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Alien plant invasions in European woodlands

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Taxonomic nomenclature: Euro+Med (2006–2016) and The Plant List (2013) for families not covered by this source.

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Abstract

Aim: Woodlands make up a third of European territory and carry out important ecosystem functions, yet a comprehensive overview of their invasion by alien plants has never been undertaken across this continent.

Location: Europe.

Methods: We extracted data from 251,740 vegetation plots stored in the recently compiled European Vegetation Archive. After filtering (resulting in 83,396 plots; 39 regions; 1970–2015 time period), we analysed the species pool and frequency of alien vascular plants with respect to geographic origin and life-forms, and the levels of invasion across the European Nature Information System (EUNIS) woodland habitats.

Results: We found a total of 386 alien plant species (comprising 7% of all recorded vascular plants). Aliens originating from outside of and from within Europe were almost equally represented in the species pool (192 vs. 181 species) but relative frequency was skewed towards the former group (77% vs. 22%) due, to some extent, to the frequent occurrence of *Impatiens parviflora* (21% frequency among alien plants). Phanerophytes were the most species-rich life-form (148 species) and had the highest representation in terms of relative frequency (39%) among aliens in the dataset. Apart from Europe (181 species), North America was the most important source of alien plants (109 species). At the local scale, temperate and boreal softwood riparian woodland (5%) and mire and mountain coniferous woodland (<1%) had the highest and lowest mean relative alien species richness (percentage of alien species per plot), respectively.

Main conclusions: Our results indicate that European woodlands are prone to alien plant invasions especially when exposed to disturbance, fragmentation, alien propagule pressure and high soil nutrient levels. Given the persistence of these factors in the landscape, competitive alien plant species with a broad niche, including alien trees and shrubs, are likely to persist and spread further into European woodlands.

KEYWORDS

EUNIS, exotic, forest, invasive plants, life-form, neophyte, non-native, origin, tree

1 | INTRODUCTION

Globalization has triggered a massive spread of plant species to areas outside their native distribution ranges (van Kleunen et al., 2015). Some alien species persist only temporarily as casuals in the new area, while others can overcome local abiotic and reproductive barriers to establish self-sustaining populations (Richardson et al., 2000). Some naturalized aliens become invasive, that is they can spread in large numbers and across considerable distances (Richardson et al., 2000) or can have detrimental environmental and socio-economic impacts (Rumlerová, Vilà, Pergl, Nentwig, & Pyšek, 2016). Alien plant invasions (defined here broadly as alien plant colonization) are determined by the invasiveness of the species, invasibility of the receiving site and propagule pressure (Richardson & Pyšek, 2006). An unresolved question with important implications for policy is to what extent human activities, such as road construction, woodland fragmentation, planting

of alien species and forest management practices, accelerate alien plant invasions, and whether habitats differ in their invasibility, irrespective of propagule pressure (Chytrý, Jarošík et al., 2008).

In Europe, a total of 5,789 alien plant taxa have been reported (Lambdon et al., 2008), including those that have arrived between the Neolithic and the Mediaeval Age (archaeophytes) and after AD 1500 (neophytes). Given the potentially detrimental environmental and socio-economic impact of invasive alien species (Rumlerová et al., 2016), the regulation of invasive alien species has become a top priority for conservation policy at the national and European levels (European Parliament, 2012; EU Regulation 1143/2014). The European Habitat Directive also requires their recording during assessments (Council Directive 92/43/EEC).

Woodlands cover a third of Europe's terrestrial area (Forest Europe, 2015; note that we use "woodland" as a synonym of "forest" in our article). In the past, they were logged and transformed to cropland and

other open landscape types on a massive scale (Behre, 1988). Today, most European woodlands are composed of stands where the mean tree age is only 60 years (Vilén et al., 2012). Woodlands—and stands with old trees in particular—are generally thought to be resistant to alien plant invasions given the specific abiotic conditions in their herb layer, such as a dense canopy cover and a thick litter layer (Rejmánek, 2015). However, an increasing number of studies has questioned this assumption (e.g., Essl, Mang, & Moser, 2012; Kohli, Jose, Pal Singh, & Batish, 2009; Martin, Canham, & Marks, 2009; Rejmánek, 2015). Their high biological inertia (slow ecosystem turnover) could make woodlands more resistant to alien plant invasion (Rose & Hermanutz, 2004; Von Holle, Delcourt, & Simberloff, 2003). Given the dominance of long-lived life-forms among alien species, such as phanerophytes, invasion in woodlands could be subject to time-lags and the level of invasion could increase in the future (Berg, Essl, Wagner, & Drescher, 2016; Essl et al., 2012).

Intercontinental trade plays an important role in driving alien plant invasions across the globe (Westphal, Browne, MacKinnon, & Noble, 2008). For Europe, recent studies by Seebens et al. (2015) and van Kleunen et al. (2015) found that species originating outside of Europe outnumbered those originating from within. However, this ratio was never tested specifically for woodlands (but see Rejmánek, 2015) and other factors such as climatic and edaphic congruence might also play an important role. If intercontinental trade were a main driver of alien plant invasions in European woodlands, we would expect that aliens with an origin from outside of the continent outnumber those with an origin from within. Furthermore, given a higher introduction rate for alien species from outside of Europe, the chance that aliens with a high dispersal capacity and strong competitive ability enter the region could increase, which should result in a high frequency of alien species from outside of Europe than of alien species from within (sampling hypothesis, Catford, Jansson, & Nilsson, 2009).

In the last two decades, scientists have used vegetation survey data and plant species lists to compare the levels of alien plant invasion across habitats in Europe, for example in Catalonia (Vilà, Pino, & Font, 2007), Basque Country (Campos, Biurrun, García-Mijangos, Loidi, & Herrera, 2013), Czech Republic (Chytrý, Pyšek, Tichý, Knollová, & Danihelka, 2005) and Slovakia (Medvecká, Jarolímek, Senko, & Svitok, 2014) (see also review by Pyšek & Chytrý, 2014). While not a surrogate of invasibility per se (see Chytrý, Jarošík et al., 2008; Lonsdale, 1999; Richardson & Pyšek, 2006), the levels of alien plant invasion can point to mechanisms underlying plant invasions, particularly if levels are similar in corresponding habitats across regions. However, the mentioned studies had a regional scope and differed strongly in their methodological approach, especially in their habitat classification schemes, which hampers an unbiased extrapolation of particular findings to the European level.

By analysing vegetation data from Catalonia, Great Britain and the Czech Republic, Chytrý, Maskell et al. (2008) performed the most comprehensive analysis of plant invasions across all habitats in Europe so far. The study reported on invasion levels across habitat types defined by the European Nature Information System (EUNIS; Davies & Moss, 2003; <http://eunis.eea.europa.eu/habitats.jsp>), which facilitates

knowledge transfer to European environmental policy. However, the analysis was based on the coarse EUNIS level 2 classification, which differentiates between deciduous (G1), evergreen broadleaved (G2), coniferous (G3), mixed (G4) and disturbed (G5) woodlands. This classification scheme precludes a comparison across a more detailed spectrum of woodland habitats.

In this study, we used data from the European Vegetation Archive (EVA) and additional regional datasets to evaluate the levels of alien plant invasions in European native woodlands. EVA is a recently compiled, large consolidation of multiple vegetation-plot databases (Chytrý et al., 2016). In our analysis, we first considered European woodlands as an entity and then inspected patterns across individual woodland habitat types of the recently revised EUNIS classification (henceforth: “habitats”). We asked the following questions: (1) Do aliens originating from outside of Europe reach the same species numbers and frequencies as those originating from within Europe? (2) Do phanerophytes contribute more to the number and frequency of alien species than other life-forms? (3) Which geographic regions have donated most alien plant species to European woodlands? (4) How do habitats compare in their levels of invasion at the local scale?

2 | METHODS

2.1 | Data extraction and habitat classification

At the time of data extraction (13 January 2016), EVA encompassed data from approximately 1.1 million vegetation plots. We pooled these data with additional vegetation databases from European regions (see Appendix S1 for an overview of databases). As vegetation databases often lack information on stand age or total tree cover, we defined woodlands based on the cover of individual tree species. Plots were included if they encompassed tree species that can form dense canopies (most broad-leaved deciduous trees, *Picea* and *Abies* species) and that had an individual cover of at least 25%. In addition, we included plots which contained tree species that form more open canopies (*Pinus*, *Betula*, *Quercus*, *Taxus*, *Larix*) and that reached an individual cover of at least 15%. This step resulted in an initial dataset of 251,740 plots.

Plots were assigned to a habitat (see Appendix S2 for an overview of considered habitats) using an expert system developed for the revised version of EUNIS woodland habitat classification (Schaminée et al., 2014). We used the version “2016-05-05” of this expert system, compatible with the modified version of the EUNIS habitat classification used in the European Red List of Habitats (Janssen et al., 2016). This expert system was applied in the JUICE software (Tichý, 2002). Only those plots that were unambiguously assigned to a habitat were considered for further analysis (intermediate dataset, $n = 158,827$ plots).

2.2 | Status of taxa

We assigned a residence status (“alien,” “native” and “uncertain”) to all vascular plant species \times region combinations in the intermediate

dataset. Regions equalled countries, except for the Balearic Islands, Corsica, Crete, Sardinia and Sicily, which were treated as independent regions due to the large size of these islands and their distinct natural history. Furthermore, the European part of Russia was divided into five distinct subregions, in line with Euro+Med (2006–2016), due to its vast area and large macroclimatic contrasts.

We considered only neophytes as alien species, that is those that arrived in the region after 1500 AD (Pyšek et al., 2004), as the status of archaeophytes is poorly known in some countries. For the purpose of this study, archaeophytes were considered as natives. Taxa of “uncertain” status were those unknown to the region (e.g., *Cirsium palustre* in Greece) or whose status in the region is unclear (e.g., *Cicerbita plumieri* in Montenegro). We also assigned an “uncertain” status to taxa that were defined only above the species level (e.g., *Rubus* in Austria), except for those whose daughter taxa are all alien in the region (e.g., *Tsuga* in Poland; these cases were treated as “alien”).

Given the lack of an up-to-date and taxonomically complete database on the status of European plant species, we used a variety of sources to identify the residence status, including Euro+Med (2006–2016) and other sources (see Appendix S3: List S1), as well as knowledge among authors and other regional experts mentioned in the Acknowledgements.

2.3 | Origin of alien plants

In the intermediate dataset, we further classified all alien taxa in each vegetation plot according to their origin, distinguishing between: (1) aliens from within Europe, that is alien in the respective region but native to another European region (as in Lambdon et al., 2008); (2) aliens from outside of Europe; and (3) anecophytes (alien species with an unknown native origin) and hybrids (hybrid taxa with at least one alien parent). When distinguishing between (1) and (2), we defined Europe as the territory bordered by the Mediterranean Sea and the Atlantic Ocean, including the European part of Russia, the Caucasus and Ural Mountains, Iceland, Malta and Svalbard but excluding Madeira, the Canary Islands, the Azores, Kazakhstan, Cyprus and all of Turkey. We identified the specific region of origin based on sources listed in Appendix S3: List 2. Species with a native distribution across multiple geographic regions were scored for each region.

2.4 | Life-form

We retrieved information on the life-form (chamaephyte, geophyte, hemicryptophyte, herbaceous climber, hydrophyte, phanerophyte, therophyte, woody climber) of alien and native plants from sources listed in Appendix S3: List S3, and from expert knowledge available among the authors. Some taxa were associated with more than one life-form.

2.5 | Data filtering

We applied several filters to the intermediate dataset. In order to be included in the final dataset, plots had to be sampled during the period

of 1970–2015 and to have an area between 100 and 1,000 m². Our study aimed to analyse the results of spontaneous invasion processes. To account for the bias of alien trees planted for timber, fruit or honey production, and ornamental purposes (“planted alien trees”), we excluded all plots with an alien species that is only known from planted populations in the region (e.g., *Abies alba* in Belgium, *Pinus strobus* in Slovenia), as derived from Euro+Med (2006–2016). Furthermore, we excluded plots with alien tree species that are naturalized but widely planted (see Appendix S3: List S4) if they covered more than 20% in the tree layer or an unidentified layer. Plots in which these taxa occurred in the shrub or herb layer (e.g., as seedlings) were retained in the dataset. Last, but not least, we excluded all plots in which the cover of species with an uncertain status exceeded 20%. After filtering, the final dataset comprised 83,396 plots from 39 regions (Figure 1) and 23 habitats (see Appendix S2 for the list of habitats and their regional coverage).

2.6 | Data analysis

We assessed the levels of alien plant invasion across (1) all European woodlands as one entity and (2) individual habitats and quantified it as: (i) the number and percentage of alien species in the species pool; (ii) the relative frequency of alien species (sum of frequencies of alien species divided by the sum of frequencies of all species: a species record in a plot was counted as one species occurrence, irrespective of the vegetation layer); and (iii) the mean relative alien species richness per plot (number of alien species divided by the total number of species in a plot, averaged across plots; Chytrý, Maskell et al., 2008; Catford, Vesik, Richardson, & Pyšek, 2012; for habitats only). Species with “uncertain” status were excluded from all calculations. Furthermore, we only included taxa at the species level, except for index (iii), for which we considered also taxa at the above-species level (e.g., *Symphoricarpos* in the Netherlands).

The number of plots differed strongly among regions and habitats. Some small regions were over-represented (e.g., Czech Republic, the Netherlands, Switzerland), while some large regions were under-represented (e.g., European subregions of Russia, Romania, Ukraine). This imbalance can bias the estimates of frequencies and relative alien species richness. While we were unable to address the latter shortcoming, we decreased the over-representation of some small regions using randomized, stratified sampling across habitats weighted by the region's size (hereafter: resampled dataset). We set a maximum number of plots for a habitat × region combination as 2,000, 1,000, 800, 500 and 400 if the size of the region was above 700, 550, 400, 250 and 100 × 10³ km², respectively, or to 300 if the size of the region was below 100 × 10³ km². If plots were over-represented for a habitat × region combination, we applied random sampling to reduce their number to the allowable threshold for that region. We used a region's size for weighing because complete information on the spatial distribution of habitats per regions was lacking and because the density of vegetation plots differed strongly among countries. In our final filtering step, we included only habitats represented by at least 300 plots across the entire dataset.

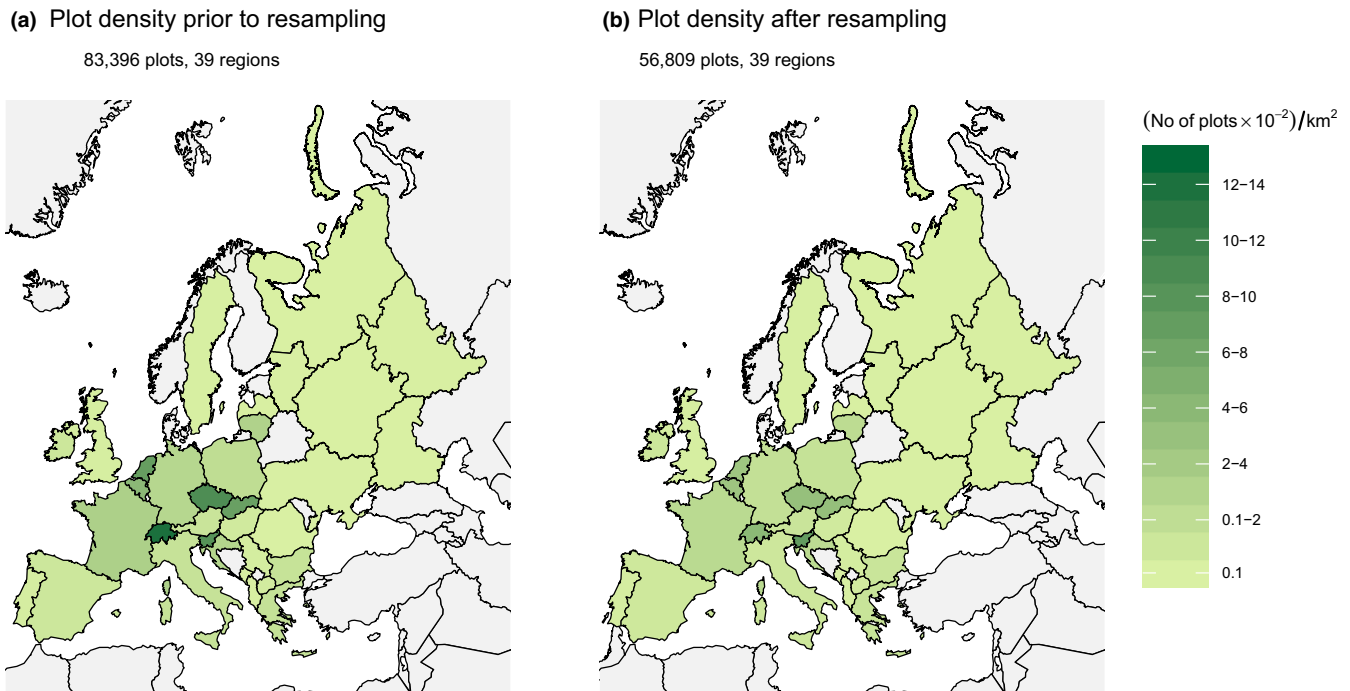


FIGURE 1 Plot density across European countries (a) prior to and (b) after filtering by stratified and weighted resampling (resampled dataset), with one exemplary run displayed in (b). [Colour figure can be viewed at wileyonlinelibrary.com]

We used two-sided exact tests of goodness-of-fit (exact binomial tests) to compare the percentages of European and non-European alien species and two-sided chi-square tests to compare the percentages of individual life-forms between the alien and native species pools. We also applied a chi-square test to compare relative frequencies of individual life-forms between alien and native plants but included also an effect size threshold of $\Delta \geq 20\%$ to account for large sample sizes, and consequently for the high power in our tests.

We used a Venn diagram to compare the alien flora among riparian (habitats G1.1, G1.2a, G1.2b, G1.3; see Appendix S2, Table S1, for a definition of habitat codes), broadleaved deciduous (G1.6a, G1.6b, G1.7a, G1.8, G1.9a, G1.Aa, G1.Ab) and coniferous (G3.1a, G3.1b, G3.2, G3.4a, G3.4b, G3.4c, G3.7, G3.Da, G3.Db) woodlands. We discarded evergreen woodlands (G2.1) and swamp and bog woodlands (G1.4, G1.5) from the Venn diagram because they were represented by few habitats.

3 | RESULTS

3.1 | General patterns across European woodlands

The final dataset included 386 alien species (7% of all recorded vascular plant species) in European woodlands. In general, species originating from outside of and from within Europe were almost equally represented in the alien species pool (192 vs. 181 species or 50% vs. 47%, Figure 2a, Appendix S4: Table S1). However, when measured in terms of relative frequency, the representation of aliens originating from outside of Europe much exceeded that of aliens originating from within Europe (77% vs. 22% of all alien species occurrences,

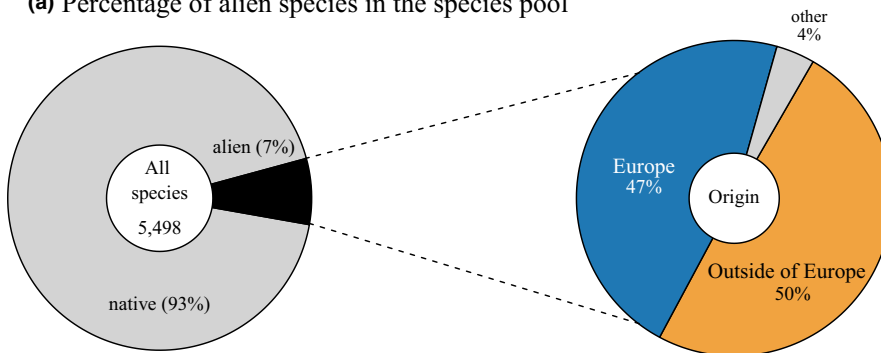
Figure 2b). Anecophytes and hybrids made up only 4% of the alien species pool and were poorly represented in terms of relative frequency (2%).

Among all life-forms, phanerophytes were the life-form richest in alien species (148 species), followed by hemicryptophytes (103 species) and therophytes (80 species; Figure 3a, Appendix S4: List S1). Herbaceous and woody climbers were represented by only 10 and 13 species, respectively. Compared to the life-form spectrum of native plants, phanerophytes were significantly over-represented (38% vs. 11%, $\chi^2 = 239$, $p < .01$) and hemicryptophytes significantly under-represented (27% vs. 51%; $\chi^2 = 80.9$, $p < .01$) in the alien species pool; therophytes (21% vs. 17%; $\chi^2 = 2.9$, $p = .09$) were equally represented among alien and native plants.

In terms of relative frequency, phanerophytes (49%) and therophytes (34%) had the highest representation among alien plants (Figure 3b). Their relative frequency was significantly higher among alien plants than among native plants (phanerophytes: 49% vs. 27%, $\chi^2 = 2,470$, $p < .01$; therophytes: 34% vs. 4%, $\chi^2 = 2,5702$, $p < .01$). Hemicryptophytes were under-represented among alien plants using this measure and compared to native species (14% vs. 48%, $\chi^2 = 4,843$, $p < .01$, Figure 3b).

When we implemented a stronger filter, excluding all plots in which commonly planted alien trees occurred in the tree layer or in an unidentified layer, the overall results did not change much, including those for the species pool across origins (aliens from outside of Europe vs. aliens from within Europe: 168 vs. 165 species, 49% vs. 48%), relative frequency across origins (83% vs. 17%), percentage of species in species pool belonging to different life-forms (phanerophytes: 36%, hemicryptophytes: 28%, therophytes: 22%) and relative

(a) Percentage of alien species in the species pool



(b) Relative frequency of alien species across plots

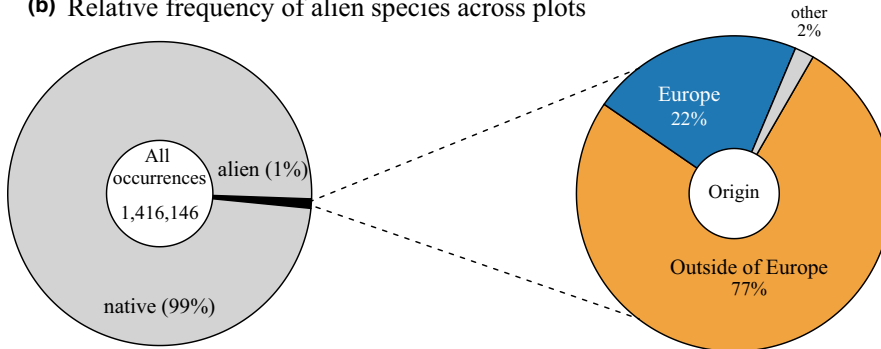


FIGURE 2 (a) Percentage of alien species in the species pool and (b) relative frequency of alien species across plots classified by their geographic origin (from Europe or outside of Europe). The “other” category includes anecophytes and hybrids. Data in (b) based on resampled dataset (standard errors of the mean < .04%). [Colour figure can be viewed at wileyonlinelibrary.com]

frequency across life-forms (phanerophytes: 36%, hemicryptophytes: 17%, therophytes: 43%) (Appendix S4: Figs. S1 and S2).

Impatiens parviflora, a therophyte from temperate Asia, was the most common alien species, accounting for 21% of occurrences of all alien plants, followed by several phanerophytes from North America (*Prunus serotina*, *Robinia pseudoacacia*, *Quercus rubra*) and Europe (*Acer pseudoplatanus*) (Table 1).

The major donors of alien plant species were other regions in Europe ($N = 181$ donated species), North America ($N = 109$), South America ($N = 52$) and temperate Asia ($N = 46$; Figure 4). The proportions of hemicryptophytes, phanerophytes and therophytes in the alien pool differed among these regions ($\chi^2 = 41.6$, $p < .01$). Life-form spectra of species that arrived from particular regions also significantly differed; most alien species from temperate Asia were phanerophytes ($\chi^2 = 29.9$, $p < .01$), from Europe phanerophytes and hemicryptophytes ($\chi^2 = 9.9$, $p < .01$), and from South America therophytes and hemicryptophytes ($\chi^2 = 8.2$, $p = .02$); among species originating from North America, these three life-forms were equally represented ($\chi^2 = 4.3$, $p = .12$).

3.2 | Differences in invasion across woodland habitats

At the local scale, habitats differed strongly in their levels of invasion (Figure 5a). Temperate and boreal softwood riparian woodlands (G1.1) had by far the highest mean relative alien species richness per plot (4.7%). Values among the remaining habitats differed strongly, with broadleaved bog woodland on acid peat (G1.5) and Mediterranean and Macaronesian riparian woodlands (G1.3) having the highest, and

mire woodlands (G3.Da, G3.Db) and mountain coniferous woodlands (G3.1a, G3.1b, G3.2, G3.4b, G3.4c) the lowest ranks. When only aliens originating from outside of Europe were considered, the mean relative alien species richness showed a similar pattern across habitats (Figure 5b). However, when only aliens originating from Europe were included, the mean relative alien species richness was smaller and the pattern more even across habitats (Figure 5c).

Temperate and boreal softwood riparian woodland (G1.1) showed the highest proportion of aliens in the species pool (8.7%) and the highest frequency of alien species (5%, Appendix S5: Tables S1 and S2) among all habitats. Similar to the pattern described above, alien plants originating from within and from outside of Europe were almost equally represented in the alien species pool of most woodlands, except for some riparian woodlands (G1.1, G1.2a, G1.3), broadleaved swamp woodland on non-acid peat (G1.4) and broadleaved bog woodland on acid peat (G1.5) (Appendix S5: Tables S1 and S3). In terms of relative frequency, aliens from outside of Europe were significantly better represented than aliens from within Europe in 74% of habitats (Appendix S5: Table S2). Phanerophytes were over-represented in the alien species pool compared to the native species pool, in most habitats (Appendix S5: Table S1). When we quantified the relative frequency of life-forms, alien phanerophytes were represented comparably to their native counterparts in many habitats (Appendix S5: Table S2).

The composition of the alien flora differed to some extent among riparian, coniferous and broadleaved deciduous woodlands; only eight alien plant species (6.8% of all alien species) were recorded in all three groups (Figure 6). Alien species that occurred in more than half of habitats represented only 2.5% of the alien species pool but accounted

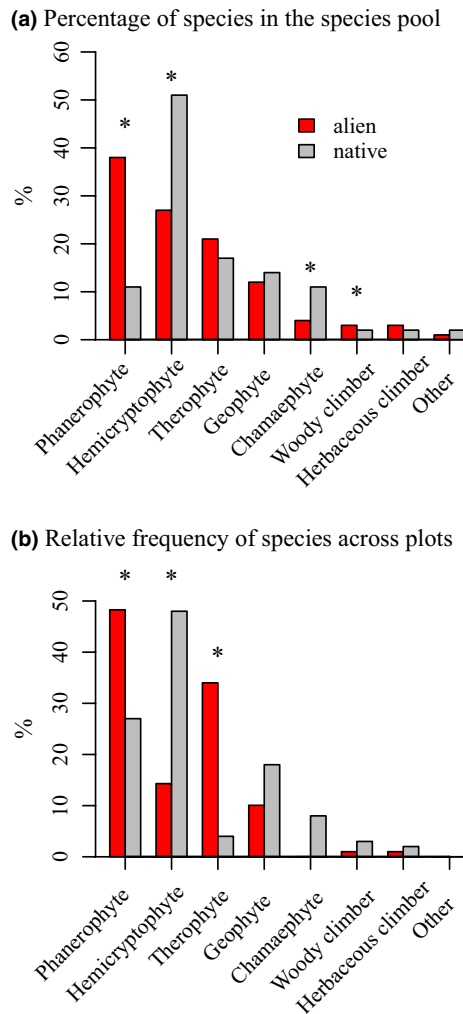


FIGURE 3 (a) Percentage of species in alien and native species pools belonging to different life-forms and (b) their relative frequency across plots. Asterisks indicate significant differences between native and alien species in life-form percentages in species pools (two-sided chi-square test, $p \leq .05$) and frequencies (two-sided chi-square test, $p \leq .05$, effect size threshold of $\Delta \geq 20\%$). Data in (b) are based on resampled dataset (standard error of the mean $< .05\%$). [Colour figure can be viewed at wileyonlinelibrary.com]

for 62% of all alien species occurrences. Overall, the alien floras from within and outside of Europe did not differ significantly in their species composition among the three groups (data not shown).

4 | DISCUSSION

4.1 | Origin

Our study found 47% of alien species in European woodlands to originate from other European regions. This value is similar to the estimate by Lambdon et al. (2008) and is consistent with earlier suggestions of natural postglacial dispersal limitation in the European flora (e.g., Svenning & Skov, 2007). The introduction pathways of alien plants to European woodlands have never been explored, but Lambdon et al. (2008) found that, irrespective of the habitat, the majority of alien

species from other regions of Europe had been introduced deliberately rather than accidentally. Short distances between native and alien range could have facilitated species introductions to adjacent regions within Europe, such as the introduction of *Acer pseudoplatanus* from Central Europe to Great Britain in the 16th century (Online Atlas of the British and Irish Flora, 2016).

Surprisingly, although the species pool sizes were nearly equal for aliens from outside of Europe and aliens from within Europe, the latter were represented by only 22%, in terms of species relative frequency across vegetation plots. In theory, this result could be explained by the enemy-release hypothesis (Keane & Crawley, 2002), according to which alien species from Europe should have evolved under similar environmental conditions and in close proximity to enemies in their invaded ranges, hence facing a stronger herbivore and pathogen pressure upon arrival than alien species from outside of Europe. However, the relatively low frequency of alien plants from within Europe could also occur by chance because of the high frequency of a few alien species from outside Europe (especially *Impatiens parviflora*, *Prunus serotina* and *Robinia pseudoacacia*), or because alien species originating from Europe can be alien only to a smaller region on this continent, as they are native to other European regions.

Our analysis was based on species status in a region, which means that the results do not necessarily reflect more fine-grained, biological patterns within regions. On the one hand, this means that our study probably underestimated the levels of invasion for larger regions because alien species originating from a different part of the region were treated as native (e.g., *Acer pseudoplatanus* in France; *Picea abies* in Germany). On the other hand, our analysis was probably oversensitive for smaller regions as alien species originating from spatially adjacent countries were treated as alien (e.g., *Pinus sylvestris* in the Netherlands).

4.2 | Life-forms

Phanerophytes were the most species-rich life-form among aliens and over-represented in the alien species pool. This result is in contrast to a recent assessment (RBG Kew, 2016), which found phanerophytes to rank behind hemicryptophytes and therophytes in terms of alien plant species numbers on a global scale. However, this comparison should be treated with caution as the previous study was not restricted to woodlands, and considered only invasive alien plants while we considered all alien species, irrespective of their invasion status.

Our finding could indicate a bias towards alien tree plantations in our data. When we implemented a stronger filter—excluding all plots in which commonly planted alien trees occurred in the tree layer or unidentified layers—the relative frequencies of phanerophytes dropped from 49% to 36%. Still, together with therophytes, they accounted for the highest percentages among alien plants (Appendix S4, Fig. S2b). The high percentage of phanerophytes in the alien species pool did not change after stronger filtering, either (39% vs. 36%, Appendix S4: Fig. S2a). Both facts suggest that even under a conservative assumption, alien phanerophytes are the life-form richest in species in European woodlands and—apart from *Impatiens parviflora*—phanerophytes had the highest frequencies among alien species.

Species name	Life-form	<i>n</i>	% Frequency among alien plants	<i>k</i>
<i>Impatiens parviflora</i>	T	2,214	21.1	16
<i>Prunus serotina</i>	P	921	8.8	17
<i>Robinia pseudoacacia</i>	P	790	7.5	19
<i>Quercus rubra</i>	P	517	4.9	16
<i>Acer pseudoplatanus</i> *	P	458	4.4	13
<i>Impatiens glandulifera</i>	T	453	4.3	11
<i>Fraxinus ornus</i> *	P	348	3.3	8
<i>Solidago gigantea</i>	G	341	3.3	13
<i>Pinus sylvestris</i> *	P	263	2.5	7
<i>Bidens frondosa</i>	T	258	2.5	7
<i>Acer negundo</i>	P	242	2.3	10
<i>Amelanchier lamarckii</i>	P	221	2.1	10
<i>Erigeron canadensis</i>	H	148	1.4	15
<i>Aesculus hippocastanum</i> *	P	133	1.3	13
<i>Erigeron annuus</i>	H	123	1.2	9

G, geophyte; H, hemicryptophyte; P, phanerophyte; T, therophyte.

Species native to some regions in Europe, although non-native to others are marked with asterisks.

TABLE 1 The most common alien plant species in European woodlands. *n* = number of plots and *k* = total number of EUNIS habitats in which the species occurred. Values for *n* and *k* are means across 100 resampled datasets (*n*: standard error ≤ 2). See Appendix S4: List S1 for a complete list of alien species grouped by life-form

The high number of alien phanerophytes likely reflects the high introduction pressure of trees since the 17th century (Goeze, 1916), the facilitation of alien tree spread through deliberate and massive

planting (Křivánek & Pyšek, 2008; Richardson, 1998), and human management practices and landscape fragmentation (Iannone et al., 2015; Mortensen, Rauschert, Nord, & Jones, 2009; Schulz & Gray,

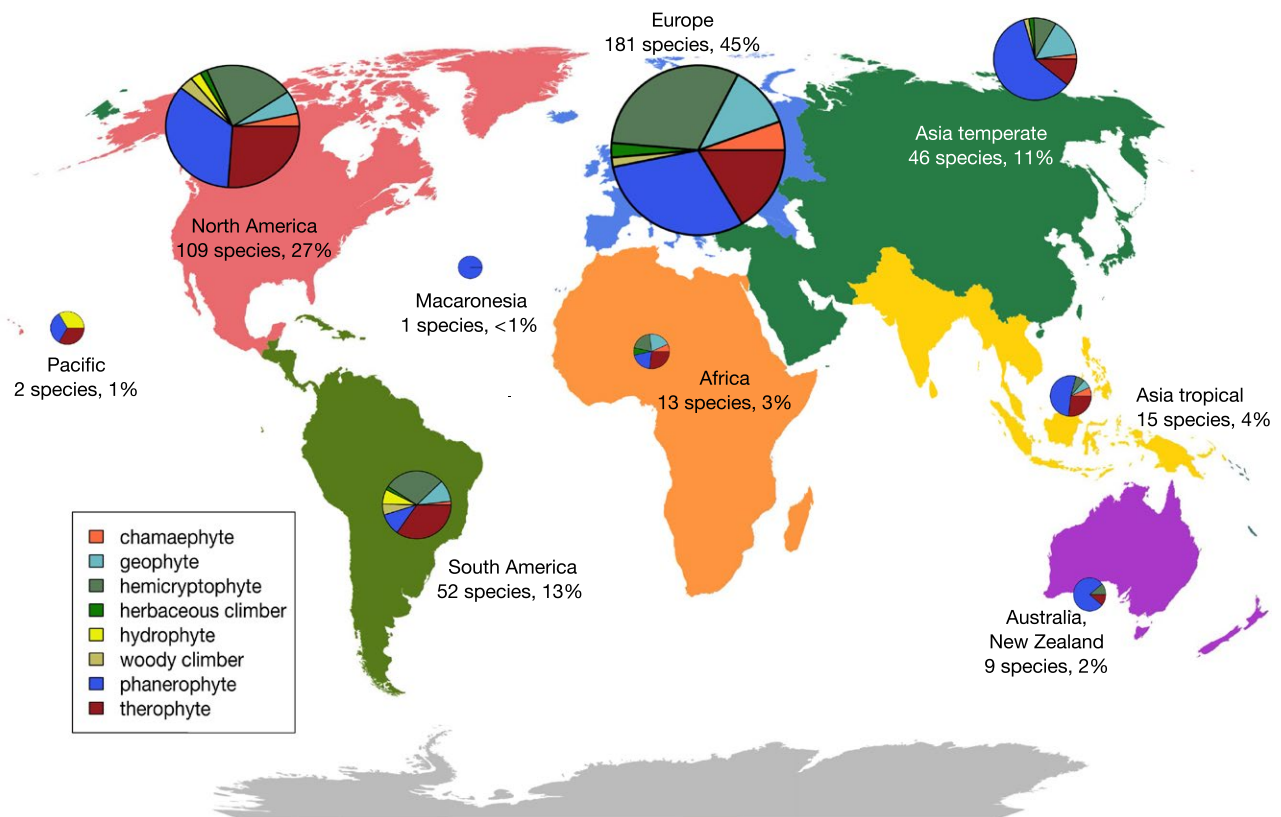


FIGURE 4 Geographic origin of alien plants in European woodlands. Pie colours represent life-forms; pie size increases with number of species but is not strictly scaled. Percentages show the share of the species pool of European woodland alien flora that is native to the region. Species can be native to more than one continent (percentages sum up to > 100%). [Colour figure can be viewed at wileyonlinelibrary.com]

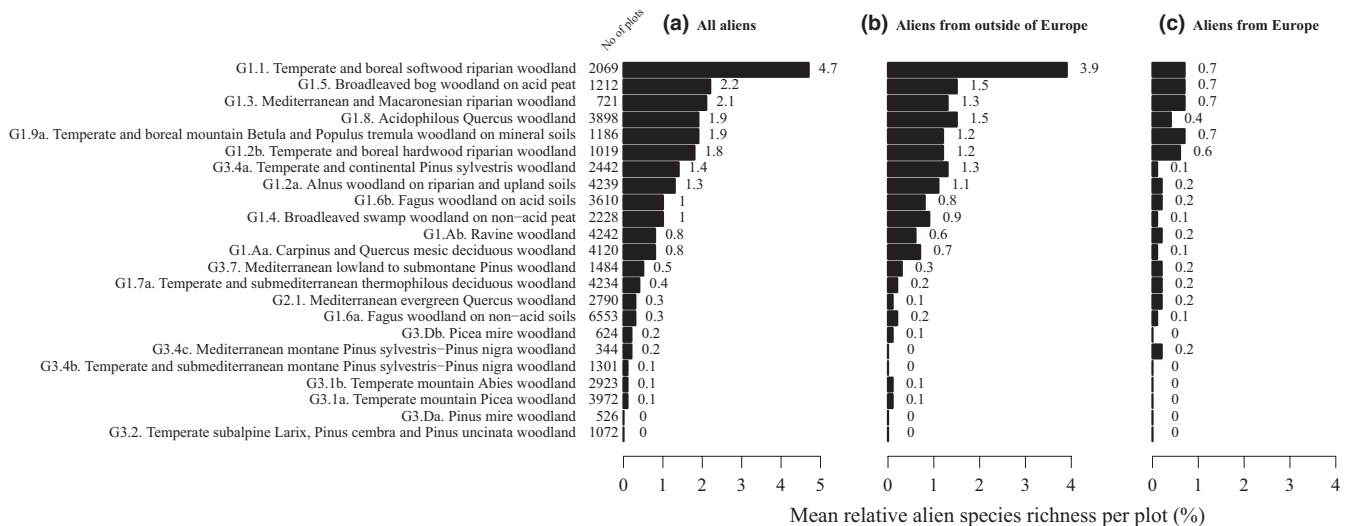


FIGURE 5 Mean relative alien species richness per plot (mean percentage of alien species in a plot compared to all species) across habitats when (a) all aliens, (b) only aliens originating from outside of Europe and (c) only aliens originating from within Europe were considered in the analysis. Data based on resampled dataset (standard errors of the mean < .01%)

2013; Webster & Wangen, 2009). The high frequency of *Acer negundo*, *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia*, in particular, could also be linked to their wide habitat niche (Table 1), a relationship that was previously found in alien plants of the Basque Country (Campos et al., 2013). Furthermore, *Acer negundo*, *Prunus serotina* and *Robinia pseudoacacia* reproduce vegetatively by resprouting, which renders them competitive in their specific habitats. *Robinia pseudoacacia* (Cierjacks et al., 2013; Vítková, Müllerová, Sádlo, Pergl, & Pyšek, 2017) and, to a lesser degree, *Acer negundo* (Walter, Essl, Englisch, & Kiehn, 2005) can colonize fallow land and urban wastelands. Given the ongoing land-use change across Europe, abandoned fields and the urban periphery could continue to provide a habitat and dispersal corridors for alien phanerophytes.

Hemipterophytes were under-represented in the species pool and the relative frequency among aliens compared to native species, although this life-form was the most species-rich and frequent among natives. Assuming that horticulture is an important pathway for the introduction of alien hemipterophytes (Pergl et al., 2016), the small species number might be explained by the low suitability of the shade-adapted and slow-growing woodland herbs for the garden market. Furthermore, the low dispersal ability of woodland hemipterophytes (Bierzychudek, 1982) could be responsible for the relatively low frequency of alien hemipterophytes.

Therophytes made up only the third largest species group among alien plants, but they had a second rank for relative frequency due to the predominance of *Impatiens parviflora*. Its high frequency in European woodlands is astonishing, considering that it arrived in Europe as recently as in 1837 (Trepl, 1984) and, unlike many alien trees, was not planted on a large scale. Its success is likely linked to its wide habitat niche, high shade tolerance, broad range of pollen vectors, high seed production and long flowering period (Čuda, Skálová, Janovský, & Pyšek, 2014; Trepl, 1984). Some studies suggested that this species prefers soils with an intermediate and high nutrient

content (Čuda et al., 2014; Jarčuška, Slezák, Hrivnák, & Senko, 2016; Reczyńska, Swierkosz, & Dajdok, 2015). Consequently, its high frequency could also reflect high nutrient deposition (Jenssen, 2009) and historic land-use dynamics in the European landscape, that is widespread afforestation on former fertilized arable land and an accompanying nutrient legacy in some European woodlands (Koerner, Dupouey, Dambrine, & Benoît, 1997). However, a good understanding of the edaphic niche of the species is still pending as Chmura, Sierka, and Orczewska (2007) found the species to grow mostly in soils with a low and intermediate nutrient content. Despite its high frequency in European woodlands, the species does not seem to have any adverse effects on native plant communities (Hejda, 2012), and it is not controlled.

4.3 | Differences in the levels of invasion across habitats

Mean relative alien species richness ranged from 0% to 4.7% in European woodlands, matching roughly values reported for natural and semi-natural habitats in Catalonia, the Czech Republic and Great Britain (0%–10%, Chytrý, Maskell et al., 2008).

Despite the relatively low estimates, we found profound habitat differences in alien plant invasion at the local scale. All four riparian habitats had high mean relative alien species richness per plot (1.3%–4.7%), especially temperate and boreal softwood riparian woodlands (G1.1). The mean relative alien species richness in the latter EUNIS habitat type (4.7%) was comparable to values reported for ruderal vegetation in Europe (4.5%–6.9%) by Chytrý, Maskell et al. (2008). High levels of invasion in riparian habitats are well documented for Europe (e.g., Liendo, García-Mijangos, Campos, López-Muniain, & Biurrun, 2016; Schnitzer, Hale, & Alsum, 2007) and regions outside of Europe (Kalusová, Chytrý, Peet, & Wentworth, 2015; Parks et al., 2005).

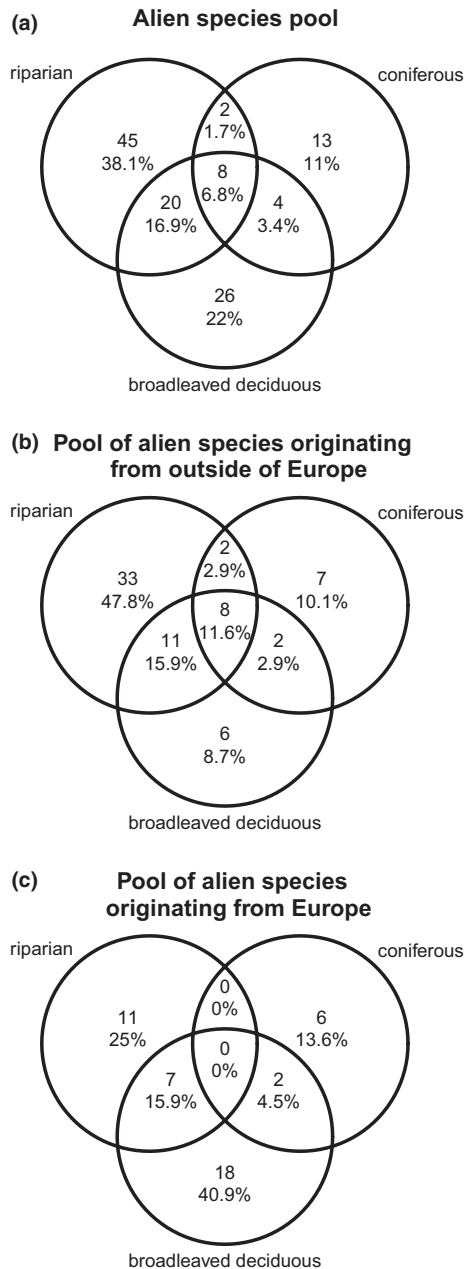


FIGURE 6 Overlap in alien plant species composition among coniferous, broadleaved deciduous and riparian habitats, considering (a) all alien species, and alien species originating from (b) outside of Europe, and (c) Europe. Values indicate the number of alien species found for the set. Only species occurring in at least five plots per group were included in the counts. In (a), the eight species occurring in all three habitat sets included: *Acer negundo*, *Erigeron canadensis*, *Impatiens parviflora*, *Oxalis pes-caprae*, *Prunus serotina*, *Quercus rubra*, *Robinia pseudoacacia* and *Symphoricarpos albus*

Although an increasing number of studies documented differences in the levels of invasion across habitats, the relative importance of individual mechanisms underlying the observed patterns, such as intrinsic vulnerability (invasibility) and human activities (e.g., proximity to gardens, habitat fragmentation, management practices), is not well understood (but see Conedera, Wohlgemuth, Tanadini & Pezzatti

2017; Chytrý, Jarošík et al., 2008). The fact that all riparian woodland habitats had high levels of alien plant invasion suggests a common set of factors that benefits alien plant colonization in these habitats. Their narrow geometric shape and hence the high ratio of edge-area versus core-area, and their function as ecological corridors, might have facilitated high propagule pressure and encroachment in these habitats (Goldblum & Beatty, 1999). In accordance with the fluctuating resource hypothesis (Davis, Grime, & Thompson, 2000), periodic flooding and accompanying exposure to nutrient pulses could also be responsible for an intrinsically high invasibility of riparian woodlands (e.g., Rejmánek, 2015; Richardson et al., 2007; Thébaud & Debussche, 1991). This should be particularly true for temperate and boreal softwood riparian woodland (G1.1), as this habitat is most proximate to rivers and exposed to a dynamic flood regime, with periodically bare soil and ample supply of nutrients and light. The high percentage of alien therophytes in this habitat type (33%) supports the importance of transient competition-free bare places, that is empty niches for alien plant establishment. In addition, extrinsic factors such as human disturbance could also explain the high levels of invasion in riparian woodlands (Liendo et al., 2016). Riparian habitats are highly degraded worldwide due to damming, canalization, drainage, dredging and straightening (Naiman, Decamps, & McClain, 2010) and were exposed to a high total emission of nitrogen and phosphorous in the last century (ICPDR, 2005). Temperate softwood riparian woodlands are particularly exposed to eutrophication because they receive the collective agricultural runoff from watersheds (Mölder & Schneider, 2011).

By contrast, *Picea* and *Pinus* mire woodlands (G3.Da, G3.Db) and temperate and Mediterranean mountain coniferous woodlands (G3.1a, G3.1b, G3.2, G3.4b, G3.4c) showed the lowest mean relative alien species richness per plot (<0.2%). The low estimate for mire woodlands might be attributed to their strong abiotic filters, such as low soil pH, and low soil oxygen and nutrient contents (Rydin & Jeglum, 2013). Interestingly, broadleaved bog woodland on acid peat (G1.5) showed the second highest mean relative alien species richness per plot (2.2%), although it also possesses strong abiotic filters. At first glance, these high relative values could be due to the low absolute values of native species richness in this habitat. However, *Picea* and *Pinus* mire woodlands were similar in this regard (Appendix S5: Fig. S1). This finding deserves further research, but a possible factor could be a stronger degree of human disturbance in the broadleaved bog woodland, such as peat extraction and the ability of the prevailing alien species in this habitat, for example *Prunus serotina*, to colonize bogs (Schrader & Starfinger, 2009).

Low levels of invasion in mountain coniferous woodlands could be due to their occurrence at higher altitudes. Decreasing levels of invasions with altitude are well documented and attributed to diminished propagule pressure (Alexander et al., 2011) and lower levels of human disturbance (Pyšek, Jarošík, Pergl, & Wild, 2011). In theory, the low levels of invasion could also be due to the intrinsic properties of conifer woodlands, such as slow circulation of nutrients and nutrient leaches (Schlesinger, 1997; and references herein). However, the intermediate mean relative alien species richness per plot in temperate and continental *Pinus sylvestris* woodland (G3.4a, 1.4%) argues against this explanation. Estimates of the levels of invasion for boreal coniferous

woodlands (lowland ecosystems) could help to disentangle this question, but they were not represented in our dataset. Previous studies from boreal ecosystems in other parts of the world show that boreal woodlands can become susceptible to alien plant invasions under strong disturbance, fire events and propagule pressure (Khapugin, Vargot, Chugunov, & Shugaev, 2016; Rose & Hermanutz, 2004).

5 | CONCLUSIONS

Our study is the most comprehensive, to date, to provide a robust and balanced assessment of alien plant invasions in a widespread vegetation type at the continental scale. It demonstrates that European woodlands have been generally invaded by many alien plant species. Our results indicate that intrinsic and human disturbance, propagule pressure and high nutrient levels could be important drivers underlying invasion processes in woodlands. Given the persistence of these factors in the landscape, competitive alien species with a broad niche and introduced alien phanerophytes will likely continue to persist and spread in this habitat. As invasions are dynamic processes operating across time and space, large vegetation archives must be updated regularly, especially by surveys from undersampled regions and from sites with recent or local alien plant introductions. The reanalysis of these data and resampling of plots with accurate geographic information could help track invasion trends at the regional and local scale, and provide insights for invasive species regulation in Europe.

The European Union regulation on the prevention and management of alien species (No 1143/2014) laid the foundations for the first and recently published list of invasive alien species of Union concern (Commission Implementing Regulation [EU] 2016/1141, 13 July 2016). Although we did not address the impact of alien species in European woodlands, our results imply that alien species originating outside of Europe could pose a particular threat because this species group had a higher frequency in European woodlands than the group originating from within Europe. Furthermore, the high frequency of alien phanerophytes shows that pathways of deliberate species introductions for timber, fruit and honey, and ornamental purposes should be more strictly regulated. Specifically, our results reinforce the argument that alien tree species introduced in the course of adaptive forest management as new timber sources to mitigate global warming should undergo a thorough risk assessment (Bolte et al., 2009). An integrated approach that includes stakeholders in science, horticulture and forestry (Sitzia, Campagnaro, Kowarik, & Trentanovi, 2016) and adheres to a Code of Conduct (Brundu & Richardson, 2016) could strengthen a Europe-wide regulation of invasive phanerophytes. Last but not least, our study indicates that differences in the levels of invasion across habitats should be taken into account when planning and implementing monitoring and management actions in protected areas.

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DATA ACCESSIBILITY

R scripts for the data analysis and information on data accessibility are deposited at <https://doi.org/10.6084/m9.figshare.5057041.v1>.

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BIOSKETCH

Viktoria Wagner is a postdoctoral researcher with an interest in invasion ecology and macroecology. Her team of co-authors consists of experts in invasion and vegetation ecology and ecological modelling. This study is part of the InvasEVe project, a pan-European initiative that aims to elucidate the patterns and mechanisms underlying alien plant invasions in European woodlands.

Author contributions: Viktoria Wagner and Milan Chytrý were responsible for the idea and study design. Stephan Hennekens and Ilona Knollová assisted with software and data handling. Viktoria Wagner led the data preparation, statistical analysis, and writing. Co-authors supplied data, checked species status and life form assignments, provided expertise on the statistical analysis, and/or helped develop the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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