archaeophytes; values above bars are counts (number of plant species). Expected frequencies are based on the observed values for native plants and significantly differ from the observed values, pooled across all pollination modes, for both neophytes and archaeophytes. Statistics are given in the *Results: Pollination modes of alien and native species*. Species using multiple pollination modes were assigned to each of them. Self-pollination includes geitonogamy, cleistogamy, and pseudocleistogamy. Pollination by water is omitted due to insufficient frequency for testing (expected value less than 5).

pollinators in northwestern Europe is also pollinated by many species in Central Europe. This can be assumed based on the fact that generalist pollinators in e.g., the UK are also generalist pollinators in Central Europe; for this correspondence there is a robust evidence for butterflies (compare Settele et al. 2009 with Thomas and Lewington 2010).

Distributional characteristics of plant species were related to the Czech Republic and included: (1) number of grid cells from which the species has been reported, based on the Central-European phytogeographical mapping grid (Schönfelder 1999) of $10' \times 6'$ (minutes, longitude \times latitude), which at 50° N is 12.0×11.1 km or 133.2 km² (mean 135.7; range 1–679; total number of grid cells 679); and (2) number of habitat types in which the species grows (mean 13.8; range 1–78; total number of habitat types 88; data from Sádlo et al. [2007]).

Statistical analyses

Pollination modes of alien and native species.—Three questions were tested: (1) whether the frequency of the pollination modes of alien plants, regardless of their invasion status, are the same as those of native plants (Fig. 1); (2) whether the frequencies of the pollination

modes of casual and naturalized neophytes are the same as those of invasive neophytes (Fig. 2); and (3) whether the frequencies of the pollination modes of invasive neophytes are the same as those of native plants (Fig. 3). All questions were examined based on a G statistic, following Sokal and Rohlf (1995:685–743). The first and second questions were analyzed by G tests for goodness of fit with expected frequencies based on the extrinsic hypothesis (Sokal and Rohlf 1995: Box 17.1). The third question was tested by G tests on contingency tables, using generalized linear models with log-link function and Poisson distribution of errors (e.g., Crawley 1993:231–237). Unlike in the test of the third hypothesis, which allows for low frequencies, only categories with sufficient frequencies for analyses with unequal expected frequencies (Sokal and Rohlf 1995:698–702) were used to test the first two hypotheses. Calculations were made in SPSS version 15 and S-Plus version 6.2.

Effect of the pollination mode on the number of grid cells occupied by plants.—To ascertain whether plants with different pollination modes differ in distribution, the numbers of grid cells occupied by native species, archaeophytes, and neophytes were compared for different pollination modes by two-way fixed-effects

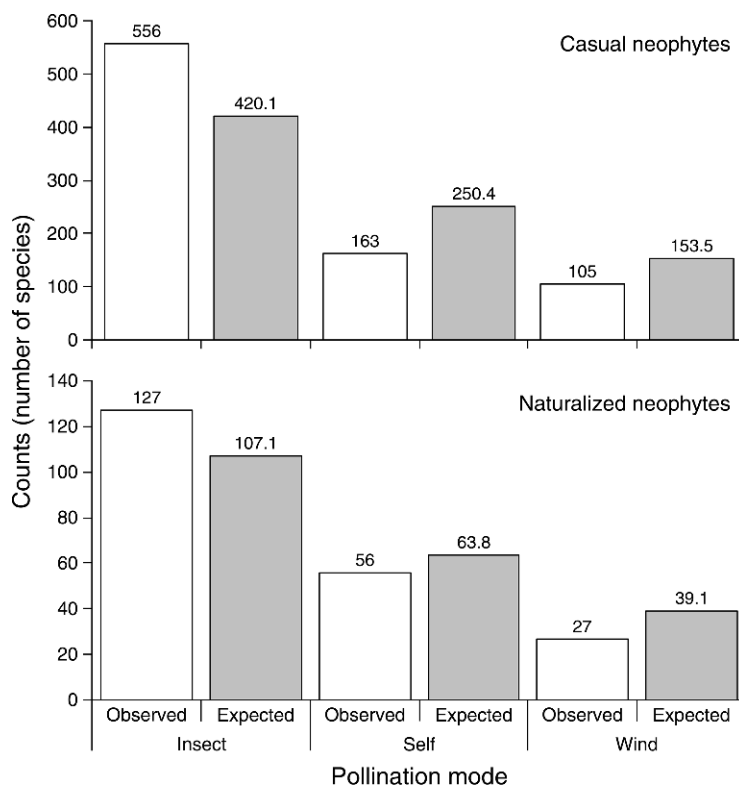


FIG. 2. Observed and expected frequencies of pollination modes for casual and naturalized neophytes. Expected frequencies are based on the observed values for invasive neophytes and significantly differ from the observed values both for casual and naturalized neophytes. Other details are as in Fig. 1.

ANOVA (Table 1). Casual species were excluded from the analysis, as they have much smaller and intrinsically more haphazard distributions compared to naturalized and invasive aliens and native plants. Differences in the number of grid cells occupied were tested in relation to the interaction between the previously defined three plant groups and their pollination modes. Because the

interaction appeared significant, numbers of grid cells for individual modes of pollination were compared separately for native plants, archaeophytes, and neophytes by one-way ANOVAs (Table 2). Number of grid cells was ln-transformed before analyses to normalize the data (e.g., Sokal and Rohlf 1995), and the homogeneity of variance checked by Levene's test

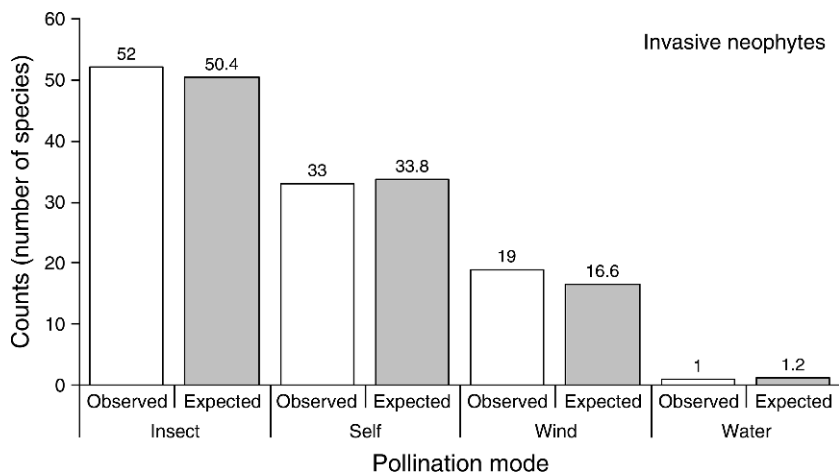


FIG. 3. Observed and expected frequencies of pollination modes for invasive neophytes. Expected frequencies are based on the observed values for native species and do not differ significantly from the observed values. All pollination types are included, because the G test on the contingency table is not affected by small frequencies. Other details are as in Fig. 1.

TABLE 1. Two-way ANOVA for the number of grid cells in the Czech Republic occupied by different groups of plants (native plant species, archaeophytes, and neophytes) with different pollination modes.

Source of variation	df	SS	F	P
Group of plants	2	242.10	38.34	<0.0001
Pollination mode	5	36.75	2.33	0.04
(Group of plants) × (pollination mode)	10	167.55	5.31	<0.0001
Residuals	1767	5578.40		

Note: Pollination modes include insect-only, insect- and self-pollinated, insect- and wind-pollinated, wind-pollinated only, self- and wind-pollinated, and self-pollinated only.

(e.g., Underwood 1997:183). In the case of heterogeneous variance, nonparametric one-way ANOVAs were repeated using Kruskal-Wallis tests (Sokal and Rohlf 1995:423–427; but see Underwood 1997:223–224).

Differences among means for the individual pollination modes were tested by a posteriori multiple comparison tests for unequal sample sizes (Table 3). Because these methods are not settled (e.g., Sokal and Rohlf 1995:244, Underwood 1997:234–242), for data with homogeneous variance both a method testing all possible pairs of means (Tukey’s method with 95% simultaneous confidence intervals in S-Plus version 6.2; Crawley 2002:274–279) and a sequential procedure on ordered means (SNK test with harmonic mean on group sizes in SPSS version 15; Underwood 1997:234–240) were used. The results of both tests were consistent, and only those based on the SNK test are presented. For data with heterogeneous variance, all possible pairs of means were compared by Tamhane’s T2 conservative pairwise comparisons test in SPSS version 15. Following Underwood (1997:234–235 and 239–240), only means in such groups that showed no differences among the means within a homogeneous group (i.e., a group with no significant differences within the group), and simultaneously, having every mean in the homogeneous group different from all means in any other homogeneous group, were considered as significantly different.

Diversity of insect pollinators.—Two questions were tested: whether the number of (1) insect pollinator species and (2) insect pollinator functional groups associated with plant species of a different status differ. Pollinator diversity of these groups of plant species was compared using number of pollinator species and number of pollinator functional groups as the response variables and the seven groups of plant status as the individual levels of a factor group of plants. All data

were analyzed by generalized linear models (GLM) on counts with logit link function, using Poisson errors, which were checked for overdispersion. Numbers of pollinator groups were slightly overdispersed. This overdispersion was treated by using a dispersion factor, to inflate the standard errors of the parameters, calculated by dividing Pearson’s chi-square by the residual degrees of freedom (McCullagh and Nelder 1989). Numbers of pollinator species were very strongly overdispersed. Consequently, the data were analyzed using quasi error structure with variance increasing with the square of the mean (e.g., Crawley 2002:544, Mitchell and Power 2003).

Because common plant species are likely to host more pollinators and also to have received a greater sampling effort in the CrypTra database than rare species, we controlled for this bias by including the number of grid cells and that of habitats occupied by plant species as covariates. All analyses were first run with plant distribution in grid cells (i.e., frequency of occupancy) as a covariate, and the analyses were then repeated with the number of habitats added as the second covariate. We initially included interactions between plant status classes and the covariates in the full model. We used backward selection to yield a minimal adequate model (MAM) and to prevent overfitting. The covariates were ln-transformed to normalize the data (e.g., Sokal and Rohlf 1995), and in analyses with both of them they were standardized to zero mean and unit variance in order to achieve their comparable influence. Using these standardized values, collinearity was checked by calculating tolerance values (Quinn and Keough 2002:128). All fitted models were checked by plotting standardized residuals against fitted values and by normal probability plots (e.g., Crawley 1993).

TABLE 2. One-way ANOVAs for the number of grid cells in the Czech Republic occupied by native plants, archaeophytes, and neophytes, by pollination mode.

Source of variation	Native species				Archaeophytes				Neophytes			
	df	SS	F	P	df	SS	F	P	df	SS	F	P
Pollination mode	5	38.73	2.45	0.03	5	65.69	4.91	0.0003	5	99.87	5.42	0.0001
Residuals	1295	4101.28			259	692.78			213	784.35		

Note: Kruskal-Wallis nonparametric tests were used for data with heterogeneous variances in one-way ANOVAs: for archaeophytes, $\chi^2 = 18.55$, df = 5, $P = 0.002$; for neophytes, $\chi^2 = 23.72$, df = 5, $P = 0.0002$.

TABLE 3. Number of grid cells (ln-transformed) in the Czech Republic occupied by native plants, archaeophytes, and neophytes, ranked by pollination mode (top to bottom: lowest to highest number of occupied cells).

Native species				Archaeophytes				Neophytes			
Pollination		ln(occupied cells)		Pollination		ln(occupied cells)		Pollination		ln(occupied cells)	
Mode	<i>n</i>	Mean	SD	Mode	<i>n</i>	Mean	SD	Mode	<i>n</i>	Mean	SD
Self	44	3.52 ^a	1.68	insect	82	3.73 ^a	2.02	insect	100	2.52 ^a	2.11
Self + wind	40	3.89 ^a	1.92	self + wind	11	3.98 ^a	1.77	wind	31	3.43 ^{ac}	1.58
Wind	249	4.03 ^a	1.85	self	11	4.16 ^{ab}	1.06	insect + self	72	3.48 ^{bc}	1.86
Insect + self	548	4.24 ^a	1.80	wind	23	4.60 ^{ab}	1.18	insect + wind	5	3.5 ^{abc}	1.84
Insect	396	4.32 ^a	1.67	insect + self	131	4.79 ^b	1.49	self + wind	5	5.23 ^b	0.82
Insect + wind	24	4.42 ^a	1.75	insect + wind	7	5.27 ^b	0.42	self	6	5.29 ^{bc}	1.11

Notes: Sample size (*n*) is the number of species within a plant group and pollination mode. Within a column (plant group), pollination modes that do not share a common superscript letter differ significantly ($P < 0.05$) in the number of cells occupied, using the SNK test (for native species) and Tamhane's T2 test for data with heterogeneous variance (archaeophytes and neophytes).

Phylogenetic corrections.—Closely related species are more likely to share the same biological traits due to their common evolutionary history compared to more distantly related species (Felsenstein 1985, Harvey and Pagel 1991). Therefore, it is necessary to check for the influence of phylogeny on model results when analyzing biological invasions (Sol et al. 2008). To test the different questions, we used different approaches using the phylogenetic supertree provided by Durka (2002), based on more than 200 published sources. We tested the differences in the frequency of pollination modes of alien and native species by using contingency tables of phylogenetic diversity of the groups instead of species numbers. Though usually used with integer numbers, contingency tables can also be applied with nonnegative, non-integer entries, which represent phylogenetic diversity. From the different measures for phylogenetic diversity available, average taxonomic distinctness (AvTD; Warwick and Clarke 1995) proved to be the best in providing genuine information on phylogenetic branching instead of species richness (Schweiger et al. 2008a). It is calculated as the mean distance between two randomly chosen species of a triangular distance matrix: $AvTD = [\sum_{i < j} d_{ij}] / [s(s-1)/2]$, where *i* and *j* are two species, *d* is the distance, and *s* is the number of species. The analyses showed no differences between the groups.

To correct for phylogenetic effects in linear models (ANOVA, GLM), we used the eigenvector filtering approach (Diniz-Filho et al. 1998). In particular, we employed a phylogenetic modification of the approach proposed by Bini et al. (2009) for spatial analyses, namely SEVM-v3. To this end, we used the triangular phylogenetic distance matrix (also called patristic distance matrix) and subjected it to principal coordinates analysis (PCoA). The resulting eigenvector matrix was regressed on the residuals of the MAM. Significant eigenvectors (called phylogenetic filters) were then added as covariates to the model. This approach is roughly comparable to the approach described by Griffith and Peres-Neto (2006) of selecting eigenvectors that minimize Moran's *I* coefficient of autocorrelation in regression residuals (Bini et al. 2009) but is computationally much faster.

In no tested case did we find a deviation in the general relationships from the phylogenetically uninformed analyses. For reasons of simplicity and because the phylogenetic signal was uninformative, we only present the results without phylogenetic correction.

RESULTS

Pollination modes of alien and native species

Alien and native species differed in the frequency of their pollination modes ($G = 108.15$, $df = 4$, $P < 0.0001$). Compared to native species, insect pollination was overrepresented, while self- and wind pollination were underrepresented among neophytes ($G = 125.08$, $df = 2$, $P < 0.0001$). Frequencies of pollination modes of archaeophytes and native species were more similar ($G = 14.19$, $df = 2$, $P = 0.0008$), with wind pollination slightly underrepresented and self-pollination slightly overrepresented in the former group (Fig. 1).

The differences in the frequencies of pollination modes of neophytes with different invasion status were also significant ($G = 13.69$, $df = 4$, $P = 0.008$). There was a clear increase in self- and wind pollination and a decrease in insect pollination during the invasion process, from casual through naturalized to invasive species. These differences, compared to expected values derived from the frequencies of pollination modes of invasive neophytes, are more distinct for casual ($G = 92.00$, $df = 2$, $P < 0.0001$) than naturalized ($G = 8.72$, $df = 2$, $P = 0.01$) neophytes. Compared to expected 100% values based on invasive neophytes, casuals had 132.3% insect-pollinated, but only 65.1% self-pollinated and 68.4% wind-pollinated species; corresponding numbers for naturalized neophytes were 118.5%, 87.8%, and 69.0%, respectively (Fig. 2). Finally, invasive neophytes did not differ ($G = 0.79$, $df = 3$, NS, not significant) in the frequency of their pollination modes from native species (Fig. 3).

Effect of the pollination mode on the number of grid cells occupied

The effect of pollination mode on invasion success, expressed as the number of grid cells occupied by the

TABLE 4. Minimal adequate model (MAM) for the number of pollinator species explained by plant status and by the number of occupied grid cells and habitats ($F = 99.63$, $df = 2$, 789 , $P < 0.0001$).

Explanatory variable	Parameter	SE	F	df	P
Common intercept for residential status of all groups of plants	3.12	0.052			
Slope on the number of habitats for arch-nat and neo-inv	0.31	0.074			
Slope on the number of habitats for native and arch-inv	0.83	0.066†	28.27‡	1, 788‡	<0.0001‡

Notes: Abbreviations for plant status: arch-nat, naturalized archaeophytes; arch-inv, invasive archaeophytes; neo-nat, naturalized neophytes; neo-inv, invasive neophytes; native, native plants. Note that the model is described using the log-link function to linearize the relationships, so counts must be calculated from the model parameters as exponential values.

† Standard error of the difference in slopes on the number of habitats between arch-nat and neo-inv, and native and arch-inv.

‡ Test for common slope of the number of habitats for arch-nat, neo-inv, native, and arch-inv.

plants, significantly depended on plant group (interaction between group of plants and pollination mode in Table 1: $F = 5.31$, $df = 10$, 1767 , $P < 0.0001$). When analyzed separately for native plants, archaeophytes, and neophytes, differences among means for the individual pollination modes indicated that neophytes pollinated exclusively by insects were significantly less widely distributed than neophytes with exclusive self-pollination (Table 3). Although one-way ANOVAs indicated that the number of grid cells according to pollination mode also differed for native plants and archaeophytes (Table 2), the multiple comparisons for these two groups just suggested but did not yield unequivocal significant differences (Table 3).

Diversity of insect pollinators

Among plant species pollinated by insects, the number of pollinator species and the number of pollinator functional groups significantly depended not only on the number of grid cells but also on the number of habitats occupied, and the relationships were plant status-specific and different for pollinator species (Table 4) and functional groups (Table 5).

The number of pollinator species increased with increasing number of grid cells occupied by a plant species ($F = 76.89$, $df = 2$, 960 , $P < 0.0001$), and the rate of this increase was independent of the plant invasion status, as indicated by the common slope for all groups of plants. However, differences in intercept indicated that casual neophytes, and casual and invasive archaeophytes (number of pollinator species = $2.09 + 0.39 \times$ number of grid cells) harbored more pollinator species than naturalized and invasive neophytes, naturalized

archaeophytes, and native species (number of pollinator species = $1.42 + 0.39 \times$ number of grid cells).

When habitats were added as a covariate to the analysis, the number of pollinator species no longer depended on the number of grid cells occupied (deletion test on the number of grid cells: $F = 0.45$; $df = 1$, 776 ; NS), but for several plant status groups it increased with the number of habitats occupied (slopes in Table 4). This increase was slower for invasive neophytes and naturalized archaeophytes than for native plants and invasive archaeophytes (Table 4). Within the latter group, the increase in the number of pollinator species was even higher for invasive archaeophytes (slope on the number of habitats for invasive archaeophytes = 1.42) than for native plants (slope on the number of habitats for native plants = 0.81). However, this difference was only marginally significant (deletion test on common slope for native plants and invasive archaeophytes: $F = 3.10$, $df = 1$, 787 , $P = 0.08$), due to a large variance in the number of pollinators of invasive archaeophytes (standard error of the difference in the slope on the number of habitats between invasive archaeophytes and native plants = 0.47). Finally, there was no increase in the number of pollinator species with increasing number of habitats for casual archaeophytes and neophytes, nor for naturalized neophytes (deletion test for the slope on the number of habitats for casual plants and naturalized neophytes: $F = 1.90$, $df = 3$, 785 , NS). These plant groups harbored on average approximately 23 pollinator species, independently of the numbers of grid cells and habitats occupied by the plants (common intercept 3.12 for residential status of all groups of plants in Table 4).

TABLE 5. Minimal adequate model (MAM) for the number of pollinator functional groups ($F = 46.54$, $df = 4$, 785 , $P < 0.0001$).

Explanatory variable	Parameter	SE	F	df	P
Intercept for arch-cas and neo-cas	2.14	0.079			
Intercept for arch-inv, arch-nat and neo-nat	1.60	0.089†	24.51‡	2, 785‡	<0.0001‡
Intercept for native and neo-inv	1.32	0.087§	24.51‡	2, 785‡	<0.0001‡
Common slope on the number of grid cells for all groups	0.16	0.030	14.53	1, 785	<0.001
Common slope on the number of habitats for all groups	0.29	0.029	50.88	1, 785	<0.0001

Notes: See Table 4 for plant status abbreviations. Additional abbreviations for plant status: arch-cas, casual archaeophytes; neo-cas, casual neophytes.

† Standard error of the difference in the intercept between arch-cas and neo-cas, and arch-inv, arch-nat, and neo-nat.

‡ Test on common intercept for the plant status of all groups of plant status.

§ Standard error of the difference in the intercept between arch-cas and neo-cas, and native and neo-inv.

For the number of pollinator functional groups, the rate of increase with increasing numbers of grid cells occupied by a plant ($F = 41.82$, $df = 5$, 955 , $P < 0.0001$) depended on plant status (Appendix). When the number of habitats was added in the model (Table 5), the number of pollinator functional groups significantly depended on both the number of grid cells and habitats occupied by a plant species. The rate of increase in the number of functional groups with increasing number of grid cells and habitats was the same for all plants regardless of their status (common slopes on the number of grid cells and habitats for all groups of plants in Table 5). This pattern thus differed from that for pollinator species, for which there was no effect of the number of grid cells after adding the number of habitats into the analysis, and for which the increase with increasing number of habitats differed according to plant status (Table 4). For pollinator functional groups, the increase with increasing number of habitats (common slope 0.29 in Table 5) was nearly twice as high compared to that with increasing number of grid cells (common slope 0.16 in Table 5). Holding the effect of the number of grid cells and habitats constant by the common slopes in Table 5, casual archaeophytes and casual neophytes harbored the highest number of functional groups (intercept 2.14 in Table 5), native species and invasive neophytes the lowest (intercept 1.32 in Table 5), and invasive and naturalized archaeophytes, and naturalized neophytes harbored intermediate numbers of pollinator functional groups (intercept 1.60 in Table 5).

DISCUSSION

Frequencies of pollination modes of aliens shift over time toward those of native species

Most alien plants are well served by generalist insect pollinators, and it has been suggested that pollinator limitation is not a major barrier for the spread of introduced plants (Richardson et al. 2000a, Traveset and Richardson 2006). Only a tiny proportion of potential invaders are known to be prevented from spreading because of the absence of pollinators. However, the striking differences in the frequencies of pollination modes of plants that we found at different stages of invasion indicate that forming of the relationships between newly arriving plants and their pollinators is an important part of the invasion process, and that general patterns derived from a thorough comparative analysis of the whole native and alien floras may differ from anecdotal evidence of individual case studies of a limited number of highly invasive alien species (Pyšek et al. 2008).

We show that alien and native species markedly differ in the frequency of pollination modes used by the species (see also Crawley et al. 1996, Williamson and Fitter 1996, Klotz et al. 2002, van Kleunen and Johnson 2007, van Kleunen et al. 2008). There is a disproportionately high representation of pollination by insects in early stages of invasion, followed by shifts to progressively

more wind- and self-pollination as species become naturalized or invasive. A possible explanation for the initial overrepresentation of insect pollination among casual species might be introduction bias; as noted previously, one major pathway for the introduction of alien plant species is via garden escapes (Hanspach et al. 2008, Hulme et al. 2008, Lambdon et al. 2008), and garden plants are often selected for their showy flowers, indicative of animal pollination. However, such introduction bias is not likely to explain the effect reported here because the representation of neophytes introduced as garden ornamentals or species planted by beekeepers in our data set increases from 44.9% among casual species to 63.1% and 65.8% among naturalized and invasive species, respectively.

The difference in the frequency of pollination modes between neophytes and native species diminishes as the invasion process continues toward naturalization, and eventually, at the stage of invasion, there is no difference in the frequency of the modes of pollination between invasive neophytes and native species. This implies that among all introduced neophytes, selfers are quicker to spread and become naturalized or even invasive due to ecological trait-based sorting. This progressively shifts the frequency of pollination modes within the group of more invasive aliens away from animal pollination, and thus toward the modes shown in native flora. Higher similarity of the pollination spectra of archaeophytes to native flora than of neophytes fits this overall picture.

In a similar manner, the difference in pollination modes observed between archaeophytes and neophytes can be interpreted in terms of a continuous invasion process. Archaeophytes are a distinct group of aliens in Central Europe, which invaded between the beginning of Neolithic agriculture about 7500 years ago and the end of the Middle Ages (Pyšek et al. 2004b, Pyšek and Jarošík 2005). This provided them with enough time to adapt to the new region and has resulted in their intermediate position between neophytes, the modern invaders, and native species as far as the response to climate and habitat affinities is concerned (Deuschewitz et al. 2003, Kühn et al. 2003, Pyšek et al. 2005, Chytrý et al. 2008). By definition, each “neophyte” eventually becomes an “archaeophyte” if it persists long enough, because the division based on residence time is arbitrary. Assuming that invasion by neophytes tells a story of the archaeophytes’ past, it may be inferred that the set of the most successful alien species tend to utilize the same spectrum of pollination modes as native species. Of course, both groups currently differ in several aspects of ecology, distribution, and evolutionary history (e.g., Kühn and Klotz 2003, Pyšek et al. 2005, Chytrý et al. 2008, Williamson et al. 2009) and must have arrived in their new range using different pathways (Hulme et al. 2008). Therefore one may ask whether this analogy is acceptable. Different pathways would mean different preselection of species being introduced into Central Europe. As the environment into which these newly

arriving species colonized was different from the pristine environment in which the native species evolved or assembled, it is likely that both groups of aliens at their time of arrival were characterized by trait compositions different from that of the native species pool. Finding a high similarity in the composition of pollination mode between native species and archaeophytes now indicates some filtering and converging trajectories in the time after establishment.

There are, however, two potentially confounding factors to be borne in mind: (1) the covariation of pollination mode with other traits relevant for invasion success, and (2) the different biogeographic history of archaeophytes and neophytes. Different plant traits are usually correlated, either negatively (i.e., they are trade-offs) or positively (e.g., forming specific syndromes) (see e.g., Diaz et al. 2004, Wright et al. 2004). This may potentially lead to spurious correlations or associations, i.e., the mode pollination being associated with a species status or invasion stage although some correlated traits are in fact responsible for this pattern. In a comprehensive analysis on the invasion success of alien species in Central Europe, Küster et al. (2008) analyzed more than 380 species and 40 traits. While mode of pollination was significant in a single variable regression, it could only explain <2% of the variation. In a multiple regression model, pollination mode remained as an important predictor, but was only significant in interactions, specifically with duration of flowering, which in itself was again nonsignificant. No interference with any other traits was found in the final analysis, based on an Akaike information criterion (AIC) simplification approach. This concerns also life span that explained merely 1.3% of the variation in invasion success in the analysis of Küster et al. (2008) and supports our assumption that life history (whether the species was annual, biennial, or perennial) was unimportant and hence unlikely to be confounded with pollination mode in our data set. We hence conclude that the observed relationships with pollination modes are genuine.

Archaeophytes, which reached Central Europe before the discovery of America by Europeans in 1492, are of Eurasian origin, while neophytes were introduced also from other continents. However, the majority of neophytes in the Czech flora has their native range in other parts of Europe (39.8%) and Asia (27.6%), and only 15.1% are from North America (Pyšek et al. 2002). Therefore, the proportion of species from other continents seems to be too low to explain the higher incidence of animal pollination, or patterns in plant–animal associations among neophytes. So, while the biogeographical background of the species and its influence on the pollination mode and capacity to co-opt the native fauna needs to be generally taken into account, the above arguments suggest that it is acceptable to hypothesize that invasion by neophytes tells a story of the archaeophytes' past.

Overall, this indicates that the process of becoming a successful invader is associated with utilizing pollinator assemblages that are typical for the invaded region and reflected in the frequency of pollination modes of native flora. In this respect, it is relevant that in Europe there have not been many human-induced pollinator introductions in the past so that the alien plants had to associate with already available native pollinators, unlike alien plants in, e.g., Australia, New Zealand, or South America that could also associate with newly arriving pollinators, such as honey bees and some bumble bees. On a more general level, these results support the idea that successful invaders need to be, especially at the beginning of invasion, sufficiently similar to resident species (Sax and Brown 2000), rather than suggesting that empty niches in terms of pollination modes are colonized (Mack et al. 2000). This is further supported by the finding of Morales and Traveset (2009) who found in their meta-analysis that the effect of alien plants on the visitation and reproductive success of co-occurring native species was most detrimental if both groups of species had a similar flower symmetry or color.

Selfing is associated with invasion success of neophytes

We show that pollination modes are associated with the invasion success of neophytes. In this plant group, we found not only that the relative representation of self-pollination increases from the initial toward more advanced stages of the invasion process, but also that this pollination mode is associated with a wide geographical distribution. No such effect was found for archaeophytes or native species; in these two groups, none of the pollination modes is superior to the others in terms of species distributions. This implies that the capability for self-pollination is most important at the earlier (viewed at the historical time scale of centuries), dynamic phase of invasion associated with establishment and spread, and less so after the alien species has become an integral part of regional flora and, presumably, reached most or all of its potential distribution.

The importance of self-compatibility and unspecialized pollination requirements has been suggested since the first attempts to define traits of a successful invader (Baker 1965, 1974). The reproductive assurance hypothesis (Baker 1955), also referred to as Baker's law (e.g., van Kleunen and Johnson 2007, van Kleunen et al. 2008) states that selfing may be a selective advantage in population establishment after long-distance dispersal and when pollinators are absent. This is often associated with poor or unpredictable climatic conditions and/or frequent disturbance; for example, in the flora of Germany, selfing is overrepresented in regions where natural disturbance is high due to floods or storms (Kühn et al. 2006). The observed wider distribution (in terms of occupied grid cells) of selfing neophytes (compared to insect-pollinated neophytes) in the Czech Republic results in a scale-dependent effect. At each

location (fine scale) one can find a higher proportion of selfing species from the available species pool whereas insect-pollinated species with a smaller range make up only a smaller proportion of the available species pool. Therefore, e.g., the proportion of selfing neophytes is significantly higher at a local scale ($\sim 130 \text{ km}^2$) in Germany than for Germany as a whole (Küster et al. 2010).

Unfortunately, little quantitative information is available on the breeding biology and pollination requirements of most invasive alien plants. Both entirely autogamous and obligatory outcrossing species can be found among highly successful alien plants (Richardson et al. 2000a). Recently it was shown that self-compatible alien species have spread more quickly than self-incompatible ones, which strongly suggests that pollination failure may be a factor constraining invasion success (van Kleunen and Johnson 2007, Küster et al. 2008, van Kleunen et al. 2008); our data support this. However, although selfing is generally considered as a convenient mating strategy in colonizing species, as it allows for the founding of new populations from single propagules and for persistence during initial periods of low population density (Barrett 2000), its role has not previously been analyzed in terms of the progressive change in the pollination strategies of alien species at different stages of the invasion process.

The results discussed previously suggest that the role of specific traits in plant invasions (pollination in this case) is stage dependent (Heger and Trepl 2003, Pyšek et al. 2009a), thus suggesting that it is worthwhile to explore aliens at different stages of the invasion process separately (Dietz and Edwards 2006); while some differences among native and alien species can be detected at the stage of casual occurrence or naturalization, they may no longer be obvious if only highly invasive species are analyzed (Pyšek et al. 2008). This may also be the reason why studies lumping aliens together at different stages of invasion (Pyšek et al. 1995, Cadotte and Lovett-Doust 2001, Sutherland 2004, Lloret et al. 2005) often do not identify the mode of pollination among traits favoring invasion success; these studies compared native with alien species or invasive with noninvasive aliens and did not distinguish between aliens of different residence times in the regions invaded.

Diversity of pollinators correlates with habitat range and distribution of alien species

In this study, we found strong associations between plants' distribution and status and the diversity of their pollinators. The number of pollinator species does not directly depend on how widely distributed a host plant species is, in terms of the number of grid cells occupied; it is determined by the plant's habitat versatility. However, it is impossible to disentangle which of the two factors is a primary driver as they act in concert; the range of occupied habitats increases with larger distribution of the species ($r = 0.73$, $t = 37.392$, $df = 1251$, $P <$

0.0001 ; Pearson's product-moment correlation on ln-transformed and standardized data). Therefore, an alternative explanation might be that the more widespread an alien plant species is, the more habitats it colonizes, which brings about opportunities to "sample" pollinators associated with these habitats.

Yet, our results indicate that the range of habitats occupied by a plant species is a more important factor influencing the diversity of insect pollinators than its distribution. A wide distribution of host plants only resulted in increased diversity of pollinator functional groups, not individual species, but even here this factor acts in concert with the breadth of a plant species' habitat niche, which is more important in affecting this measure of pollinator diversity. That the effect of plant distribution on the diversity of functional groups of pollinators remained significant when the number of habitats was added into the model can be associated with functionally specific life histories of insects belonging to functional groups. For example, bees depend not only on host plants for nectar but also need specific sites for nest building, or, butterflies use different food plants for caterpillars and adults, and some species even need specific sites for ritualized mating behavior. The probability that a suite of species from a given functional group find a combination of suitable sites for their development increases with the wider geographical distribution of their host plants regardless of the number of habitat types in which these plants occur.

Associations with insect pollinators change with residence time of alien plant species

There are striking differences in the speed at which plant species of different origin, invasion status, and residence time accumulate new species of pollinating insects as the range of habitats they invade increases. Interestingly, these differences can be associated with the length of the period for which plant species are present in the region and interpreted in terms of time available for forming associations with pollinators and sampling habitats in the landscape, i.e., for ecological sorting. In our data set, residence time in the region increases from neophytes to archaeophytes to native species, but also from casual to naturalized to invasive aliens (it has been shown that the stage in the invasion process a species reaches in the secondary range positively depends on its residence time; Pyšek and Jarošík 2005, Williamson et al. 2009). Plants with longer associations with their pollinators, i.e., native species and the most successful aliens, invasive archaeophytes, exhibit faster increase in the number of pollinator species with the breadth of habitat niche than invasive neophytes and those archaeophytes that have only reached the stage of naturalization. Finally, casual species, regardless of their residence status, and naturalized neophytes that have not reached the stage of invasion, do not profit from extending habitat niche by accumulating more pollinator species. In other words, if native species and invasive

archaeophytes occupy the same range of habitats as the other groups, they harbor more insect pollinators. It can be thus hypothesized that plant species that have had more time to sample a given habitat have formed more associations with insect pollinators occurring in that habitat than plant species that have only recently colonized the habitat. This process might have been associated with that of pollinator learning; there is some evidence of learned behavioral preferences among insect pollinators, mostly social bees (Chittka et al. 1999, Biernaskie et al. 2009), which could create greater preferences for long-present, more common flowers. This would typically relate to local abundance rather than the extent of regional distribution, but local abundance of plants has been shown to be correlated with their regional distribution if considered separately within habitats (Thompson et al. 1998).

Casual plant species did not profit from increasing habitat range but generally exhibited a high diversity of pollinator functional groups. This can be explained by the fact that this group recruits from many different habitats in their native range (Hejda et al. 2009). Therefore casual aliens, as a group, arrive in a new region already adapted to pollination by very different insect species belonging to a wide range of functional groups. However, as some specialized pollinator groups are rare or do not make the best services in the secondary range of introduced plants, many casual species never naturalize.

*Was there competition for pollinators
on a historical time scale?*

Despite strong environmental changes over the past two hundred years in Central Europe, there is some evidence that the composition of pollination modes in native species and archaeophytes did not change over more than three centuries, but it did in neophytes (Knapp et al. 2010). While the comparison of neophytes with native species therefore provides an insight into the process of forming new plant–insect relationships at the scale of centuries, comparison of archaeophytes with native flora reflects this process at a much longer scale of millennia. Most archaeophytes in the focal region are native to southeastern Europe and western Asia and arrived in Central Europe with Neolithic agriculture (Pyšek and Jarošík 2005), or coevolved with humans, having no known “native range” (Klotz et al. 2002, Kühn and Klotz 2003). Although most of them are typical weeds of arable land or species of disturbed man-made habitats, and hence rather habitat-specific (Chytrý et al. 2005, Sádlo et al. 2007), this was not the case with invasive archaeophytes in our data set. Those 16 species with available data on the number of habitats occupy a broader spectrum of habitats (median = 21, range = 3–44) than is typical of native species (median = 12, range = 1–77, $n = 990$) and invasive neophytes (median = 9.5, range = 1–45, $n = 44$). Therefore, the comparison of pollination patterns of invasive archaeophytes with

other groups was not biased by their often assumed habitat specificity mentioned previously (weeds of arable land) or by the differences in the spectrum of habitats occupied, and the major characteristic in which they differed was the time since invasion. In our data set, invasive archaeophytes tended to harbor even more species of insect pollinators than native plant species. However, this difference was only marginally significant, and the high variation in numbers of pollinators associated with individual species of invasive archaeophytes indicates that during the process of forming relationships with native pollinators, archaeophytes sampled as many pollinators as possible and eventually reached pollinator diversity more or less comparable with native species. The question is whether there was competition for pollinators between native and invasive plants at the time scale of millennia. Although invasive plant species are often considered as potential competitors of native species due to their capacity for colonization and expansion, information in the literature on whether invasive plants also compete for pollination services with natives is scarce (Hulme et al. 2008, Morales and Traveset 2009). Available evidence of alluring pollinators from native plants relates to individual invading species, e.g., *Impatiens glandulifera* (Chittka and Schürkens 2001) or *Lythrum salicaria* (Brown et al. 2002), while for other invaders, e.g., *Carpobrotus edulis*, the role in promoting or constraining the natural pollination dynamics varied considerably among native species (Hulme et al. 2008). There is evidence of impacts of invasions on plant–pollinator webs for some other species (Aizen et al. 2008, Padrón et al. 2009), but none of the studies analyzed pollinator modes of the whole flora, comparing native plants with aliens of a different invasion status and residence time.

The historical data analyzed in our study cannot provide direct evidence but the comparison of patterns found for pollinator species and their functional groups suggests possible hypotheses about the invasion process. Our results show that newly arriving alien floras are pollinated by insects from a wide range of functional groups, but that as the invasion proceeds to naturalized and invasion stages, this range is reduced to a limited number of insect pollinator groups, which is not different in breadth from that utilized by the native flora. However, at the same time the long-present alien plants widen their habitat niche, accumulate pollinator species at a faster rate than those alien plants that have not been present for so long, and do not differ from native species in this respect either. It can be thus hypothesized that as invasion proceeded on a time scale from centuries to millennia, the ability of alien species to attract pollinators from a decreasing number of functional groups increased, which in turn could have led to competition for pollinators with native plants. If this was the case, such competition would be stronger for pollinator species within functional groups, which are assumed to have more similar ecological niches. In

the light of recent findings from Britain and The Netherlands, the competition for pollinators among native plants and alien invaders may become an issue if recent declines in the diversity of pollinator communities (Biesmeijer et al. 2006) continue unabated.

DIRECTIONS FOR FUTURE RESEARCH

The results of our analyses suggest several research areas with potential to improve our understanding of the role alien plant species play in plant–pollinator networks.

1) Results of studies based on primary data collected for a given purpose can answer specific questions and test hypotheses but are difficult to generalize, because they are usually conducted on a small spatial scale, in a specific habitat, and on a single or a few species. We need to obtain deeper insights into complex plant–pollinator relationships at the level of communities and ecosystems (Memmot and Waser 2002, Aizen et al. 2008, Morales and Traveset 2009, Padrón et al. 2009, Vilà et al. 2009) at broad spatial scales. Therefore, we need more field data based on carefully designed sampling (e.g., using communities with both native and alien species well represented, with alien species at different stages of invasion, or conducting studies addressing different habitats and different spatial scales [Jakobsson et al. 2009]; or making it possible to analyze the invasion process through long-term monitoring [Müller et al. 2010]) to bridge the gap between detailed knowledge from small scales and understanding of the emerging patterns in multispecies assemblages of both plants and pollinators on a geographical scale (cf. Brown and Maurer 1989). Such empirical research is especially vital in the face of increasing invasion rates of alien plants and pollinators (Hulme et al. 2009) and associated decreases in the diversity of native pollinators (Biesmeijer et al. 2006).

2) Research on biological invasions often infers the knowledge of past processes from current observations. Yet, the history of invasions provided us with natural experiments in that alien plants were being introduced at different times. The existence of two groups of alien plants differing in their residence time in a region, traditionally recognized in Europe, provides an opportunity to draw inferences about invasion events that occurred on a time scale from millennia to centuries. The differences between archaeophytes and neophytes in ecology, distribution, habitat affinities, and invasion dynamics can still be tracked after several millennia and ascribed to residence time (Pyšek et al. 2004b, Pyšek and Jarošík 2005, La Sorte and Pyšek 2009). Future empirical studies should take into account residence time because many modern invaders (neophytes) have not yet filled their potential secondary ranges and are still in the process of spreading (Williamson et al. 2009, Gassó et al. 2010). In the same vein, data should be collected with the invasion status of target species in mind. It has been shown that different processes act at

different stages of invasion, and factors as well as traits that play an important role at one stage need not be important at another (Williamson 2006, Pyšek et al. 2009a, b). On a more recent time scale, important insights can be achieved by identification of historical data sets that can be used to infer the dynamics of forming plant–pollinator relationships over time by comparing the situation on a time scale of centuries (Memmot and Waser 2002, Knapp et al. 2010).

3) Available literature on the integration of alien plants into native pollinator networks strongly suggests that the relationships of alien plants and native pollinators and the resulting effects, both direct and indirect, they have on co-occurring native plants are context dependent. Comparative studies designed so as to span across different biogeographical zones and a range of habitats differing in disturbance regimes and intensity could contribute greatly to our ability to generalize results across time and space.

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APPENDIX

Relationship between the number of pollinator groups and the natural log of the number of grid cells occupied by a plant species (*Ecological Archives* M081-010-A1).

SUPPLEMENT

Primary data used for analysis of the frequency of pollination modes and primary data used for analyses of insect-pollinated plant species (*Ecological Archives* M081-010-S1).