

Neophyte invasions in European grasslands

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Abstract

Questions: The human-related spread of alien plants has serious environmental and socioeconomic impacts. Therefore, it is important to know which habitats are most threatened by invasion and why. We studied a wide range of European grasslands to assess: (i) which alien species are the most successful invaders in grasslands; (ii) how invasion levels differ across European regions (countries or their parts) and biogeographical regions; and (iii) which habitat types are the most invaded.

Location: Europe

Methods: We selected 97,411 grassland vegetation plots from the European Vegetation Archive (EVA) and assigned a native or alien status to each of the 8,212 vascular plant species found in these plots. We considered only neophytes (alien species introduced after 1500 AD), which we further divided according to their origin. We compared the levels of invasion using relative neophyte richness in the species pool, relative neophyte richness and cover per plot, and percentages of invaded plots among regions and habitats.

Results: Only 536 species, representing 6.5% of all grassland vascular plant species, were classified as neophytes. These were mostly therophytes or hemicryptophytes with low habitat specificity. Most of them were present in very few plots, while only three species were recorded in more than 1% of all plots (*Onobrychis viciifolia*, *Erigeron annuus* and *E. canadensis*). Although invasion levels were generally low, we found more invaded plots in the Boreal and Continental region. When considering only non-European neophytes, the Pannonian region was the most invaded. Among different grassland habitats, sandy grasslands were most invaded, and alpine and oromediterranean grasslands least invaded.

Conclusions: In general, natural and semi-natural European grasslands have relatively low levels of neophyte invasions compared with human-made habitats or alluvial forests, as well as with grasslands on other continents. The most typical neophytes invading European grasslands are species with broad ecological niches.

Keywords

alien, continental scale, EUNIS habitat, Europe, European Vegetation Archive (EVA), grassland, invasion level, invasion success, neophyte, plant invasion, semi-natural vegetation

Introduction

The human-caused spread of alien plants is an important issue worldwide (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017) as many alien plant invasions have severe environmental and socioeconomic impacts (Vilà *et al.*, 2011; Pyšek *et al.*, 2020). However, there are significant differences in the levels of alien invasion among regions (Lonsdale, 1999; Kalusová *et al.*, 2015; van Kleunen *et al.*, 2015) and among habitats (Chytrý *et al.*, 2008a; 2008b; Pyšek *et al.*, 2012a; Kalusová *et al.*, 2014). To apply proper risk-assessment schemes and effective management, we need to identify the most vulnerable habitats, their successful invaders and the factors responsible for their high levels of alien plant invasion.

Europe is an important source of numerous neophytes (species native in some European countries and introduced by man to other continents or European countries after 1500 AD, hereafter European neophytes), but also receives many neophytes from elsewhere (hereafter non-European neophytes; Kalusová *et al.*, 2015; van Kleunen *et al.*, 2015; 2019). The first overviews of alien plants across European countries were based on the data from national and regional floras and additional plant distribution data (Weber *et al.*, 1997; Lambdon *et al.*, 2008), and these efforts continued with the assessment of naturalized neophytes at the global scale (van Kleunen *et al.*, 2015; 2019). However, assessing the number of neophytes in regional floras does not necessarily reflect their abundance across habitats, which largely determines the impact of neophytes on natural ecosystems (Bradley *et al.*, 2018; Sofaer *et al.*, 2018).

Recent studies have focused on fine-scale data related to habitat types to get a different perspective on invasion levels (see Pyšek and Chytrý, 2014, for a review). For example, the analysis of three climatically distinct regions using vegetation-plot data showed that broadly defined habitats such as forests or grasslands had comparable numbers of neophytes in different geographical locations (Chytrý *et al.*, 2008b). Moreover, despite different absolute invasion levels, the most and least invaded habitats were the same when comparing European and North American regions (Kalusová *et al.*, 2015). The above-mentioned studies suggest that habitat typologies are a key factor for understanding plant invasions. Generally, human-made habitats (e.g. arable fields, wastelands, ruderal sites in settlements) are most invaded, while habitats with natural vegetation are less invaded, especially at high elevations (Chytrý *et al.*, 2008b; Lambdon *et al.*, 2008). Comparisons of these broadly defined habitat types showed that different levels of alien plant invasion could be explained by several factors, especially by intensity and frequency of disturbances and related fluctuations in resource availability, propagule pressure and climate (Davis *et al.*, 2000; Chytrý *et al.*, 2008a). The recently compiled European Vegetation Archive (EVA; Chytrý *et al.*, 2016) has enabled to obtain even more in-depth insights into the neophyte invasion patterns at the level of narrowly defined habitats, already analysed for European woodlands (Wagner *et al.*, 2017) and coastal dunes (Giulio *et al.*, 2020).

Grasslands represent the second most widespread broad vegetation type in Europe after forests. Although they are typically maintained by livestock grazing or mowing for hay, we consider them as mainly semi-natural vegetation, as they are a widely distributed natural component of European vegetation. For example, they often occur in places where the succession towards forest is blocked by harsh environmental conditions or regular disturbances such as floods or

grazing by wild herbivores (Svenning, 2002; Kuneš *et al.*, 2015; Feurdean *et al.*, 2018). European grasslands occur across large gradients of soil moisture and pH, nutrient availability and climate. Grassland habitats also bear the imprint of the past, including glacial-interglacial cycles, postglacial migration and traditional management practices (Pärtel *et al.*, 2005; Feurdean *et al.*, 2018). All of these factors shape current grassland vegetation in Europe and result in high variability of vegetation types (Squires *et al.*, 2018; Chytrý *et al.*, 2020). We might expect that large ecological differences among grassland habitat types are also reflected in their different levels of invasions and species that invade them. However, neophyte invasions across grassland habitats have not been studied at the European scale so far.

Some parts of the European continent are clearly more invaded than others (Chytrý *et al.*, 2009; Pyšek *et al.*, 2017). The patterns are further differentiated with respect to various origins of neophytes. Long-term presence on the continent and relatively short distances between European countries, as opposed to intercontinental distances, can cause neophytes of European origin to be on average more common in the secondary part of their European range than neophytes originated from outside Europe (Lambdon *et al.*, 2008). For non-European neophytes, establishment success is influenced by the time since the introduction (Pyšek and Jarošík, 2005) and the degree to which the invaded area in Europe resembles their native range, expressed by climate matching at a coarse scale (Thuiller *et al.*, 2005; Cao Pinna *et al.*, 2021). Since geographical patterns of neophyte invasions might considerably differ among broad vegetation types at the country level (Divíšek and Chytrý, 2018), we need to explore the patterns in grasslands and other vegetation types at the European level separately, rather than inferring them from the patterns found for the whole flora or other vegetation types.

In this study, we used the largest European vegetation-plot database (EVA; Chytrý *et al.*, 2016) to provide a synthetic overview of neophyte invasions in European grassland vegetation, asking the following questions: (i) Which neophyte species are the most successful invaders of European grasslands, and are they habitat specialists or generalists? (ii) How do invasion levels differ across European regions (countries or their parts) and biogeographical regions? (iii) Which grassland types are the most invaded?

Methods

Initial dataset

We used 465,629 grassland vegetation plots provided by the European Vegetation Archive (EVA; Chytrý *et al.*, 2016). We then classified these plots to grassland habitat types according to the European Nature Information System (hereafter EUNIS habitats or habitats). The classification was based on species composition and cover and performed using the EUNIS-ESy expert system (v. 2020-06-08; Chytrý *et al.*, 2020) in the JUICE software (Tichý, 2002). Apart from grasslands in a narrow sense (EUNIS group R), we also recognised coastal grasslands of grey dunes, which belong to EUNIS group N (coastal habitats). An overview of contributing databases and numbers of plots assigned to particular

EUNIS habitat types are available in Appendices S1 and S2 in the Supplementary Materials. We also merged these habitats to broader habitat types (habitat groups, see Appendix S2 for details), enabling us to detect more general patterns at a coarser scale.

Geographical units

Regions used in our study mostly correspond to the whole countries. However, large islands or archipelagos with distinct biogeographical positions were treated as separate units (Balears, Corsica, Crete, Sardinia, and Sicily with Malta). For the European part of the Russian Federation, we followed the regional division suggested in the Euro+Med PlantBase (2006–2020), considering seven units (Russia North, Russia Northwest, Russia Kaliningrad, Russia Central, Russia South, Russia Caucasus and Russia East). The list of all 49 studied regions (countries or their parts) with the numbers of plots is in Appendix S3.

Each plot was also assigned to a biogeographical region defined by the European Environmental Agency (EEA, 2016), namely Alpine, Atlantic, Boreal (including Arctic), Continental, Mediterranean, Pannonian and Steppic (including Black Sea) biogeographical regions. These broad regions were delimited to reflect the main climatic gradients, landscape and soil characteristics across the continent. For the map of biogeographical regions and the corresponding number of the assigned plots, see Appendix S4.

Data filtering and the final dataset

We filtered the vegetation plots using the following criteria. First, we removed (i) plots that could not be assigned to any EUNIS grassland habitat type at the third level of classification (transitional between different grassland habitat types); (ii) plots with a cover of woody species (trees or shrubs taller than 0.5 m) higher than 10%; (iii) plots dominated by *Pteridium aquilinum* (classified as R54 habitat) or plots from forest clearings (R57). Second, we excluded plots without geographical coordinates or with a location uncertainty ≥ 7000 m. Third, we selected only plots with a surface area between 10 and 100 m² to limit the area effect. However, we retained plots with a size between 1 and 100 m² for Nordic countries since the small-size plots traditionally prevail there. We also kept plots with unknown sizes (based on the plot size histogram, 85% of the plots with known size were within the range of 10–100 m²; therefore, we assumed a similar distribution for the plots with unknown sizes). Fourth, we kept only the vegetation plots sampled between 1970 and 2018 to reduce the effect of vegetation changes through time. Fifth, we used geographical position and compositional dissimilarity of plots to limit potential pseudoreplications in the data. From pairs of plots with the compositional dissimilarity of 20% or lower (i.e. ≤ 0.2 of Simpson dissimilarity index) sampled within a distance of less than 1 km, we randomly selected just one. Sixth, to further reduce the over-representation of plots in some regions (countries or their parts), we set a maximum number of plots per region for each habitat type. Initially, we calculated the density of plots belonging to a given habitat type for each region (number of plots relative to the region's area). From the distribution of densities across all regions, we defined an outlier value (upper quartile $+1.5 \times$ interquartile range) for each habitat type, which was subsequently used as a threshold. If the habitat type was in some region

represented by more plots than the respective threshold, we randomly selected a subset of plots to match the desired maximum number of plots per region. After filtering, the final dataset used for the analyses included 97,411 plots.

Species status assignment

We considered only vascular plants in our study, including trees and shrubs. The taxonomic concepts were unified to follow the Euro+Med (2006–2020) PlantBase, or The Plant List (TPL, 2013) if the taxon was not included in Euro+Med. We assigned the native, alien or uncertain status to all the plant taxa for the region where they were recorded. We considered only neophytes in our study (i.e. alien species that arrived in the region after 1500 AD, see Pyšek and Jarošík, 2005). Archaeophytes were included among native plants and not treated separately because their lists are lacking or incomplete in many regions (countries or their parts). In many cases, it is doubtful whether a species is an archaeophyte or native in a region. If a species was reported as native in at least part of a region, we considered its status for that region as native. We assigned the native/alien status using the Euro+Med PlantBase (2006–2020), DAISIE (2009), the GLONAF database (van Kleunen *et al.*, 2019) and national or regional species checklists. In the case of contrasting status provided in different sources, our final decision was based on the most up-to-date information, status in the neighbouring regions and knowledge of local experts in our author team. All sources are listed in Appendix S5. Taxa for which we could not decide their status were excluded (mostly genus-level records). For a status assignment at the plot level, we used infraspecific taxa, as sometimes one subspecies can be native while another subspecies is considered as a neophyte. For comparison of regions and habitats, we summarized the results at the species level: when more than one subspecies were classified as neophytes, we counted them as one neophyte species, and in rare cases when both a native and neophyte subspecies occurred, we included them as both native and neophyte species. This made our results comparable with recent studies of other European habitats (e.g. Wagner *et al.*, 2017; Giulio *et al.*, 2020).

We further classified neophytes according to their origin: A, neophyte species originating from outside of Europe (Africa, America, Asia, Australia); E, species native to some parts of Europe but considered to be neophytes elsewhere in Europe, and C, other origins, i.e. anecophytes (species with unknown native distribution) or species with hybrid origin (similarly as in Wagner *et al.*, 2017). We also classified all neophytes by their prevailing life form: phanerophytes (trees and shrubs), chamaephytes (perennial herbs or dwarf shrubs with regenerative buds above the ground, but lower than 30 cm), hemicryptophytes (perennial herbs with regenerative buds at the ground level), geophytes (perennial herbs with regenerative buds belowground), therophytes (annual herbs), hydrophytes (regenerative buds underwater) and woody lianas (perennial plants with woody climbing stem). The sources used for this assignment are listed in Appendix S6.

Data analyses

We assessed the levels of invasions using different metrics (compare Catford *et al.*, 2012; Wagner *et al.*, 2017; Giulio *et al.*, 2020): (1) absolute neophyte richness in the species pool (number of neophyte species) and relative neophyte richness in the species pool (number of neophyte species relative to all species; %), (2) absolute occurrence frequency

of neophytes (count of individual plot records of neophytes) and relative occurrence frequency of neophytes (count of plot records of neophytes relative to the count of plot records of all species), (3) mean, median or quantile of absolute plot-level neophyte richness (number of neophytes in the plot) and relative plot-level neophyte richness (number of neophytes in the plot relative to all species in the plot, %) calculated per plots, (4) mean and median absolute neophyte cover and relative neophyte cover per plots, and (5) percentage proportion of invaded plots (i.e. plots with at least one neophyte present) from all the plots. We applied these metrics to the whole dataset and its specific subsets, i.e. habitat groups or regions, or considering separate neophyte categories according to their origin.

Species affinity to grassland habitat types was analyzed using the Juice software (Tichý, 2002). We calculated the degree of concentration of occurrences (i.e. fidelity) of each neophyte species in individual habitat groups using the *phi* coefficient of association. For the analysis, the size of all groups was standardized to equal size, and the significance of species concentration was evaluated using Fisher's exact test (Tichý & Chytrý, 2006). Only the associations significant at $p < 0.05$ were interpreted.

The differences in absolute/relative neophyte richness and absolute/relative neophyte cover among habitat groups and biogeographical regions were tested using the Kruskal-Wallis multiple comparison test in the package 'pgirmess' (Giraudeau, 2013) in the R software v.3.6.0 (R Core Team, 2020). Total plant cover and neophyte cover were calculated as a sum of the individual plant covers considering their possible overlap using the Jennings-Fischer formula (Jennings *et al.*, 2009; Fischer, 2015).

To track geographical patterns in the level of invasions, we assigned vegetation plots to the UTM grid cells of 50 km × 50 km. We calculated the percentage proportion of invaded plots for each cell, i.e. what percentage of plots within a given grid cell have at least one neophyte present. We prepared separate maps with respect to habitat groups and different origin categories of neophytes using the R packages 'raster' (Hijmans *et al.*, 2020), 'rgdal' (Bivand *et al.*, 2020), 'spatialEco' (Evans *et al.*, 2020) and 'berryFunctions' (Boessenkool, 2020). We mapped only grid cells containing more than 10 plots in order to avoid interpreting random patterns. We further prepared comparison of main geographical patterns using different invasion metrics.

Results

Successful neophytes

The final grassland dataset included 8,212 species, of which 536 were neophytes (approximately 6.5% of all species) with almost the same number of neophytes originating from Europe (3.0%) and outside of Europe (3.1%, Figure 1a). A list of all neophytes recorded per region (country or its part) is in Appendix S7. The majority of neophytes in grasslands were present in very few plots (median: 2 plots), while only three species, namely *Onobrychis viciifolia*, *Erigeron annuus* and *E. canadensis*, were recorded in more than 1% of all plots (Table 1). When comparing the frequency of species occurrences in plots, the prevalence of native species was even more pronounced: European neophytes corresponded only to 0.17% (4,259 of all 2,565,674 occurrences), while those from outside of Europe to 0.33% (8,473) (Figure 1b). The prevailing life forms of neophytes in the species pool were hemicryptophytes (32%) and therophytes (31%), followed by phanerophytes (21%) (Figure 2).

Most neophyte species (90% when considering only species recorded in at least five plots) occurred in more than one habitat group, indicating their low degree of specialization. This was also confirmed in the analysis of fidelity (results not shown), where only five species had a higher probability of association with some vegetation type, namely *Erigeron canadensis*, *Oenothera biennis* and *Senecio leucanthemifolius*, concentrated in sandy habitats (*phi coefficient*=0.26, 0.16 and 0.13, respectively), *Onobrychis viciifolia* in dry habitats (0.15) and *Grindelia squarrosa* in saline habitats (0.12). The most frequent neophytes per habitat group are listed in Table 2.

Geographical patterns

Summary statistics for the whole of Europe and individual regions (countries or their parts) can be found in Appendix S8 and S9, while geographical patterns are shown in Figure 3 and Appendix S14. Most vegetation-plot records included only native species and archaeophytes, while invaded plots, i.e. plots with at least one neophyte, represented only 11.9% of all plots (7.1% of plots if only non-European neophytes were considered; Appendix S8). Higher percentages of invaded plots can be seen in northern part of Europe such as in Fennoscandia, Baltic countries and Poland. This pattern is also affected by the increasing number of European neophytes towards the north, while most of the plots in southern and south-eastern Europe are only invaded by non-European neophytes (Figure 3b, c, see also Appendix S8). A slightly higher frequency of invaded plots can also be seen in coastal areas. When comparing the species pools of individual regions, those with the highest relative richness of European neophytes were Poland (3.9% of all species), the Netherlands (3.8%), Lithuania (3.5%), Denmark (3.0%) and Germany (3.0%) (see Appendix S8 for a full list).

A comparison of biogeographical regions revealed the highest percentage of invaded plots and also the highest mean neophyte richness per plot in the Boreal, Continental and Pannonian regions (in a decreasing order), while the Alpine region was least invaded (summary statistics and comparison in Tables 3 and 4 and Figure 4). When considering only non-European neophytes, the highest levels of invasion were in the Pannonian region (see Appendix S10 for details).

Habitat comparison

Summary statistics for habitat groups can be found in Tables 3b, 4b and Appendix S11. We revealed the highest species-pool neophyte richness in mesic, wet and dry grasslands, followed by sandy grasslands (see Table 3 for a summary). While rocky, dry and mesic habitat groups appeared to have a higher number of European neophytes than those of non-European origin, sandy, wet and saline habitats showed a reverse pattern. We revealed the highest prevalence of non-European neophytes in wet grasslands (Table 3). When excluding rare species from the comparison and comparing only neophytes recorded in at least 1% of the plots from the respective habitats, sandy, wet and mesic habitats had the highest species-pool neophyte richness (in decreasing order), while the oromediterranean and alpine grasslands had the lowest.

A similar pattern can also be seen in the percentage proportion of invaded plots per habitat group (Table 3) and mean relative neophyte richness per plot (Table 4, Figure 4, Appendix S11). This measure indicated sandy habitats to be most invaded, followed by wet and mesic habitat group, while oromediterranean and alpine habitat group were the least and second least invaded, respectively. Kruskal-Wallis multiple comparisons of the mean relative neophyte richness, absolute neophyte richness and the mean relative neophyte cover per plot confirmed the above-described pattern (Table 4).

Analyses at the third hierarchical level of EUNIS habitat classification support the results found at the coarse scale of habitat groups (see summary statistics in Appendix S12 and S13). Sandy habitats (both inland and coastal) had the highest percentages of invaded plots across different types and geographical regions (on average around 20%, with a maximum of 31% in R1P – Oceanic to subcontinental inland sand grassland on dry acid and neutral soils). Comparable percentages of invaded plots were also found in lowland wet tall-herb grasslands in both temperate and Mediterranean types. In contrast, high-elevation grasslands, especially alpine and oromediterranean, had the lowest percentages of invaded plots (Figure 5).

Discussion

Successful neophytes

Neophytes are a heterogeneous group with species differing in their ability to overcome abiotic and reproductive barriers and to establish sustainable populations in new environments. Some species can invade only the same or similar habitats from which they originated and to which they are adapted in their native range. Therefore, the more habitats a species occupies in its native range, the higher its chances to become a successful invader (Hejda *et al.*, 2015; Kalusová *et al.*, 2017). The association with human-made habitats and disturbances in the native range also seems to support invasion success (Kalusová *et al.*, 2017). This is in agreement with our finding of low habitat specificity for the majority of neophytes. It indicates that either they have broad habitat niches developed already in their native range or their niche has been extended in the invaded regions compared to the region of origin (see also Hejda *et al.*, 2009). A large group of neophytes in our dataset are short-lived ruderal species that use opportunities of establishing in gaps after disturbances. Although rare in semi-natural grasslands (most neophytes had few occurrences only), many of these species are more abundant in intensively disturbed habitats of the same region, either in human-made habitats or in river bars where natural hydrological disturbances support high invasion levels (Liendo *et al.*, 2021). This further suggests that they have low habitat specificity also at the level of broadly defined habitats. Similarly, Giulio *et al.* (2020) concluded that 94% of the neophytes found in European coastal dunes were generalists also occurring in other than coastal habitats.

The most frequent neophyte in our dataset was *Onobrychis viciifolia*, a perennial species native to southern and south-eastern Europe and western Asia, from where it was intentionally introduced to the rest of Europe as a forage crop (Mora-Ortiz and Smith, 2018). The second most frequent species was *Erigeron canadensis*, an annual or overwintering species native to North America. Although it is mostly found in human-made habitats (orchards, vineyards, roadsides, arable fields, ruderal sites), it is adaptable to different environments across a broad range of climates. Thanks to effective wind dispersal, it can quickly establish in open gaps after disturbance and start to grow rapidly (Weaver, 2001). It was reported as the most successful alien species also in European coastal dunes (Giulio *et al.*, 2020) and across Europe in general (Lambdon *et al.*, 2008). The third most frequent species was *Erigeron annuus*, an annual species with prevailing apomictic reproduction, native to North America. This species is also effectively dispersed by wind and is widespread across Europe. Although it has been shown that its frequency declines towards higher elevations, growth performance and seed production of the mountain populations are comparable to those in the lowland populations, and the reason for its lower frequency in the mountains is probably its greater winter mortality (Trtikova *et al.*, 2011). In contrast to *Onobrychis*, the spread of which was directly supported by humans, both *Erigeron* species seem to be so successful mostly due to high seed production and efficient seed dispersal (Weaver, 2001).

Geographical patterns

We found a relatively low proportion of neophyte species in the species pool of European grasslands (only 6.5% of all species in the dataset). Such low levels of invasion are similar to values reported from European forests (Wagner *et al.*, 2017) and coastal vegetation (Giulio *et al.*, 2020), but they are in contrast to those reported from North American habitats (Lonsdale, 1999; Kalusová *et al.*, 2015). The several times higher numbers of neophytes in North America, even when comparing similar grasslands (15% reported from prairies by Stohlgren *et al.*, 1999), support the view that Europe is donating more alien species than it is receiving in exchange (Seastedt and Pyšek, 2011; Stohlgren *et al.*, 2011; Hejda *et al.*, 2015; but see Seebens *et al.*, 2015). This also holds in comparisons within specific species groups, such as grasses (Monnet *et al.*, 2020).

The shares of non-European and European neophytes were almost equal in the species pool, but the former group prevailed when considering the relative frequency of occurrences across the plots (accounting for 58.6% of all neophyte occurrences, most of them from North America). This agrees with the greater representation of species from other continents reported by previous large-scale European studies (Wagner *et al.*, 2017; Giulio *et al.*, 2020). The neophytes of European origin in grasslands were mostly native to southern Europe from where they spread to suitable habitats in other regions. This is especially notable in the map of invaded plots, where European neophytes are almost completely lacking in southern and south-eastern Europe. Depending on when these species reached individual regions, they can be classified as either an archaeophyte or neophyte (Pyšek *et al.*, 2005). As a result, we observed a gradual increase of European neophytes towards the north. Moreover, plant species ranges do not reflect only recent climate but also the regional history, especially Pleistocene glaciations, as many species have been dispersal-limited in their postglacial expansion from their mostly southern glacial refugia (Normand *et al.*, 2011). A large number of otherwise frequent European species have probably been able to colonize northern countries only as a consequence of human-induced changes of habitats and human-assisted species dispersal (Lambdon *et al.*, 2008).

We found higher percentages of invaded plots in northern Europe (partly as a result of higher abundance of neophytes of European origin there) and in coastal habitats. The highest neophyte richness in the species pool was found in Poland, the Netherlands, Lithuania, Denmark and Germany, where both European and non-European neophytes were present in relatively high numbers. The corresponding biogeographical regions, Boreal and Continental, also have the highest percentages of invaded plots and mean neophyte richness per plot. We suggest that in these biogeographical regions, the high incidence of neophytes is partly the legacy of postglacial expansion and partly a result of the presence of coastal habitats, which are generally more invaded (Chytrý *et al.*, 2008b; Dawson *et al.* 2017; Giulio *et al.*, 2020). When considering only non-European neophytes, the Pannonian biogeographical region reached the highest mean neophyte richness per plot, which can point at suitable environmental conditions for a large number of neophytes and at the same time reflect a high abundance of open habitats in this biogeographical region.

Another important factor supporting higher invasion levels can also be the recent changes in grassland management (e.g. Timmermann *et al.*, 2015). Nowadays grasslands widely experience both reduced wild herbivore grazing and

reduced management, leading to secondary succession and vegetation changes that can support the success of neophytes (e.g. Timmermann *et al.*, 2015; Swacha *et al.*, 2018).

Habitat comparison

Our study based on a comprehensive continental-scale dataset confirmed observations from earlier regional studies that European grasslands generally have low levels of invasion, which is in contrast to highly invaded human-made habitats (fields, urban habitats) and riparian habitats (Chytrý *et al.*, 2008b; Campos *et al.*, 2013; Kalusová *et al.*, 2015). However, despite the low overall frequency of invaded plots (less than 12% of all plots), EUNIS habitat types varied in the proportion of invaded plots from 0 to 31%. The highest percentages of invaded plots were found in sandy habitats (in both inland and coastal types) and in lowland tall-herb wet meadows, while grasslands at high elevations were almost free of neophytes. Such pattern is in accordance with conclusions of earlier studies that neophytes preferably invade habitats with the temporal surplus of resources, frequent disturbances and no climatic extremes (Chytrý *et al.*, 2008a; Pyšek and Chytrý, 2014).

Since sandy and wet grasslands differ in many habitat characteristics, we can also expect different strategies of neophytes invading them. Life-form comparison revealed a relatively high representation of two distinct groups in our grassland dataset species list of neophytes, namely therophytes and hemicryptophytes (each group represented by around 30%). Wet grasslands mostly have a high total cover, and gaps occur only rarely after disturbances; thus, competitive hemicryptophytes are more successful. In contrast, the unstable substrate in sandy habitats does not allow the formation of closed stands, and many open gaps are available to support establishment of new species (disturbance effect; Hobbs and Huenneke, 1992; Lozon and MacIsaac, 1997), in our study mostly therophytes. The spread of these short-lived species, often with ruderal tendency, has been recently detected also in other vegetation types, such as dry grasslands (Essl and Dirnböck, 2008). As present weather fluctuations and drought events lead to decreased cover or even disappearance of some native species, new gaps emerge in the stands and opportunities arise for fast spreading and easily germinating therophytes (Fischer *et al.*, 2020).

The least invaded grasslands, which occur in the oromediterranean and alpine belts, have extreme climatic conditions and usually nutrient-poor soils; therefore, the number of potential neophytes is limited (Chytrý *et al.*, 2008b). Grasslands at high elevations historically experienced lower human impact and intensity of disturbances, which suppressed or at least reduced the success of neophytes (Medvecká *et al.*, 2014; Alexander *et al.*, 2016; Lembrechts *et al.*, 2016). Even the current level of human impact is usually lower at high elevations, which is reflected in lower propagule pressure of alien plants (Alexander *et al.*, 2011). Therefore, disturbance plays a crucial role, and only the most intensively disturbed mountain habitats are colonized (Pauchard *et al.*, 2009; Dainese *et al.*, 2014; Alexander *et al.*, 2016). Although we might expect that successful neophytes are habitat specialist adapted to stress of harsh climate,

alien species found at higher elevations are mostly generalist with wide ecological amplitudes and widest elevation ranges (Haider *et al.*, 2010; Alexander *et al.*, 2011).

Dataset limitations

Although the results based on our comprehensive European dataset are quite robust, it is important to be aware of possible limitations. Firstly, the EVA database (Chytrý *et al.*, 2016) comprises primarily data originally sampled for phytosociological surveys. Therefore, most of them originate from preferential sampling (Michalcová *et al.*, 2011), which may have included some tendency to avoid sampling plots with a higher incidence of alien plants. Secondly, the dataset does not include information on the site history, such as recent disturbances or the abandonment of traditional management, although these are important factors with strong effects on the invasion processes. Third, the data density across regions is unequal, and although we performed stratified resampling to reduce the disproportions among regions, some of them were still underrepresented in the dataset. Finally, the questionable status of some species can affect the overall patterns (but see Courchamp *et al.*, 2020). Grasses are most problematic in this respect because they were traditionally supported by humans and are hard to distinguish in archaeological findings, for example, *Lolium multiflorum*, *Festuca brevipila*, and most notably *Arrhenatherum elatius*. Although some sources suggest neophyte status of *A. elatius* in parts of Europe (e.g. Poschlod, 2015), based on previous archaeological findings, we classified it as an archaeophyte (see Pyšek *et al.*, 2012b). If it was considered as a neophyte, it would be one of the most successful neophytes across European grasslands, and because of its high abundance, it could change the patterns of invasions across habitats described here.

Conclusions

We provided the first overview of neophyte invasion patterns in grassland vegetation across Europe based on the most comprehensive dataset of vegetation plots existing to date. In general, natural or semi-natural European grassland habitats have relatively low levels of neophyte invasions compared with human-made habitats or riparian habitats in Europe. They are also less invaded than extratropical grasslands in the New World. Still, specific sites in European grasslands can be highly invaded. At such sites, the most typical neophytes are therophytes with broad ecological niches.

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Author contributions

MC and IA conceived the research idea. FA, IB, SB, TC, JDe, RGG, BJA, AK, JL, JM, JEM, JCS, IT, KV contributed the data and together with JP, PP, AL and DOP helped with the species status assignment. IK provided technical support with the original data preparation. IA, VK and JDa compiled the final neophyte lists. IA prepared the data, performed statistical analyses and led the writing. IA and MV prepared the maps. All co-authors commented on the manuscript.

Data availability statement

The vegetation-plot data used in this study are stored in the European Vegetation Archive database (EVA; <http://euroveg.org/eva-database>) under project number 56 – 2017-10-11. Maps can be downloaded from the Zenodo repository ([10.5281/zenodo.4497207](https://doi.org/10.5281/zenodo.4497207)).

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Supporting information

Appendix S1 Overview of contributing vegetation-plot databases.

Appendix S2 Overview of habitat types.

Appendix S3 List of regions (countries or their parts).

Appendix S4 Overview of biogeographical regions.

Appendix S5 Literature used for status assessment.

Appendix S6 References used for life-form assessment of neophytes.

Appendix S7 List of neophytes recorded per regions (countries or their parts).

Appendix S8 Species-pool summary statistics for Europe and individual regions.

Appendix S9 Plot-level summary statistics for Europe and individual regions.

Appendix S10 Plot-level summary statistics for biogeographical regions.

Appendix S11 Plot-level summary statistics for habitat groups.

Appendix S12 Species-pool summary statistics for EUNIS habitats.

Appendix S13 Plot-level summary statistics for EUNIS habitats.

Appendix S14 Additional maps.

Table 1. A list of the most frequent neophyte species recorded in European grasslands assessed by **(a)** number of plot records of the species across all regions (countries or their parts) where the species is considered neophyte (from a total of 97,411 plots) and **(b)** number of regions where the species occurred as a neophyte (from a total of 49; for more details on regions, see Appendices S7–S9); E – species with origin within Europe (they are considered neophytes only in some European regions, and their occurrences in the regions with native status were not counted), A – non-European origin, C – other origins (anecophytes, hybrids).

(a)				(b)		
Taxon	Origin	No. of plots	%	Taxon	Origin	No. of regions (max. 49)
<i>Onobrychis viciifolia</i>	E	1442	1.5	<i>Erigeron canadensis</i>	A	27
<i>Erigeron annuus</i> *	A	1312	1.3	<i>Medicago sativa</i> *	C	22
<i>Erigeron canadensis</i>	A	1188	1.2	<i>Oenothera biennis</i> agg.	A	20
<i>Trifolium hybridum</i> *	C	794	0.8	<i>Erigeron annuus</i> *	A	19
<i>Medicago sativa</i> *	C	743	0.8	<i>Matricaria discoidea</i>	A	19
<i>Solidago gigantea</i>	A	609	0.6	<i>Xanthium orientale</i> *	A	19
<i>Epilobium ciliatum</i> *	A	408	0.4	<i>Juncus tenuis</i>	A	18
<i>Matricaria discoidea</i>	A	348	0.4	<i>Bidens frondosus</i>	A	17
<i>Juncus tenuis</i>	A	323	0.3	<i>Onobrychis viciifolia</i>	E	17
<i>Impatiens glandulifera</i>	A	304	0.3	<i>Veronica persica</i>	A	17
<i>Oenothera biennis</i> agg.	A	244	0.3	<i>Robinia pseudoacacia</i>	A	16
<i>Solidago canadensis</i>	A	241	0.2	<i>Epilobium ciliatum</i> *	A	15
<i>Senecio leucanthemifolius</i> *	E	212	0.2	<i>Impatiens glandulifera</i>	A	15
<i>Impatiens parviflora</i>	A	210	0.2	<i>Solidago canadensis</i>	A	15
<i>Lolium multiflorum</i>	E	208	0.2	<i>Impatiens parviflora</i>	A	14
<i>Bidens frondosus</i>	A	199	0.2	<i>Solidago gigantea</i>	A	14
<i>Berteroa incana</i>	E	186	0.2	<i>Amaranthus retroflexus</i>	A	13
<i>Veronica persica</i>	A	178	0.2	<i>Galinsoga quadriradiata</i>	A	12
<i>Achillea ptarmica</i>	E	171	0.2	<i>Lolium multiflorum</i>	E	12
<i>Xanthium orientale</i> *	A	167	0.2	<i>Oxalis stricta</i>	A	12

*Species marked by asterisk include the following subspecies: *Epilobium ciliatum* (subsp. *ciliatum*, subsp. *adenocaulon*), *Erigeron annuus* (subsp. *annuus*, subsp. *septentrionalis*), *Medicago sativa* (subsp. *sativa*, nothosubsp. *varia*), *Senecio leucanthemifolius* subsp. *vernalis*, *Trifolium hybridum* (subsp. *hybridum*, subsp. *elegans*), *Xanthium orientale* (subsp. *orientale*, subsp. *californicum*, subsp. *italicum*, subsp. *riparium*). *Oenothera biennis* agg. refers to a group of taxa which are difficult to determine and usually not distinguished.

Table 2. A list of the most frequent neophyte species per habitat group assessed by **(a)** number of plot records of the species across all regions (countries or their parts) where the species is considered to be a neophyte and **(b)** number of regions where the species is considered to be a neophyte; the group of oromediterranean habitats (recorded in six regions) is excluded here due to the absence of neophytes; all the neophyte species in the group of alpine habitats were recorded in one region only; therefore, they cannot be sorted by the number of regions in **(b)**; origin 'A' refers to non-European origin, 'E' to European origin and 'C' to other origins (anecophytes, hybrids); see Table 1 for details on infraspecific taxa.

(a)					(b)		
Habitat group (plots)	Taxon	Origin	No. of plots	%	Taxon	Origin	No. of regions (max)
Sandy (4359)	<i>Erigeron canadensis</i>	A	492	11.3	<i>Erigeron canadensis</i>	A	20 (38)
	<i>Oenothera biennis</i> agg.	A	148	3.4	<i>Oenothera biennis</i> agg.	A	10 (38)
	<i>Senecio leucanthemifolius</i>	E	113	2.6	<i>Xanthium orientale</i>	A	8 (38)
	<i>Xanthium orientale</i>	A	79	1.8	<i>Robinia pseudoacacia</i>	A	7 (38)
	<i>Berteroa incana</i>	E	71	1.6	<i>Ambrosia artemisiifolia</i>	A	6 (38)
Rocky (4671)	<i>Berteroa incana</i>	E	42	0.9	<i>Erigeron canadensis</i>	A	10 (33)
	<i>Erigeron canadensis</i>	A	36	0.8	<i>Onobrychis viciifolia</i>	E	7 (33)
	<i>Onobrychis viciifolia</i>	E	36	0.8	<i>Erigeron annuus</i>	A	5 (33)
	<i>Dianthus caryophyllus</i>	E	34	0.7	<i>Medicago sativa</i>	C	5 (33)
	<i>Oxalis dillenii</i>	A	20	0.4	<i>Oenothera biennis</i> agg.	A	4 (33)
Dry (25430)	<i>Onobrychis viciifolia</i>	E	1073	4.2	<i>Erigeron canadensis</i>	A	17 (43)
	<i>Erigeron annuus</i>	A	307	1.2	<i>Medicago sativa</i>	C	17 (43)
	<i>Medicago sativa</i>	C	272	1.1	<i>Erigeron annuus</i>	A	16 (43)
	<i>Erigeron canadensis</i>	A	158	0.6	<i>Onobrychis viciifolia</i>	E	16 (43)
	<i>Crassula lycopodioides</i>	A	119	0.5	<i>Robinia pseudoacacia</i>	A	12 (43)
Mesic (32740)	<i>Erigeron annuus</i>	A	819	2.5	<i>Erigeron canadensis</i>	A	22 (45)
	<i>Trifolium hybridum</i>	C	533	1.6	<i>Erigeron annuus</i>	A	18 (45)
	<i>Medicago sativa</i>	C	435	1.3	<i>Matricaria discoidea</i>	A	18 (45)
	<i>Erigeron canadensis</i>	A	366	1.1	<i>Medicago sativa</i>	C	18 (45)
	<i>Onobrychis viciifolia</i>	E	320	1.0	<i>Juncus tenuis</i>	A	16 (45)
Wet (22763)	<i>Solidago gigantea</i>	A	417	1.8	<i>Bidens frondosus</i>	A	16 (47)
	<i>Epilobium ciliatum</i>	A	324	1.4	<i>Erigeron annuus</i>	A	16 (47)
	<i>Impatiens glandulifera</i>	A	283	1.2	<i>Erigeron canadensis</i>	A	16 (47)
	<i>Trifolium hybridum</i>	C	254	1.1	<i>Epilobium ciliatum</i>	A	15 (47)
	<i>Bidens frondosus</i>	A	188	0.8	<i>Impatiens glandulifera</i>	A	15 (47)
Alpine (6086)	<i>Onobrychis viciifolia</i>	E	9	0.1			1 (26)
	<i>Amorpha fruticosa</i>	A	4	0.1			1 (26)
	<i>Alchemilla conjuncta</i>	E	3	0.0			1 (26)
	<i>Cota triumfettii</i>	E	2	0.0			1 (26)
	<i>Oenothera glazioviana</i>	A	2	0.0			1 (26)
Saline (988)	<i>Grindelia squarrosa</i>	A	17	1.7	<i>Erigeron canadensis</i>	A	6 (22)
	<i>Xanthium orientale</i>	A	17	1.7	<i>Symphyotrichum squamatum</i>	A	3 (22)
	<i>Erigeron canadensis</i>	A	8	0.8	<i>Xanthium orientale</i>	A	3 (22)
	<i>Ambrosia artemisiifolia</i>	A	7	0.7	<i>Xanthium spinosum</i>	A	3 (22)
	<i>Symphyotrichum squamatum</i>	A	4	0.4	<i>Cotula coronopifolia</i>	A	2 (22)

Table 3. Absolute and relative species richness in the species-pool and percentage proportion of invaded plots for (a) biogeographical regions and (b) habitat groups; Medit. = Mediterranean region, Oromedit. = oromediterranean habitat group; percentages are calculated for the corresponding habitat group or region.

(a) Biogeographical region	Alpine	Atlantic	Boreal	Continental	Medit.	Pannonian	Steppic	
Species richness	4430	2360	1126	4492	4536	1464	2177	
Native plants richness	4320	2162	1047	4176	4437	1400	2120	
Neophyte richness - all neophytes	110	198	79	316	99	64	57	
- Non-European origin	51	110	30	142	75	41	32	
- European origin	50	74	44	149	16	20	21	
- Other origin	9	14	5	25	8	3	4	
Relative neophyte richness - all neophytes [%]	2.5	8.4	7.0	7.0	2.2	4.4	2.6	
- non-European [%]	1.2	4.7	2.7	3.2	1.7	2.8	1.5	
All plots	18105	13193	3103	49589	6573	1983	4865	
Invaded plots	1124	1061	548	7445	626	292	449	
% of invaded plots	6.2	8.0	17.7	15.0	9.5	14.7	9.2	
% of plots invaded by at least one non-European neophyte	2.4	5.7	7.1	9.1	7.1	10.8	5.4	
(b) Habitat group	Sandy	Rocky	Dry	Oromedit.	Mesic	Wet	Alpine	Saline
Species richness	2150	3354	6016	957	4014	3584	3180	846
Native plants richness	2020	3293	5798	957	3736	3323	3167	828
Neophyte richness - all neophytes	130	61	218	0	278	261	13	18
- Non-European origin	80	24	89	0	115	158	6	13
- European origin	46	33	111	0	141	85	7	2
- Other origin	4	4	18	0	22	18	0	3
Relative neophyte richness - all neophytes [%]	6.0	1.8	3.6	0.0	6.9	7.3	0.4	2.1
Relative neophyte richness - non-European [%]	3.7	0.7	1.5	0	2.9	4.4	0.2	1.5
All plots	4354	4671	25430	380	32740	22762	6086	988
Invaded plots	1122	263	2729	0	4413	2915	30	73
% of invaded plots	25.8	5.6	10.7	0	13.5	12.8	0.5	7.4
% of plots invaded by at least one non-European neophyte	21.8	2.3	3.9	0	7.5	10.2	0.2	6.4

Table 4. Selected summary statistics for **(a)** biogeographical regions and **(b)** habitat groups; comparison of mean species richness, mean absolute and relative neophyte richness and mean neophyte cover calculated across plots; Medit. = Mediterranean region, Oromedit. = oromediterranean habitat group; species richness refers to all species recorded in the plot, neophytes include all neophyte species irrespective of their origin; Kruskal-Wallis multiple comparison test shows significant differences among groups at the level of $p=0.01$, with letters sorted according to the increasing mean; note that medians are equal to zero for all neophyte statistics; see Appendices S10 and S11 for more details and separated categories of neophytes.

(a) Biogeographical region	Alpine	Atlantic	Boreal	Continental	Medit.	Pannonian	Steppic	
Species richness	29.32	21.08	24.89	27.27	22.17	26.92	26.25	
Relative neophyte richness [%]	0.25	0.6	1.04	0.82	0.65	0.79	0.6	
Kruskal-Wallis test	a	b	d	d	bc	cd	bc	
Absolute neophyte richness	0.07	0.11	0.25	0.19	0.11	0.18	0.11	
Kruskal-Wallis test	a	ab	c	c	b	c	ab	
Relative neophyte cover [%]	0.38	1.04	1.77	1.24	0.85	0.84	0.36	
Kruskal-Wallis test	a	ab	d	d	bc	cd	ab	
Absolute neophyte cover	0.31	0.83	1.24	0.96	0.60	0.66	0.21	
Kruskal-Wallis test	a	ab	d	d	bc	cd	ab	
(b) Habitat group	Sandy	Rocky	Dry	Oromedit.	Mesic	Wet	Alpine	Saline
Species richness	15.8	26.14	31.55	19.52	28.38	21.77	21.51	9.51
Relative neophyte richness [%]	2.21	0.28	0.38	0	0.66	0.95	0.02	0.82
Kruskal-Wallis test	e	b	c	abc	d	d	a	bcd
Absolute neophyte richness	0.35	0.07	0.12	0	0.17	0.17	0	0.08
Kruskal-Wallis test	e	b	c	abc	d	d	a	abcd
Relative neophyte cover [%]	1.86	0.36	0.48	0	0.87	2	0.03	0.59
Kruskal-Wallis test	e	b	c	abc	d	d	a	abcd
Absolute neophyte cover	1.09	0.24	0.36	0	0.67	1.6	0.03	0.45
Kruskal-Wallis test	e	b	c	abc	d	d	a	abcd

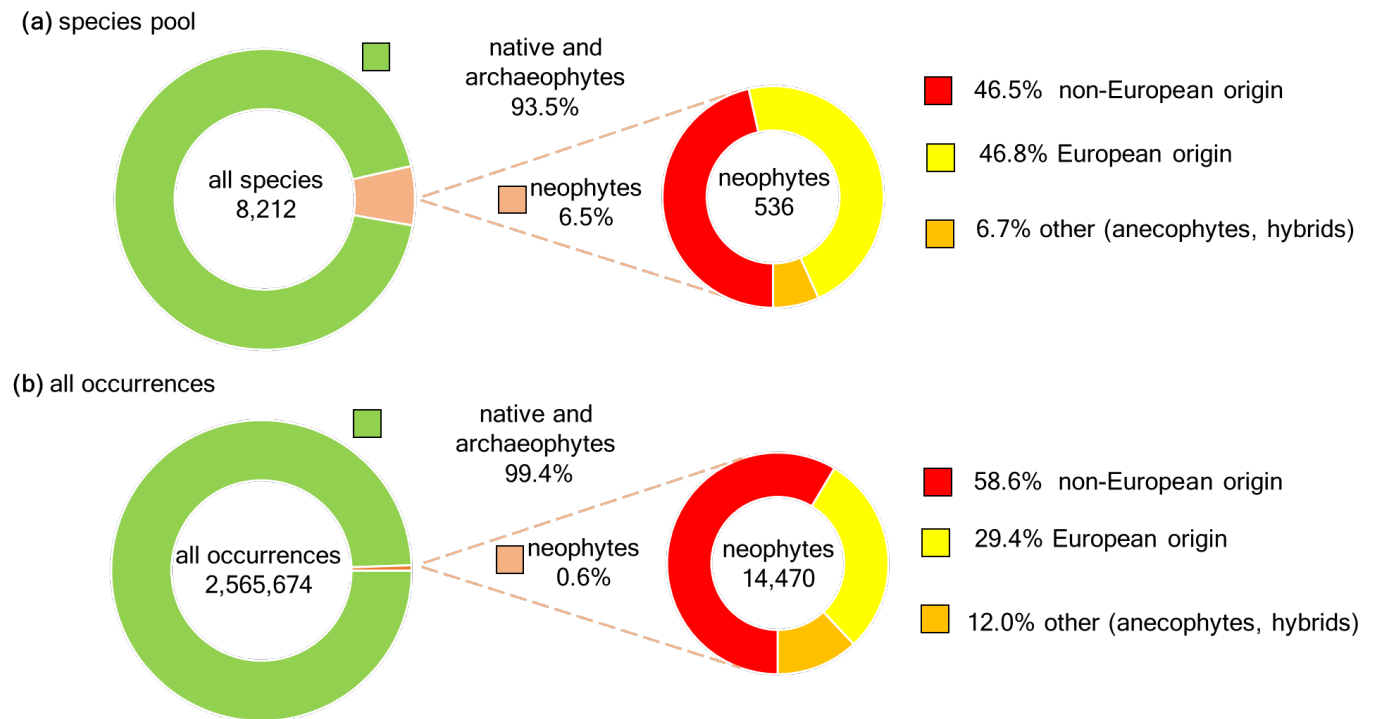


Figure 1. Overview of (a) absolute and relative richness of native species (including archaeophytes) and neophytes in European grasslands based on the whole species pool and (b) species frequency across all occurrences (number of species records in vegetation plots). For (a), we considered as native only those species that are included in the native category in all the regions, while species of European origin considered as a neophyte in at least one region were included in the neophyte numbers. In total, 242 species had double status within Europe (approximately 2.9 % of all species). The overview based on all occurrences (b) considers each record of plant species in each plot separately (see Appendix S10 for details).

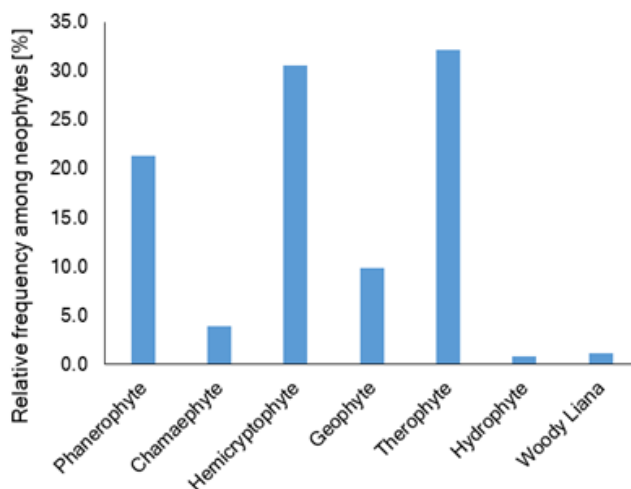
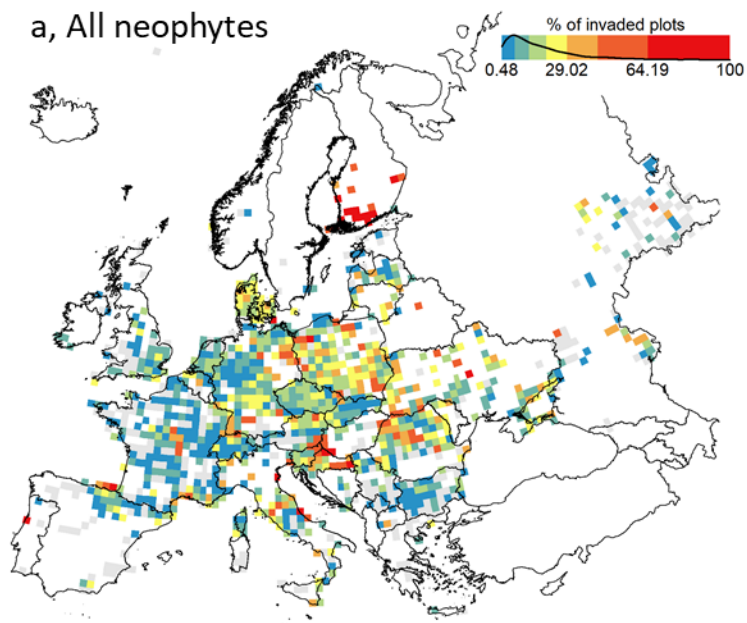
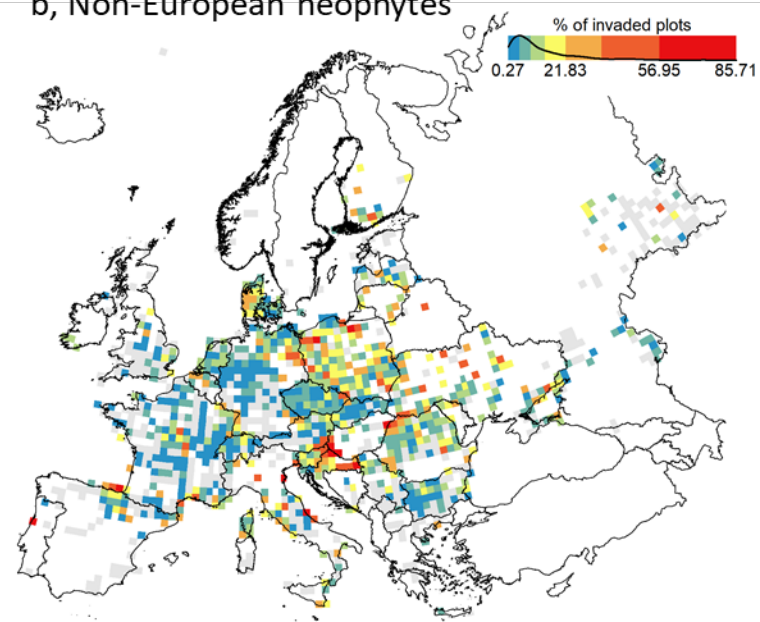


Figure 2. Life forms of neophytes in the species pool of European grasslands.

a, All neophytes



b, Non-European neophytes



c, European neophytes

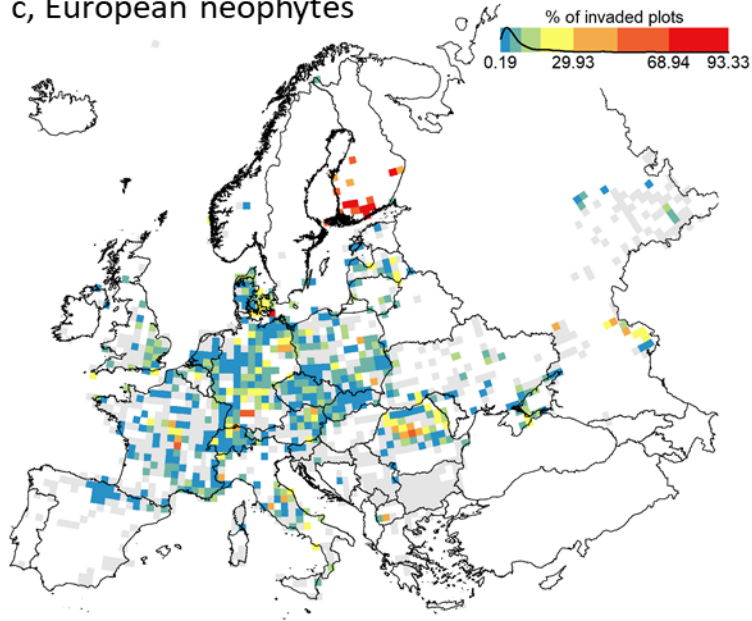
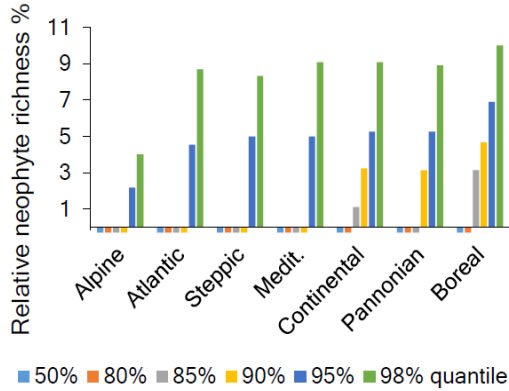
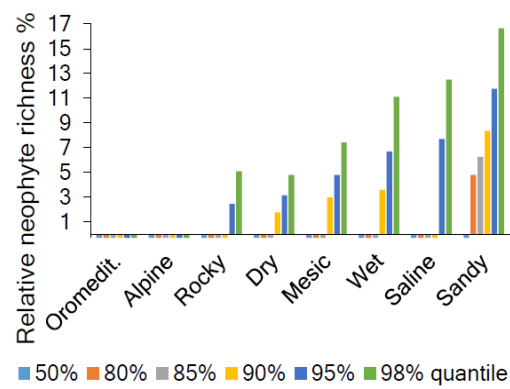


Figure 3. Percentage proportion of invaded plots calculated per UTM 50 × 50 km grid cells. Colour-scale categories were defined using the k-means algorithm, reflecting the distribution of relative frequencies of invaded plots in the data. Grey colour indicates cells with only not-invaded plots (0 %). Cells with less than ten plots are not mapped. See Appendix S3 for the number of plots recorded in each country. Maps for habitat groups and neophyte origin categories, and comparison of main patterns using different invasion metrics are in Appendix S14.

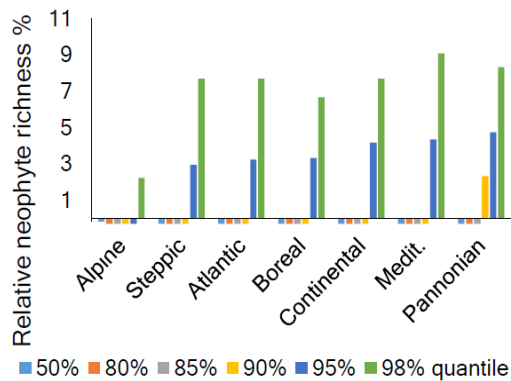
a, All neophytes



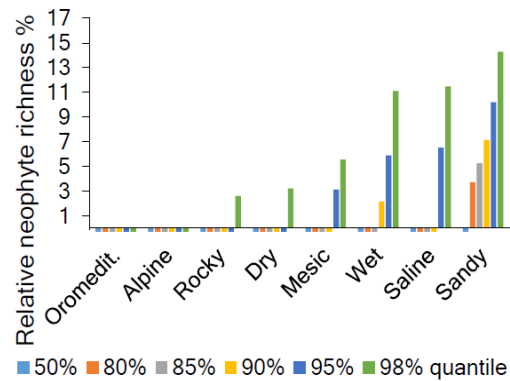
d, All neophytes



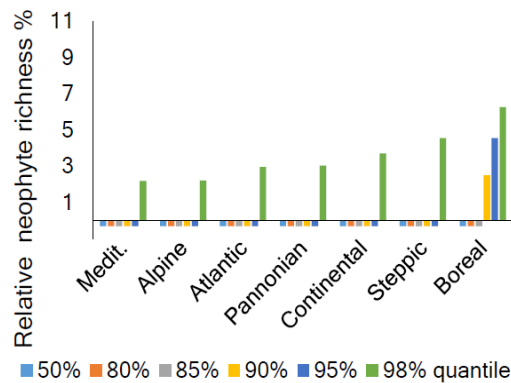
b, Non-European neophytes



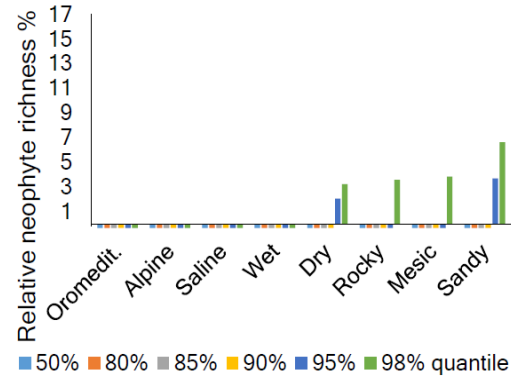
e, Non-European neophytes



c, European neophytes



f, European neophytes



Biogeographical regions

Habitat groups

Figure 4. Quantile comparison of mean relative neophyte richness per plots for (a, b, c) biogeographical regions and (d, e, f) habitat groups. In our dataset with the prevalence of non-invaded plots, the median values (here shown as 50% quantile) were all equal to zero, and the only differences were visible within higher quantiles. Therefore, we sorted the values of relative neophyte richness assessed in individual plots in ascending order within each biogeographical region or habitat group. To show the 80% quantile, we took the value at the position corresponding to 80% of the data, and did the same for other quantiles. The data are sorted by the values of the 95% quantile. Neophytes are divided by origin categories, biogeographical regions and habitat groups. Note different extents of the percentage scale between regions and habitats.

EUNIS habitats

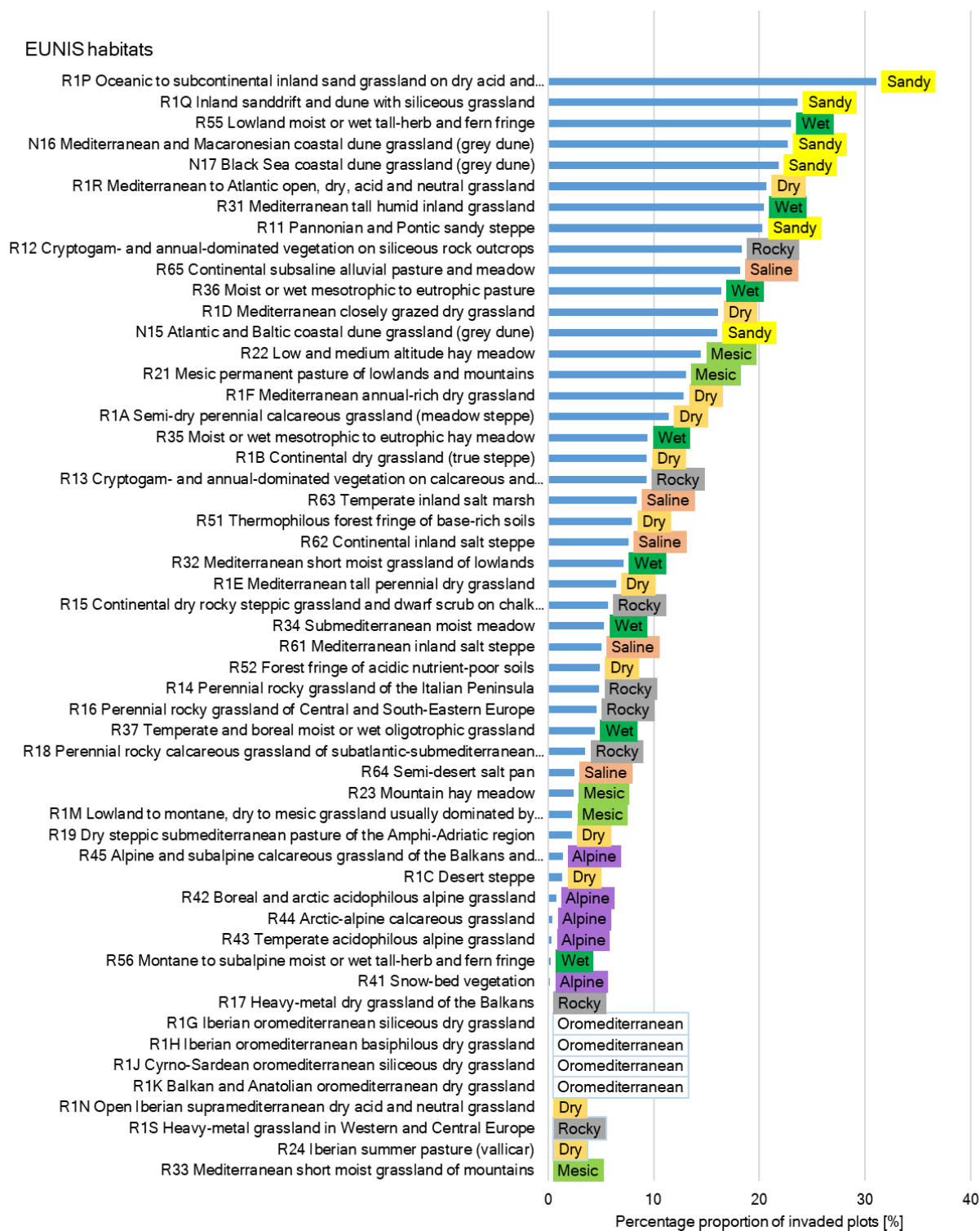


Figure 5. Percentage proportion (%) of plots with neophytes in individual EUNIS habitats. Corresponding habitat groups are indicated by the labels next to the bars. The last nine habitats (starting with R17) do not have any invaded plots and are sorted alphabetically by their EUNIS codes. For other statistics, see Appendix S12 and S13.