Biol Invasions (2023) 25:1739–1765
https://doi.org/10.1007/s10530-023-03005-7

ORIGINAL PAPER

Neophyte invasions in European heathlands and scrub

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Received: 28 June 2022 / Accepted: 12 January 2023 / Published online: 19 February 2023
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Abstract Human-assisted introduction of alien plants is causing ecosystem transformations worldwide and is considered an important threat to biodiversity. We provide a European assessment of habitat levels of invasion in heathlands and scrub and identify successful alien plants and invasion trends across biogeographical regions. We analysed a geographically stratified data set of 24,220 dwarf shrub and scrub vegetation plots sampled across Europe. Among the 6547 vascular plant taxa occurring in these plots, we identified 311 neophytes (4.8%, i.e. alien species introduced in Europe or its sub-regions after 1500 AD) and compared five metrics of the level of invasion in (i) EUNIS habitats, (ii) broad habitat groups and (iii) biogeographical regions of Europe. We related habitat-specific levels of invasion to elevation and climatic variables using generalized linear models. Among neophytes, phanerophytes of non-European origin prevailed. The most frequent neophytes in the plots were *Prunus serotina*, *Robinia pseudoacacia* and *Quercus rubra* among phanerophytes, *Impatiens parviflora* among therophytes, and *Erigeron canadensis* and *Solidago gigantea* among

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-023-03005-7.

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hemicryptophytes. Levels of invasion significantly differed among habitats and biogeographical regions. The most invaded habitat was Macaronesian lowland scrub, followed by riparian scrub, *Rubus* scrub and forest-clearing scrub of temperate Europe, and coastal dune scrub of the Atlantic region. The levels of invasion were low in the shrublands of the Arctic and Mediterranean regions and decreased with elevation within habitats. Results suggest that insularity, low elevation, frequent disturbances, and high availability or considerable fluctuation of resources promote neophyte invasions in European shrublands.

Keywords Alien plants · Biogeographical regions · EUNIS · Europe · Level of invasion · Shrubland

Introduction

Human-assisted introduction and subsequent spread of alien plant species are among the most critical causes of biodiversity loss worldwide (Courchamp et al. 2017; Pyšek et al. 2020). They have serious negative consequences for some native species, habitats and ecosystem functioning (Vilà and Hulme 2016; Carboni et al. 2021), human health and the economy (Diagne et al. 2021; Novoa et al. 2021). However, the magnitude of invasion and impacts of alien species are often context-dependent and vary by invading species, habitats and regions (Kalusová et al. 2015; Kumschick et al. 2015; Ming et al. 2021). Therefore, identifying successful invaders and vulnerable habitats across regions is crucial for effective decision-making, alien risk assessment and management (Gallardo et al. 2019).

The extent to which a habitat is invaded by alien plants is expressed as the level of invasion, which includes various metrics of alien presence and abundance at a site, in a plant community or in a habitat (Catford et al. 2012; Guo et al. 2015). Early attempts to quantify the levels of invasion focused on urbanized areas (Celesti-Grapow and Blasi 1998; Pyšek 1998). With increasing data availability, assessments of the level of invasion became available for a variety of systems with increasing complexity, such as nature reserves (Pyšek et al. 2002; Landi et al. 2020), habitats at the country level (e.g. Chytrý et al. 2005; Wiser et al. 2011; Campos et al. 2013; Medvecká et al. 2014) or entire continents (Chytrý et al. 2009). Cross-habitat comparisons based on large-scale vegetation-plot data sets showed that habitats vary considerably in their levels of invasion (Chytrý et al. 2008a), and these habitat-specific invasion patterns remain consistent across different regions (Chytrý et al. 2008a), and even continents (Kalusová et al. 2015). Chytrý et al. (2008b) showed that although the level of invasion does not equate to habitat invasibility, i.e. intrinsic susceptibility to invasion, they are usually closely related. The accumulation of such evidence has enabled the formulation of more general rules of habitat invasion by alien plants. First, the most invaded habitats are those with frequent disturbance and a high or fluctuating resource supply (Davis et al. 2000; Pyšek and Chytrý 2014). Second, the level of habitat invasion depends on the size of the species pool of potential invaders introduced into a given area (Kalusová et al. 2014). Thus, the levels of invasion decrease from human-made habitats to undisturbed, natural habitat types (Pyšek et al. 2009), as well as from lowlands to higher elevations (Medvecká et al. 2014). Third, oceanic islands have been found to have higher levels of habitat invasion because of the lower diversity of their native floras with competitively weaker species (Lonsdale 1999; Hulme 2004; Stierstofer and Gaisberg 2005). However, large continental islands exhibit similar patterns of habitat invasion levels as mainlands (Vilà et al. 2010; Guarino et al. 2021). Habitats and their characteristics are, therefore, among the most important predictors of the spread of alien plants worldwide (Bellard et al. 2016).

The availability of high-quality data on species co-occurrence across Europe (e.g., European Vegetation Archive, EVA; Chytrý et al. 2016) has motivated new studies of plant invasion patterns at the continental scale. Such studies, focused on European forests (Wagner et al. 2017, 2021) and grasslands (Axmanová et al. 2021), provided detailed information on the invasion process for a number of habitat types across the continent at fine spatial resolution. They also revealed geographical patterns in plant invasions across Europe and identified invasion hotspots and the most successful invasive species. However, such analyses have not yet been performed for all major habitat types. European shrublands have not received as much attention as forests or grasslands with respect to alien plants, probably due to their smaller spatial extent, lower economic importance and recognition as successional or degradation stages between open habitats and forests rather than as habitats themselves. The most comprehensive study of plant invasions across European habitats so far (Chytrý et al. 2008a) compared the habitat levels of invasion among three climatically contrasting regions—Mediterranean, subcontinental and oceanic. They also considered shrublands, but only distinguished among coarse units that occurred in the three study areas. Mediterranean shrublands were also considered in multiple-habitat invasion studies from the Iberian Peninsula (Vilà et al. 2007), the Balearic Islands (Vilà et al. 2010), Sicily (Guarino et al. 2021) and other Mediterranean islands (Affre et al. 2010). In temperate Europe, shrublands were included among other habitat types in alien plant assessments for the Czech Republic (Chytrý et al. 2005), Moldavia (Sîrbu et al. 2012), Slovakia (Medvecká et al. 2014) and NW Poland (Myśliwy 2014). There is insufficient information or only anecdotal evidence for other parts of Europe such as subarctic regions (Milbau et al. 2013).

Despite their smaller area compared to grasslands or forests, shrublands can be important for plant invasions because they are transitional habitats that can accumulate alien species from adjacent vegetation types and serve as a reservoir and pathway for their dispersal into other habitats (van Rensburg et al. 2013). The importance of shrublands can even increase in the future due to woody plant encroachment after management cessation (Archer et al. 2017; Deng et al. 2021). Conversion of grasslands to shrublands and woodlands has already been recognized as a global issue and is assumed to accelerate with climate change (Criado et al. 2019). In other parts of the world where shrublands occur over large areas, there is growing evidence that alien plants can have negative impacts on shrublands, including replacement of native biota (Dickens and Allen 2014) and alteration of ecosystem processes, soil properties, water availability and fire regimes (Steers et al. 2013; Goldstein and Suding 2014). Shrublands in Europe are very heterogeneous and dynamic vegetation dominated by either dwarf shrubs or taller-growing shrubs, occurring across broad elevational and latitudinal gradients (Mucina et al. 2016). In general, these shrublands are supported by environmental factors that slow or prevent vegetation succession toward woodlands. These can be harsh climates (e.g. low temperatures, droughts, high snowpack or a short growing season), waterlogging or periodical disturbances, either natural or human-induced. We expect that all of these factors influence not only the development and distribution of shrublands, but also the establishment of alien species in shrubland habitats. They can also lead to a considerable variation in the levels of invasion in different shrubland types. However, a comprehensive synthesis of plant invasions in shrubland habitats at the European scale is still pending.

In our study, we use the most comprehensive data set of European heathland and scrub vegetation available to date. We analyze these data on two scales to reveal both fine-resolution patterns of habitat invasions and more general patterns in broadly defined habitats in different regions. At the finer scale, we use EUNIS level 3 habitats based on a recently revised habitat classification system (Chytrý et al. 2020). At the coarser scale, we track the variation in invasion levels across broader habitats and biogeographical regions with different compositions of native species pools, macroclimates and landscapes. In all analyses, we also distinguish between groups of alien species according to their non-European or European origin. The European distribution of alien plants introduced from other continents depends on invasion pathways and histories (Riera et al. 2021), time since introduction (Lambdon et al. 2008) and climate match between native and invaded regions (Thuiller et al. 2005; Cao Pinna et al. 2021). Therefore, non-European aliens can be represented and distributed differently across European regions than aliens of European origin, which generally have shorter distances to overcome and a higher chance of being introduced into a similar environment.

Based on the conclusions of previous studies from other habitat types (Wagner et al. 2017, 2021; Giulio et al. 2020; Axmanová et al. 2021), we hypothesize that, at a local scale, the level of neophyte invasion in European heathland and scrub habitats is highly variable and depends on the ecology of different habitat types. In particular, (H1) high levels of invasion should occur in naturally or human-disturbed scrub habitats that have constantly or temporarily high resource availability, while in contrast, low levels of invasion are expected in heathlands and scrub on poor soils without frequent disturbance. At a coarser scale, we expect the levels of invasion in European shrublands to differ among biogeographical regions. Specifically, (H2) scrub habitats on Macaronesian islands should be more invaded than scrub habitats of mainland Europe, reflecting higher invasibility of oceanic ecosystems; and (H3) scrub habitats in warm lowland and coastal regions of the European mainland should be more invaded than those at high elevations or northern latitudes of Europe, reflecting less severe abiotic constraints and larger pools of alien species.

Methods

Data set

We used an initial data set of vegetation plots with known geographical coordinates from the European Vegetation Archive (EVA; Chytrý et al. 2016), which were classified to habitat types according to the European Nature Information System (i.e., EUNIS habitats). The classification was performed using the EUNIS-ESy expert system (v. 2020-06-08; Chytrý et al. 2020). We selected 63,318 plots belonging to EUNIS habitat group S (heathlands and scrub) and heathland and scrub habitat types belonging to EUNIS habitat group N (coastal habitats). We assessed 45 habitat types at Level 3 of the EUNIS classification and grouped them into 11 broader habitat types (i.e., broad habitats) to investigate patterns of plant invasions in both finer and coarser categories of heathland and scrub habitats.

We filtered the initial data set to allow invasion comparisons among habitats. We removed plots: (i) classified into transitional categories between different types of heathland and scrub habitats; (ii) sampled before 1970; (iii) with a size outside the range of 1–100 m^2. We also retained plots of unknown size, assuming they were within the plot-size ranges traditionally used to survey such vegetation types (see also Axmanová et al. 2021). European heathlands and scrub habitats have not been thoroughly studied by vegetation and invasion ecologists compared to European forests and grasslands, which is reflected in the smaller data set and less balanced coverage of vegetation-plot data across European countries. Therefore, we further resampled the filtered data set applying spatial and compositional criteria to reduce the effect of pseudoreplications and spatial autocorrelation in densely sampled regions. Using an iterative procedure, we randomly selected one plot from each pair of plots that had similarity in species composition > 0.8 (Bray–Curtis similarity) and, at the same time, were located within 1 km distance (following Divíšek and Chytrý 2018). We also removed plots representing rare EUNIS habitats, of which < 20 plots remained in our data set after the application of filtering and resampling procedures. The final data set used for analyses contained 24,220 plots. A list of vegetation-plot databases from EVA with their contribution to the final data set can be found in Supplementary Information, Table S1. An overview of the 45 EUNIS habitats included in the final data set with numbers of plots and their assignment to 11 broad habitat categories is available in Supplementary Information, Table S2.

Species status

We considered only vascular plant taxa and unified their nomenclature across the vegetation plots according to the Euro+Med PlantBase (2021), or The Plant List (TPL 2013) for those taxa not listed in Euro+Med. We assigned each taxon the status of native, neophyte (i.e., alien species introduced after 1500 AD) or unknown, considering each region of Europe separately (see the delimitation of regions in the next section). We distinguished only neophytes, while archaeophytes were not separated from native species following the Euro+Med PlantBase approach. To assess the status of each species, we used Euro+Med PlantBase, DAISIE (2009), the GloNAF database (van Kleunen et al. 2019), available national/regional checklists, and the knowledge of local experts (see a list of sources used for species status assignments in Supplementary Information, Table S3). We excluded taxa with unknown status. Some species or subspecies have dual status, i.e. they can be native in some European regions and neophyte in other regions. Due to this fact, we followed status assigned at the infraspecific level in statistics for particular regions, however, for habitat summaries across regions, we used the species-level status. Thus, if at least one subspecies was native, we considered the species native. Neophytes were further divided into groups according to their origin: (i) neophytes of non-European origin; (ii) neophytes of European origin (i.e. species with dual status in Europe); and (iii) neophytes of other origin (including anecophytes and hybrids). We also classified neophytes to eight life forms (see sources in Supplementary Information, Table S4) and geographical regions of origin (10 world's regions; POWO 2021; with additional categories of anecophytes and hybrids).

European regions

To assess the status of species across Europe and examine geographical patterns of invasions, we delimited 50 European regions. Regions usually corresponded to political units (i.e., countries), except for large islands or archipelagos (the Balearic Islands, Corsica, Crete, Sardinia, Sicily, Svalbard, Madeira and the Canary Islands) and the European part of Russia. For the latter, we have adopted the subdivision into seven regions from the Euro+Med PlantBase: North Russia, Northwestern Russia, Kaliningrad, Central Russia, South Russia, East Russia and Caucasus Russia. The list of regions with numbers of plots and neophytes recorded can be found in Supplementary Information, Table S5.

To analyze the main biogeographical and macroclimatic gradients in Europe, we also assigned each plot to one of nine biogeographical regions according to the European Environmental Agency (EEA 2016), including Alpine, Arctic, Atlantic, Boreal, Continental, Mediterranean, Macaronesian, Pannonian and Steppic (including Black Sea) biogeographical regions. In addition, we characterized each plot based on its geographical coordinates by two climatic variables, annual mean temperature (°C) and annual precipitation (mm), and elevation (m) using ArcGIS 10.8 (ESRI 2011). We obtained climatic variables from Chelsa (Karger et al. 2017) and elevation from Jarvis et al. (2008).

Data analyses

We calculated the level of invasion by neophytes in European heathlands and scrub vegetation for: (i) EUNIS Level 3 habitats; (ii) broad habitats; and (iii) European biogeographical regions. We used different metrics of the level of invasion (e.g. Catford et al. 2012; Wagner et al. 2017; Axmanová et al. 2021):

i. *Relative neophyte richness* in the pooled species list of all plots in the entire data set and in each broad habitat and bioregion;
ii. *Relative frequency of neophyte occurrence* (i.e., proportion of records of neophytes across all plots) in the whole data set;
iii. *Mean* or *quantiles of relative neophyte richness per plot* (i.e., percentage proportion of the number of neophyte species in a plot) across all plots of the whole data set and each EUNIS habitat, broad habitat and bioregion;
iv. *Percentage proportion of plots invaded* by at least one neophyte relative to all plots in the whole data set and each EUNIS habitat, broad habitat and bioregion;
v. *Mean relative neophyte cover* (i.e., percentage cover of neophytes in a plot) across plots of all broad habitats and biogeographical regions.

We calculated all invasion level metrics separately for neophytes of non-European and European origin and for the other origin category. The following quantiles of relative neophyte richness per plot were used: 50% to show the median and 80, 85, 90, 95 and 98% to show whether there is a stable trend in the level of invasion among broad habitats and biogeographical regions, although not evident in the lower quantiles due to the prevalence of not-invaded plots (see also Axmanová et al. 2021). Percentage cover of neophytes in a plot was calculated using the Jennings-Fischer formula (Jennings et al. 2009; Fischer 2015) as the sum of individual species covers, considering their possible overlap in a plot.

All of the following analyses were performed in R, v. 4.1.1. (R Core Team 2021). We tested for differences in mean relative neophyte richness and cover per plot among broad habitats and biogeographical regions using the Kruskal–Wallis rank-sum test with post-hoc multiple pairwise comparison among groups using Dunn's test (at $P \leq 0.05$) available in the package *rstatix* v.0.7.0 (Kassambara 2021). Differences in the counts of particular life forms for native species and neophytes compared with their expected counts in the species pool were tested with Pearson's chi-square test of independence using the package *stats*. Three categories of life forms (i.e. epiphytes, hydrophytes and lianas) with <5 species in native or neophyte groups were removed prior to the test, but passively displayed in the figure. Post-hoc tests of particular counts for the combination of life form and status (native/neophyte) were calculated comparing their standardized residuals [(observed count − expected count) / $\sqrt{\text{expected count}}$] to the normal distribution of residuals (Beasly et al. 1995) with Bonferroni correction applied on the significance levels ($P \leq 0.005$).

To characterize the geographical patterns of invasion levels across Europe, we assigned all plots to 50 km × 50 km UTM grid cells based on their geographical coordinates. We drew maps of the mean relative neophyte richness in plots and percentage proportions of invaded plots in a given grid cell across Europe using the packages *raster* 3.5-2 (Hijmans et al. 2021), *rgdal* v.1.4-3 (Bivand et al. 2020), *spatialEco* v.1.3-7 (Evans et al. 2021), *berryFunctions* v.1.20.1 (Boessenkool 2021) and *classInt* v.0.4-3 (Bivand 2020). We mapped all neophytes together and neophytes of non-European and European origin separately. To test the effects of annual mean temperature, precipitation and elevation, as well as two-way interactions of the two climate variables with elevation on mean relative neophyte richness in plots, we used a generalized linear model (GLM) with binomial error distribution and logit link function (Dobson 1990; Douma and Weedon 2019). To test for the simultaneous effects of the explanatory variables on the probability that plots are invaded by at least one neophyte (coded as 0/1), we used a GLM with the Bernoulli distribution and *cloglog* link function because of the predominance of zeros in the data (Dobson 1990). The multicollinearity of the explanatory variables was checked by the variation inflation factor (VIF) using the *VIF* function in the package *reghelper* (Hughes 2020). All explanatory variables were standardized prior to the analyses. The significance of each GLM was tested with the likelihood-ratio χ^2 test ($P \leq 0.05$). We calculated the percentage of deviance explained [D2 = (null deviance − model deviance)/null deviance], which corresponds to the proportion of variation explained (Nakagawa and Schielzeth 2013), using the *glm* and *anova* functions in the R package *stats*.

Results

Neophytes in heathland and scrub habitats

The data set contained 6547 vascular plant species, of which 311 species (4.8%) were neophytes. Neophytes of non-European origin were more frequent (52.7%) than neophytes of European origin (40.8%) or neophytes of other origins including anecophytes and hybrids (7.4%; Fig. S1a). The frequency of occurrence of neophytes in vegetation plots was generally low, accounting for 4.5% of all species records in the data set (Fig. S1b); non-European neophytes were recorded much more frequently (78.2% of neophyte records) than other neophytes. Life forms representation in the species pool of European heathlands and scrub habitats differed significantly among native species and neophytes ($\chi 2 = 241.5$, df = 4, $P < 0.001$). Neophytic phanerophytes and therophytes had higher counts, whereas neophytic chamaephytes and hemicryptophytes had lower counts than expected (Fig. 1). The recorded neophytes were mainly from the Mediterranean region (including the Mediterranean part of Europe, North Africa and the Middle East), temperate Asia, non-Mediterranean parts of Europe and North America (Fig. 2).

In general, all neophytes occurred in < 1% of the plots in the entire data set, with many species recorded in two plots only. The most common neophytes in European heathland and scrub habitats included those of non-European origin (Table 1a, b; complete list of neophytes with plot counts can be found in Supplementary Information, Table S6), namely *Impatiens parviflora*, *Prunus serotina*, *Erigeron canadensis*, and *Solidago gigantea.* Although *Impatiens parviflora* and *Prunus serotina* were among the most frequent species in the whole data set, their geographical distribution was limited, suggesting that they had invaded heathland and scrub habitats only in a part of European regions. Most neophytes had a narrow invaded range and were usually recorded in only one region. *Solidago canadensis* invaded more European regions than *Solidago gigantea*, but when *S. gigantea* was present in a region, it occurred in plots with higher frequency. *Erigeron annuus* was also widespread, but occurred less frequently in plots of heathland and scrub habitats than *E. canadensis*.

Levels of invasion in heathland and scrub habitats

Only a low proportion of plots in European heathlands and scrub habitats was invaded by at least one neophyte (7.9% of the total). More plots were invaded by non-European neophytes only (5.8% of plots) than by neophytes of European origin only (1.4%) or by neophytes of unknown origin only (0.4%). Further 0.4% of plots were invaded by both non-European and European neophytes. The mean relative richness of neophytes in all plots of European heathlands and scrub habitats was 0.7% per

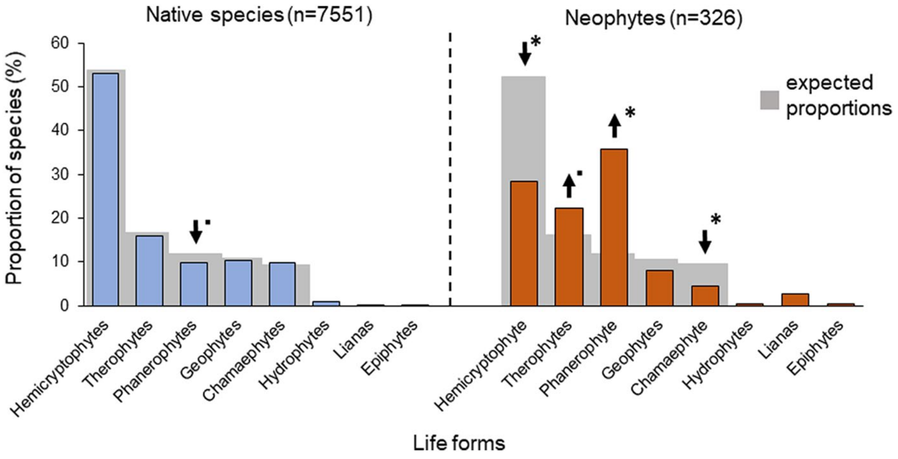
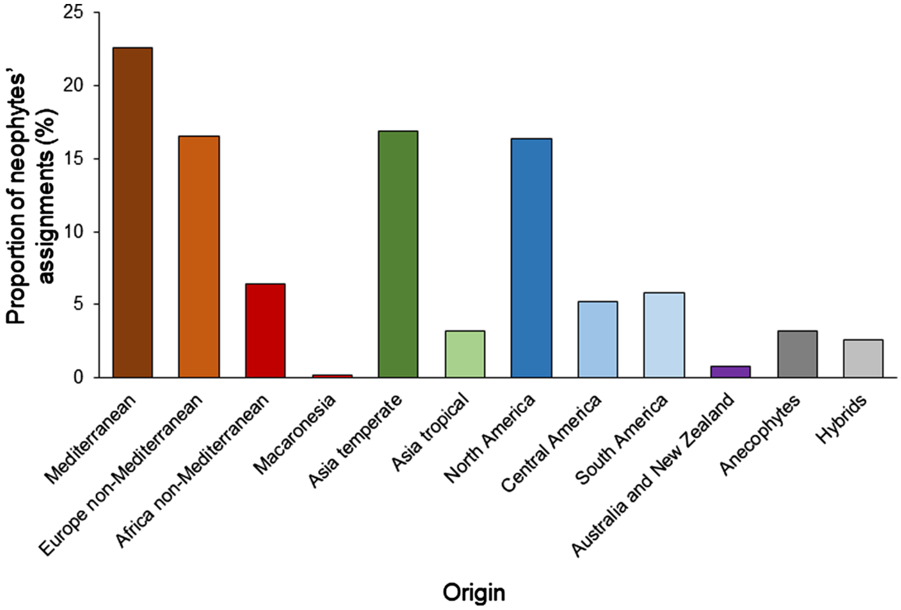


Fig. 1 Proportions of native species and neophytes in the species pool of European heathland and scrub habitats that belong to different life forms. The grey area represents the expected proportions under the hypothesis of independence of the life form and native or neophyte status (Pearson's chi-square test; $\chi 2 = 241.5$, df = 4, $P < 0.001$). Proportions of life forms with < 5 species (epiphytes, hydrophytes and lianas) were passively displayed. Arrows indicate cases where the proportion of a particular life form is significantly higher (↑) or lower (↓) than expected. The significance of the differences was tested using the comparison of standardized residuals to their normal distribution with Bonferroni correction applied; ·- marginally significant ($P \sim 0.005$); * - significant ($P < 0.005$); n = number of life forms assigned within native species and neophytes groups

Fig. 2 Proportions of neophytes of different geographical origins in the species pool of European heathland and scrub habitats. Many neophytes (37.7%) originated from two or more regions, and the percentage in a given region was calculated relative to all assignments of 311 neophytes to all regions (n = 496)



plot and the mean relative cover of neophytes was 0.9% per plot. Neophytes of non-European origin reached higher mean relative richness (0.5% per plot) as well as mean relative cover (0.7% on average) in all plots than neophytes of European origin (0.1% and 0.2%).

At the fine scale of EUNIS habitats, we found that four types of EUNIS habitats had relatively high levels of invasion, as measured by both the mean relative richness of neophytes calculated across plots (Fig. 3) and the proportion of plots that are invaded (Supplementary Information, Fig. S2). These included

Table 1 Most frequent neophytes in European heathland and scrub habitats in terms of (**a**) the percentage of the 24,220 plots in which the species occurred; (**b**) the percentage of the 50 European regions where the species occurred

(a) Species name	Life form	Plot count	%	(b) Species name	Life form	Region count	%
Impatiens parviflora	T	192	0.79	*Erigeron canadensis*	T	20	40.0
Prunus serotina	P	132	0.55	*Erigeron annuus*[a]	H	15	30.0
Erigeron canadensis	T	127	0.52	*Solidago canadensis*	H	14	28.0
Solidago gigantea	H	117	0.48	*Robinia pseudoacacia*	P	13	26.0
Bidens frondosus	T	91	0.38	*Solidago gigantea*	H	13	26.0
Robinia pseudoacacia	P	84	0.35	*Impatiens glandulifera*	T	12	24.0
Impatiens glandulifera	T	79	0.33	*Impatiens parviflora*	T	12	24.0
Erigeron annuus[a]	T	77	0.32	*Bidens frondosus*	T	11	22.0
Claytonia perfoliata	T	73	0.30	*Acer negundo*	P	10	20.0
Oxalis pes-caprae	G	55	0.23	*Reynoutria japonica*	G	10	20.0
Echinocystis lobata	L	49	0.20	*Echinocystis lobata*	L	9	18.0
Vaccinium macrocarpon	C	46	0.19	*Oenothera biennis* agg.[c]	H	9	18.0
Quercus rubra	P	41	0.17	*Oxalis stricta*	G	9	18.0
Solidago canadensis	H	38	0.16	*Veronica persica*	T	9	18.0
Epilobium ciliatum[b]	H	36	0.15	*Xanthium orientale*[d]	T	8	16.0

All listed neophytes are of non-European origin. Life forms: P – phanerophyte, C – chamaephyte, H – hemicryptophyte, G – geophyte, T – therophyte, L – liana

[a] Incl. subsp. *annuus* and subsp. *septentrionalis*; [b] incl. subsp. *adenocaulon* and subsp. *ciliatum*; [c] agg. incl. group of other non-identified *Oenothera* taxa; [d] incl. subsp. *californicum*, subsp. *italicum* and subsp. *riparium*

(i) lowland scrub habitats in Macaronesian islands, (ii) riparian scrub habitats in various biogeographical regions of Europe, (iii) *Rubus* scrub and forest-clearing scrub in lowland to montane elevation belts of temperate Europe, and (iv) sand-dune scrub on the Atlantic and Baltic coasts. In all of these habitats, neophytes originating from outside Europe prevailed, with the only exception of Macaronesian garrigue, where neophytes of European origin accounted for a higher proportion of invaders. In contrast, heathland and scrub habitats at high elevations or with xeric conditions and nutrient-poor soils, including various arctic, alpine, subalpine and Mediterranean habitats, generally had low levels of plant invasions.

At the scale of broad habitats, we found the highest relative richness of neophytes in species pools of temperate lowland to montane scrub, Macaronesian lowland scrub, and riparian scrub. Macaronesian and riparian scrub also had the highest relative richness of neophytes in their plots and highest proportions of plots invaded by at least one neophyte. Neophytes often reached high relative percentage cover there (Table 2). The lowest relative richness of neophytes was found in the species pools of broad scrub habitats at high elevations (arcto-alpine, oro-mediterranean, Macaronesian montane) and in the Mediterranean, semi-desert and saline scrub, and temperate heathlands (Table 2).

High-elevation scrub habitats usually had low mean relative richness of neophytes in plots (Fig. 4a), and neophytes reached a very low cover in plots (Table 2). Mediterranean scrub with a small pool of neophytes and low mean relative neophyte richness in plots (Fig. 4a) showed a slightly higher proportion of invaded plots and higher mean relative cover of neophytes than similarly invaded temperate heathlands (Table 2). Semi-desert and saline scrub habitats had moderate relative richness of neophytes in plots, although other invasion metrics, i.e. relative richness of the species pool, proportion of invaded plots and mean neophyte cover in plots, were low (Fig. 4a). This pattern is due to the relatively low richness of native and also to the fact that few neophytes were able to invade these habitats, but they were present quite constantly across plots.

An intermediate contribution of neophytes to species pools was found in coastal and fen scrub habitats (Table 2). However, coastal habitats showed a higher proportion of invaded plots and a relatively high mean neophyte cover compared to fen scrub (Table 2). This

Fig. 3 Mean relative richness of neophytes in European heathland and scrub habitats, calculated as the proportion of neophytes of non-European origin (brown) and European origin (orange) across all plots assigned to a given EUNIS habitat. Broad habitats are indicated by a symbol next to the habitat names. Habitats are ranked in descending order of the proportion of both neophyte groups to the total number of species

Table 2 Levels of invasion in broad European heathland and scrub habitats including relative neophyte richness (i.e. proportion of neophytes in pooled species lists of a given broad habitat), mean relative neophyte richness (i.e. mean proportion of neophytes in plots assigned to a given broad habitat), the proportion of plots invaded by neophytes and the mean relative neophyte cover (i.e. mean cover of neophytes in plots assigned to a given broad habitat)

Broad habitats	Arcto-alpine	Coastal	Fen	Maca-ronesian lowland	Maca-ronesian montane	Mediterranean	Oro-mediter-ranean	Riparian	Semi-desert and saline	Temperate heathlands	Temperate lowland to montane
Absolute species richness	2606	1081	1081	290	46	2688	1297	1627	485	1478	3046
Relative neophyte richness (%)	0.4	3.9	3.5	5.9	0	2.1	0.6	5.0	2.9	2.7	6.5
- Non-European origin	0.2	2.3	2.5	4.1	0	1.0	0.3	3.3	2.1	1.6	3.5
- European origin	0.2	1.4	1.0	1.7	0	1.0	0.2	1.2	0.8	0.9	2.5
- Other origins	0	0.2	0.2	<0.1	0	0.1	0.1	0.5	0	0.2	0.5
Mean relative neophyte richness (%)	<0.1	0.9	0.6	3.4	0	0.4	0.1	2.9	0.8	0.4	1.3
KW groups	a	bd	bc	e	abcd	bc	ab	e	abd	ac	d
- Non-European origin	<0.1	0.8	0.4	2.3	0	0.2	<0.1	2.6	0.6	0.3	1.0
KW groups	a	c	b	d	abc	b	ab	d	abc	ab	c
- European origin	<0.1	0.1	0.1	1.1	0	0.2	<0.1	0.2	0.2	0.1	0.2
KW groups	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Number of plots	4831	1933	1678	108	38	3176	544	1073	241	4631	5967
% of plots invaded by neophytes	0.3	10.5	7.6	36.1	0	5.6	1.1	32.2	7.5	3.8	13.6
- Non-European origin	0.1	9.9	6.2	26.9	0	2.5	0.6	30.0	5.4	3.0	10.6
- European origin	<0.1	<0.1	1.4	12.9	0	3.0	0.6	2.3	2.5	0.9	3.6
- Other origins	<0.1	0.4	<0.1	<0.1	0	0.3	<0.1	<0.1	<0.1	0.1	0.8
Mean relative neophyte cover (%)	<0.1	2.3	0.6	3.4	0	0.3	<0.1	2.6	0.8	0.2	1.8
KW groups	a	bd	bc	e	abcd	c	ab	e	abd	ac	d
- Non-European origin	<0.1	2.2	0.5	2.7	0	0.1	<0.1	2.5	0.5	0.2	1.3
KW groups	a	bd	bc	e	abcd	bc	ab	e	abd	ac	d
- European origin	<0.1	0.1	<0.1	0.7	0	0.1	<0.1	0.1	0.3	<0.1	0.5
KW groups	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Values were calculated for each of the 11 broad habitats and for neophyte origin categories: non-European origin, European origin, other origin (anecophytes, hybrids). Differences in mean relative neophyte richness and cover among broad habitats were tested using Kruskal–Wallis multiple comparison test (KW groups) at $P \leq 0.05$, and significant homogeneous groups based on multiple comparisons were indicated by the same letters. Mean values are shown instead of medians, which were zero. Results for other origins were all non-significant and therefore are not shown. *ns* non-significant indicates that despite the relatively small size of its neophyte pool, coastal scrub is invaded frequently, especially by non-European neophytes, which are able to dominate there.

In all broad scrub habitats, neophytes of non-European origin prevailed in the pool of neophytes. The patterns of mean relative richness and cover of neophytes in the plots were, therefore, mainly determined by neophytes of non-European origin, while the representation of European neophytes and those of other origin did not differ significantly among broad habitats. A high contribution of neophytes of European origin was only found for the geographically distinct Macaronesian lowland scrub (Table 2, Fig. 4c,f). Lists of neophyte taxa in each broad habitat can be found in Supplementary Information, Table S7.

Levels of invasion of heathland and scrub habitats across European biogeographical regions

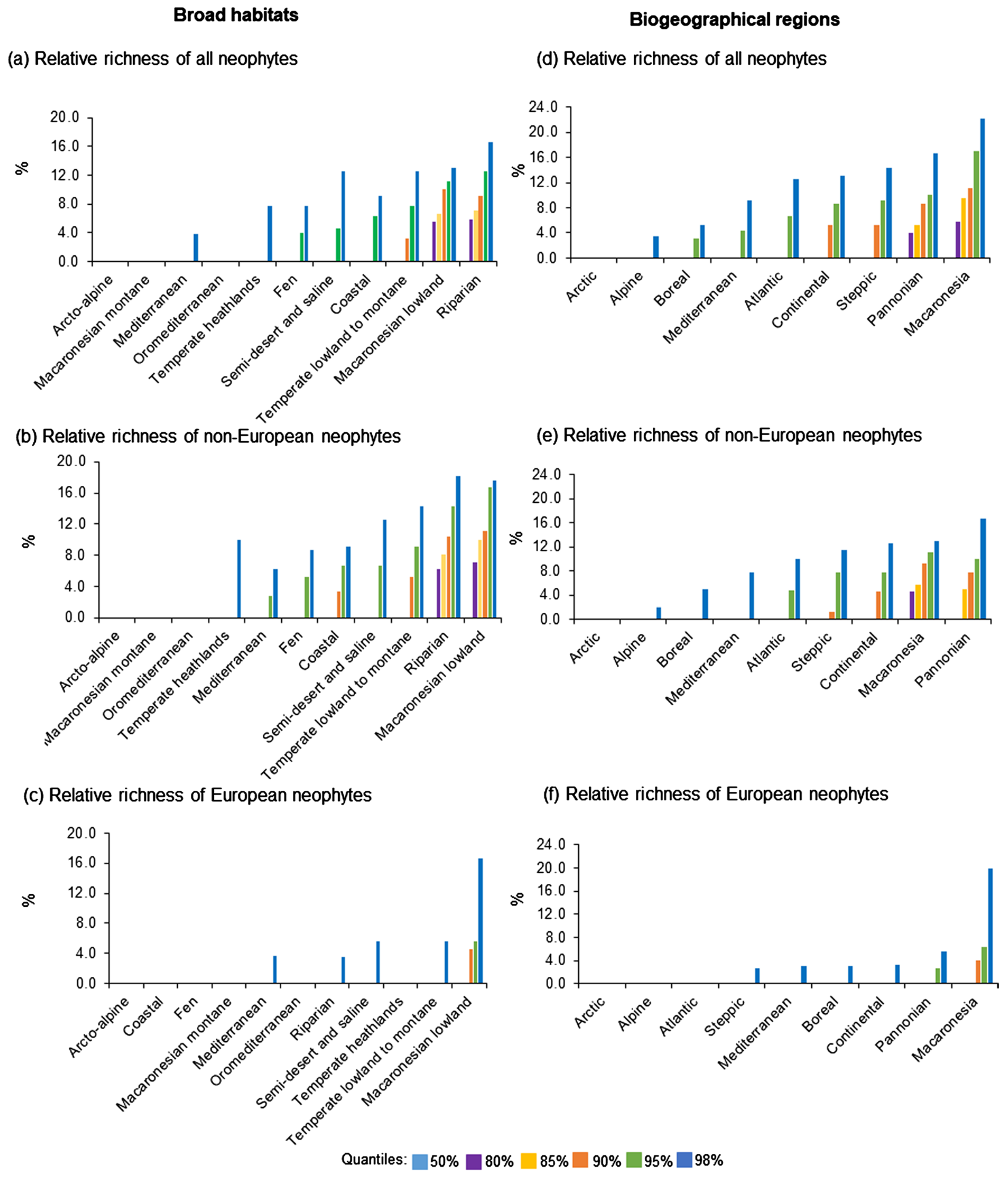
In general, there was an increase in invasion levels from southern to central Europe, followed by a decrease toward northern Europe (Fig. 5a, d). The highest relative richness of all neophytes in the species pools of European heathland and scrub habitats was found in the Atlantic, Macaronesian, Continental and Pannonian regions. The relative richness in species pools then decreased towards Steppic, Boreal and Mediterranean regions and the lowest relative richness was found at high elevations of the Alpine region and high latitudes of the Arctic region (Table 3). Similar patterns were found for the mean relative richness and cover of neophytes in plots and proportions of invaded plots (Table 3; Fig. 4d). However, the Atlantic region, which holds the highest relative richness of neophytes in species pools, showed only intermediate values for the other metrics (Table 3). Non-European and European neophytes also followed this pattern (Fig. 4e, f), but non-European neophytes were generally more frequent across biogeographical regions (Table 3). The only exception included Madeira and the Canary Islands (Macaronesian biogeographical region), where neophytes of European origin also showed relatively high levels of invasion (Table 3, Fig. 5c). Summary statistics of the invasion levels for particular European regions (countries or islands) can be found in Supplementary Information, Table S5.

Local hotspots of neophytes in mainland Europe indicated by locally high mean relative richness of neophytes in plots were found in central Europe (Fig. 5a), especially in Austria, Slovenia, the Czech Republic and SW Poland in temperate riparian, *Rubus* and forest clearings scrub. Other hotspots were found on the coast of the Balkan Peninsula (Fig. 5a) in the Mediterranean riparian scrub, in Crete and Spain in coastal sand dune scrub, and in Germany and Netherlands in temperate riparian and *Rubus* scrub habitats. Areas with high levels of invasion related to different types of riparian scrub habitats were also scattered within Germany and in the interior of the Balkan Peninsula. Local hotspots indicated by the high proportion of invaded plots (Fig. 5d) were located in coastal sand-dune scrub of Netherlands and the Baltic countries, in Mediterranean or temperate riparian scrub of Greece, Italy, Sicily and Spain, on British Isles in temperate thorn scrub and on Sicily in Mediterranean maquis (Table 3, Fig. 5d).

Determinants of the levels of invasion of heathland and scrub habitats in Europe

The relative richness of neophytes (all origins combined) in plots (Table 4a) and the probability that a given plot would be invaded by at least one neophyte in that category (Table 4b) were most strongly influenced by elevation. Both variables decreased along the elevational gradient from lowlands to high mountains. The second most important factor affecting relative richness of neophytes was annual mean temperature: plots in warm areas were more invaded than in cold areas. For the probability of plots being invaded, annual precipitation was slightly more important predictor than temperature with a decrease of invaded plot numbers with increasing precipitation. An increase in annual mean temperature showed a positive effect on the probability and relative richness of European neophytes, however, in neophytes of non-European origin, it increased only the probability of plots being invaded, not their relative richness in plots. The relative richness and probability of a plot being invaded by non-European as well as European neophytes decreased in response to increasing annual precipitation.

There was a significant interaction between elevation and annual mean temperature on the relative richness and probability of a plot being invaded (Table 4b). The negative relationship between level of invasion and elevation is not as pronounced in warm



regions. For example, in the Macaronesian biogeographical region (Supplementary Information, Fig. S3), relative richness and probability of plot invasion by all neophytes regardless of origin and European neophytes showed no response to elevation. Only the relative richness of neophytes of non-European origin and probability of a plot being invaded by them decreased with elevation there, whereas the relative richness of European neophytes peaked at mid-elevations (Fig. S3c). In contrast, in the Mediterranean

◂**Fig. 4** Comparison of quantiles of relative neophyte richness in broad habitats (**a**–**c**) and biogeographical regions (**d**–**f**). As the median proportion of neophytes in plots of all broad habitats and regions is zero due to the prevalence of non-invaded plots, we used quantiles to compare the level of invasion. All proportions of neophytes in plots within a particular broad habitat or biogeographical region were ranked in ascending order, and values corresponding to the position of 50%, 80%, 85%, 90% , 95% and 98% of the data were used. Broad habitats and biogeographical regions were sorted in ascending order by the value of the 95% quantile. Quantiles are shown for all neophytes and separately for neophytes of non-European and European origin. Neophytes of other origins (anecophytes and hybrids) are not shown because the values for all quantiles are zero

region with similarly high annual mean temperatures, the effect of increasing elevation remained significantly negative for both neophyte groups and both measures of invasion levels in plots (not shown).

Discussion

Our results show that the levels of neophyte invasions vary considerably both among individual European heathland and scrub habitats and across different biogeographical regions of Europe.

The most invaded European heathland and scrub habitats and biogeographical regions

The levels of invasion found in EUNIS shrubland habitats in our study (mean relative richness of neophytes in plots up to 3.8%) are comparable to those of shrubland habitats included in the comparative study for selected European regions by Chytrý et al. (2008b; up to 3.1%). The slightly higher maximum value in our study results from the inclusion of the heavily invaded Macaroneasian garrigue (S64) and Madeiran and Canarian xerophytic scrub (S81 + S82), which were not included in the previous study. However, the observed levels of invasion are still lower than in the most invaded European human-made habitats (mean relative richness of neophytes > 5.6%; Chytrý et al. 2008b).

We found the most invaded heathland and scrub habitats in the Macaronesian biogeographical region (Canary Islands and Madeira). This can be a result of the effect of insularity, Macaronesian flora specificity in the European context and the history of human colonization. High isolation of oceanic islands from mainlands leads to low species richness (Simberloff 1995), and therefore low functional diversity of native species and their reduced competitiveness compared to alien species from mainlands (Sol 2000; Fridley and Sax 2014). Habitats on oceanic islands and their vegetation are therefore highly vulnerable to the human-induced introductions (Castro et al. 2010) which also explains generally high levels of invasion on the studied Macaronesian islands. The effect of low native richness might not be so important on continental islands, i.e. those historically connected to the mainlands, such as those in Mediterranean Europe, which share many species with adjacent parts of the continent and where island heterogeneity and propagule pressure can be of higher importance (Vilà et al. 2010). Mediterranean Europe has a long history of alien introductions, which can be reflected in relatively lower proportions of neophytes in the species pool (Cao Pinna et al. 2021) compared to the Macaronesian islands that host high proportions of neophytes, many of which were introduced relatively late, since the nineteenth century (Silva et al. 2008).

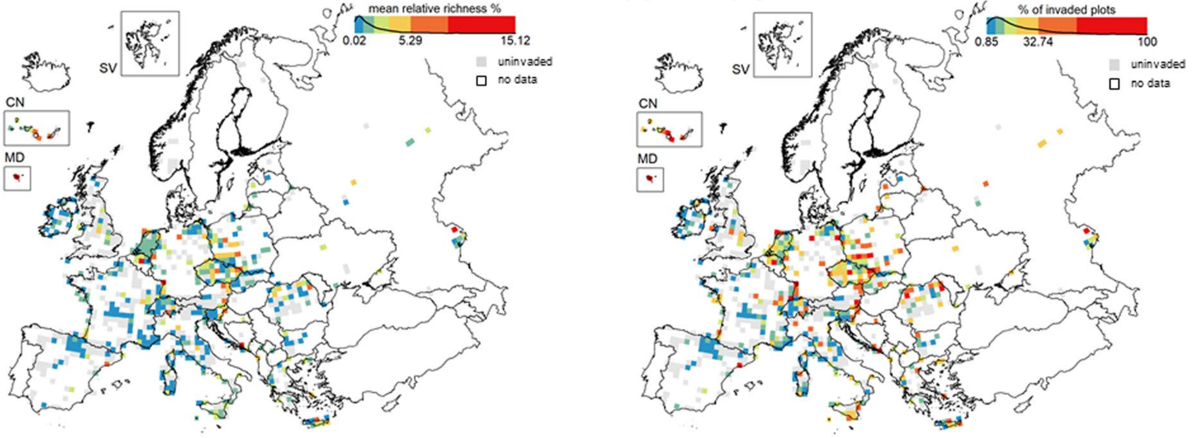
The high counts of neophytes of European origin is probably a consequence of the different structure of Macaronesian native flora, originating more from the Afrotropical biogeographical realm (Allan et al. 2004; Reyes-Betanacort et al. 2008), the occurrence of many endemics (Bramwell 1976) and the history of species introductions from Europe, especially from the Mediterranean region (Arévalo et al. 2005; Expósito et al. 2018). From this perspective, European neophytes in Macaronesia may act in a similar way as non-European neophytes in the rest of the study area as they are introduced from overseas to a unique biogeographical context. However, European neophytes exhibit a specific distribution pattern on the islands as a result of their prevalent Mediterranean origin (Expósito et al. 2018). They reach their highest richness at intermediate elevations, whereas the occurrence of non-European species usually increases towards lower elevations (Arévalo et al. 2005). Indeed, we revealed that the mid-elevational Macaronesian garrigue contained a high proportion of European neophytes with a prevalence of Mediterranean species such as *Leontodon saxatilis* subsp. *rothii*, *Lavandula multifida* or *Reichardia intermedia* (Supplementary Information, Table S7), while non-European neophytes, including common drought-tolerant

Mean relative neophyte richness

Proportion of plots invaded by neophytes

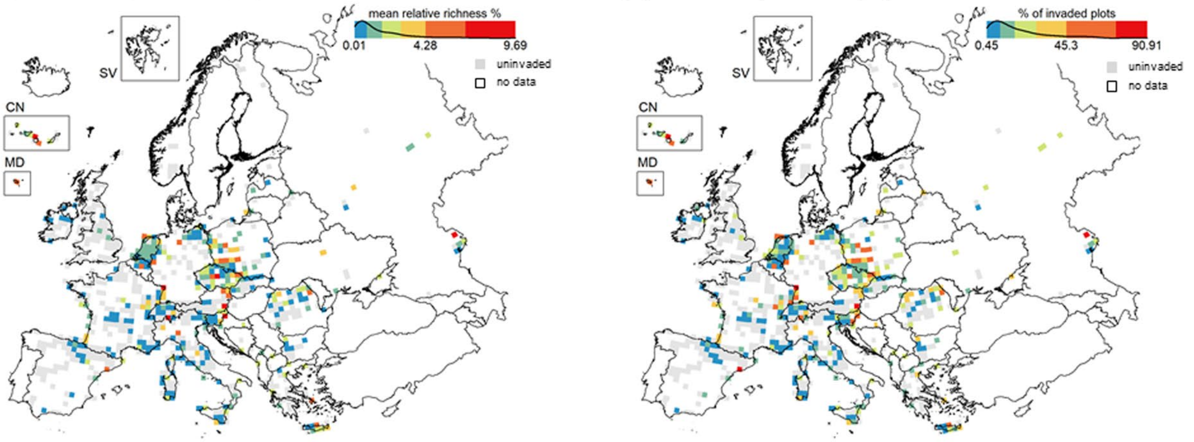
(a) All neophytes

(d) All neophytes



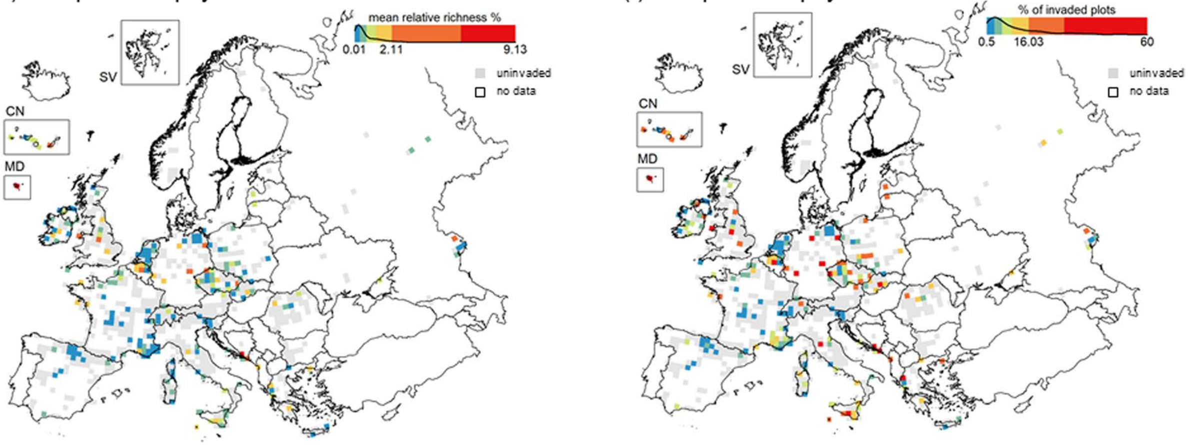
(b) Non-European neophytes

(e) Non-European neophytes



(c) European neophytes

(f) European neophytes



◂**Fig. 5** Maps of (**a**–**c**) mean relative neophyte richness (i.e. mean percentage of neophytes in all plots in a grid cell) and (**d**–**f**) percentage of plots invaded by (**a**, **d**) all neophytes, (**b**, **e**) neophytes of non-European origin, (**c**, **f**) neophytes of European origin in 50 km×50 km UTM grid cells. Only cells for which more than five plots with geographical coordinates are available are shown in color. Color scale intervals for the level of invasion were defined using the k-means algorithm based on the distribution of relative neophyte proportions and the frequency of invaded plots in the data set. *SV* Svalbard, *CN* Canary Islands, *MD* Madeira

species such as *Opuntia stricta* and *O. ficus-indica*, prevail in Madeiran and Canarian xerophytic scrub, which occur in arid lowlands (Janssen 2016) (Supplementary Information, Table S7).

The second most invaded type of European shrublands includes Temperate, Mediterranean, and Semi-desert riparian scrub (S91, S93 and S94). These azonal habitats represent local hotspots of neophyte invasion in shrublands in contrasting biogeographical regions of mainland Europe and some Mediterranean islands. Our results, therefore, expand findings of previous European studies that reported wet and riverine scrub as habitats maintaining high alien species richness (Vilà et al. 2007; Chytrý et al. 2008b; Guarino et al. 2021). Riparian habitats, including riparian forests, are known to harbour large numbers of alien plant species (Kalusová et al. 2015; Wagner et al. 2017). High invasibility of such habitats is caused by frequent natural disturbances from river dynamics as well as human-induced disturbance, both coupled with natural or artificial eutrophication and sudden increases in nutrient fluxes and water availability (Richardson et al. 2007). Together with high propagule pressure (Richardson et al. 2007) and a large species pool of potential invaders (Kalusová et al. 2017), these factors contribute to high invasion levels. In our data set, we found high mean relative neophyte richness as well as high proportion of invaded plots in riparian scrub, but not so strikingly high mean cover of neophytes. This can be a result of the frequent occurrence of neophytic therophytes (Table S9) invading from adjacent highly disturbed and open riparian sites such as river bars (Liendo et al. 2021). The importance of disturbance and high availability or fluctuation of resources (Davis et al. 2000) for neophyte invasion into European shrublands is also supported by the identity of other often invaded habitats, Temperate *Rubus* scrub (S32) and Temperate forest clearings scrub (S38). Both of them are characterized by increased nutrient availability and frequent disturbances due to forestry management. The importance of *Rubus* scrub as a reservoir for neophytes may even increase in the future as its area increases in some parts of Europe with the abandonment of pastures (Rodwell 2016).

The third most invaded heathland and scrub habitat in Europe is Atlantic and Baltic coastal dune scrub (N1A). Similarly to other studies of coastal dune vegetation (Campos et al. 2004; Giulio et al. 2020), we found that Mediterranean and Black Sea coastal dune scrub (N1B) is less invaded than coastal scrub in the Atlantic biogeographical region, both in terms of the relative richness of alien species and the proportion of invaded plots. In coastal dunes, two factors can lead to high invasion levels – their dynamic nature with frequent disturbances and high propagule pressure from human activities such as recreation and planting of aliens for sand stabilization (Guarino et al. 2021). Typical examples of dune scrub invaders in our data set (Supplementary Information, Table S7) include *Rosa rugosa,* which was planted in NW Europe for sand dune fixation and ornamental purposes (Isermann 2008), and *Prunus serotina*, originally introduced for wood plantations and now spreading on stabilized coastal dunes (Weeda 2010). Although the relative richness of alien species is generally lower in coastal dune scrub than in Macaronesian lowland and riparian scrub, neophytes, when present, achieve high cover in the vegetation. The marked inconsistency between high relative richness of neophytes in the species pool of all heathlands and scrub habitats of Atlantic biogeographical region together (8.1%, highest among all regions) and low relative richness in its coastal dune scrub can indicate a delay in the invasion process. Species can be already present in the region, but have not spread yet to all suitable habitats. In addition, the contribution of neophytes to the total species pool of coastal dune scrub is lower (3.9%) compared with coastal dune grasslands (7%; Giulio et al. 2020), which also suggest an invasion debt and a potential future increase of neophytes within coastal scrub, possibly due to increasing level of human-induced disturbances. Despite being less invaded compared to the Atlantic region, Mediterranean and Black Sea coastal dunes share the same properties and thus can be at a higher risk of invasion with the increase in human pressure too (Guarino et al. 2021).

Table 3 Levels of invasion in biogeographical regions including relative neophyte richness (i.e. the proportion of neophytes in the pooled species lists of a given broad habitat), mean relative neophyte richness (i.e. mean proportion of neophytes in plots assigned to a given bioregion), the proportion of plots invaded by neophytes and the mean relative neophyte cover (i.e. mean cover of neophytes in plots assigned to a given bioregion)

Biogeographical regions	Alpine	Arctic	Atlantic	Boreal	Continental	Macaronesia	Mediterranean	Pannonian	Steppic
Absolute species richness	2791	208	1656	546	2395	369	3783	681	584
Relative neophytes richness (%)	1.5	0	8.1	2.8	5.2	6.0	2.7	4.4	3.3
- Non-European origin	0.9	0	4.7	1.8	2.9	3.8	1.7	3.5	2.4
- European origin	0.5	0	2.9	0.9	1.8	2.2	1.0	0.9	0.5
- Other origins	0.2	0	0.5	< 0.1	0.4	< 0.1	< 0.1	< 0.1	0.3
Mean relative neophyte richness (%)	0.2	0	0.8	0.4	1.2	3.1	0.5	1.9	1.1
KW groups	b	abc	c	abcd	de	e	ac	e	abcde
- Non-European origin	0.2	0	0.6	0.3	1.0	2.0	0.4	1.6	0.9
KW groups	ab	a	b	abc	cd	d	ab	c	abcd
- European origin	< 0.1	0	0.2	0.1	0.1	1.2	0.1	0.3	0.2
KW groups	ns	ns	ns	ns	ns	ns	ns	ns	ns
Number of plots	5376	159	6817	361	5393	160	5506	146	300
% of plots invaded by neophytes	2.4	0	7.7	6.7	14.2	28.8	6.5	25.3	12.7
- Non-European origin	2.1	0	6.2	4.7	12.1	21.3	3.9	19.9	10.0
- European origin	< 0.1	0	1.6	2.5	2.4	10.6	2.5	7.5	2.0
- Other origins	0.2	0	0.4	< 0.1	0.1	< 0.1	0.5	< 0.1	2.0
Mean relative neophytes cover (%)	0.2	0	1.2	0.9	1.4	4.7	0.4	3.9	0.5
KW groups	ab	a	b	abc	cd	d	ab	c	abcd
- Non-European origin	0.2	0	1.0	0.7	0.9	2.6	0.3	3.8	0.4
KW groups	b	abc	c	abcd	de	e	ac	de	abcd
- European origin	0.0	0	0.1	0.3	0.4	2.2	0.1	0.2	0.1
KW groups	ns	ns	ns	ns	ns	ns	ns	ns	ns

Values were calculated for each of the nine biogeographical regions and for neophytes according to their origin (non-European, European and other, i.e. anecophytes and hybrids). Differences in mean relative neophyte richness and cover among biogeographical regions were tested using the Kruskal–Wallis multiple comparison test (KW groups) at $P \leq 0.05$, and significant homogeneous groups based on multiple comparisons were indicated by the same letters. Mean values are shown instead of medians, which were zero. Results for other origins were all non-significant and are therefore not shown. *ns* non-significant

The least invaded European heathland and scrub habitats and biogeographical regions

Low values of both the relative richness of neophytes in plots and the proportion of invaded plots were found in two broad groups of European heathlands and scrub habitats. The first group includes scrub of the Mediterranean biogeographical region. The second group includes heathlands and scrub of the Arctic biogeographical region, as well as at high elevations, including various types of alpine, subalpine, oro-mediterranean and Macaronesian montane habitats. Both groups experience high levels of abiotic stress affecting their vegetation, such as low nutrient availability in poor soils, drought, low temperatures or short growing seasons (Zefferman et al. 2015).

In the Mediterranean biogeographical region, heathlands and scrub habitats have previously been shown to have a low level of plant invasion (Pino et al. 2005; Vilà et al. 2007; Affre et al. 2010). We have shown that the exceptions are riparian and coastal scrub habitats, which can form local hotspots for neophyte occurrences. The lowest relative richness of neophytes was found in the driest habitats,

Table 4 Results of generalized linear models examining the effects of elevation, annual mean temperature, annual precipitation and their two-way interactions on (a) relative neophyte richness in plots (proportion of neophytes in plots; binomial distribution) and (b) the probability that a plot is invaded by neophytes (yes/no; Bernoulli distribution)

(a) Relative neophyte richness in plots	All neophytes ($D^2 = 15.2\%$)				Non-European origin ($D^2 = 15.7\%$)				European origin ($D^2 = 8.2\%$)			
	Estimate	SE	Z	*P*	Estimate	SE	Z	*P*	Estimate	SE	Z	*P*
Intercept	−5.521	0.039	−141.172	***	−5.935	0.050	−119.698	***	−6.935	0.073	−94.827	***
Elevation	−1.352	0.054	−24.839	***	−1.664	0.068	−24.377	***	−0.569	0.103	−5.485	***
Annual mean temperature	0.167	0.049	3.462	***	0.079	0.060	1.372	ns	0.515	0.097	5.295	***
Annual precipitation	−0.130	0.038	−3.421	***	−0.128	0.051	−2.497	*	−0.199	0.065	−3.073	**
Elevation:Annual mean temperature	0.234	0.064	3.663	***	0.140	0.079	1.761	ns	0.619	0.128	4.814	***
Elevation:Annual precipitation	0.011	0.053	1.903	ns	0.011	0.057	0.148	**ns**	−0.122	0.133	−0.915	ns
(b) Plot invaded/uninvaded by neophytes	All neophytes ($D^2 = 9.3\%$)				Non-European origin ($D^2 = 9.9\%$)				European origin ($D^2 = 5.1\%$)			
	Estimate	SE	Z	*P*	Estimate	SE	Z	*P*	Estimate	SE	Z	*P*
Intercept	−2.925	0.043	−68.114	***	−3.356	0.055	−60.806	***	−4.168	0.074	−57.059	***
Elevation	−0.961	0.059	−16.095	***	−1.296	0.076	−17.033	***	−0.262	0.102	−2.588	**
Annual mean temperature	0.276	0.051	5.399	***	0.181	0.063	2.875	**	0.543	0.094	5.803	***
Annual precipitation	−0.280	0.047	−5.964	***	−0.274	0.061	−4.506	***	−0.273	0.075	−3.660	***
Elevation:Annual mean temperature	0.295	0.068	4.355	***	0.221	0.084	2.622	**	0.559	0.123	4.549	***
Elevation:Annual precipitation	0.072	0.067	1.079	ns	0.040	0.086	0.468	ns	−0.069	0.128	−0.537	ns

24,220 plots sampled in European heathland and scrub habitats were analysed. Models were run separately for all neophytes and neophytes of non-European and European origin. All explanatory variables were standardized to facilitate comparison of model estimates; D^2 deviance explained, *SE* standard error, *Z* value of the Wald statistic, *ns* not significant. Significance was tested with the likelihood-ratio χ^2 test and levels indicated as *** $P < 0.001$; **$P < 0.01$; *$P < 0.05$

Mediterranean spiny heaths (S71, S72) or gypsum scrub (S65), where neophytes were absent. The presence of neophytes increased slightly in the Mediterranean acidophilous and basiphilous garrigue (S61, S62) and the other Mediterranean shrublands. Most alien species introduced to Europe are not as tolerant as native species to xeric conditions, especially summer droughts (Lambdon et al. 2008), and climatic matching is therefore critical for successful invasion to the Mediterranean ecosystem (Cao Pinna et al. 2021). Another explanation for the low neophyte numbers is the long history of human settlements and species introductions, which can have resulted in the resistance of Mediterranean vegetation to new invasions (Di Castri 1989; Guarino et al. 2021). The very low richness of neophytes was also found in the oro-mediterranean hedgehog heaths (S73-75), where xeric conditions are combined with isolation on high mountains. In our data set, neophytes in Mediterranean shrublands included (i) species of European origin native to one part of the Mediterranean and introduced to another, such as *Acanthus mollis* subsp. *mollis*, (ii) drought-tolerant non-European neophytes, such as *Opuntia ficus-indica, Carpobrotus acinaciformis* or *Oxalis pes-caprae*, and (iii) non-European species with broad ecological tolerance such as *Lantana camara* or *Robinia pseudoacacia* (Supplementary Information, Table S7).

Heathlands and scrub habitats of the Arctic and Alpine biogeographical regions share many features that may account for their low levels of invasion by neophytes. Environmental filtering caused by abiotic stress (low temperatures and short growing season), as well as sparse human population and associated low propagule pressure, are likely to reduce invasions at northern latitudes or higher elevations. Many alien species invading areas at northern latitudes originate from European regions with milder climates (Sandvik et al. 2019; Wasowitz 2016) and are concentrated mainly in human-altered habitats near settlements, roads or paths (Elven et al. 2011; Ware et al. 2012). Indeed, plots of Shrub tundra (S11) or Subarctic and subalpine *Salix* scrub (S21) in the Arctic biogeographical region contained no neophytes. However, with increasing human pressure and disturbance, subarctic *Salix* scrub may also be invaded by generalist aliens (Milbau et al. 2013). We also observed no neophytes or very low levels of invasion across all heathlands and scrub habitats at high elevations of the Alpine biogeographical region. Mountain systems are known to be less invaded than their surroundings (McDougal et al. 2011). Besides climatic filtering, isolation and low human activity resulting in low propagule pressure (Pauchard et al. 2009), invasion to high elevations is also limited by the alien species pool, which consists of species introduced to lowlands and adapted to lowland climate (Alexander et al. 2011, 2016). This is also evident in our data, where neophytes invading European alpine shrublands are a mixture of species with no clear common features such as cold adaptations (Supplementary Information, Table S7). However, some alpine habitats in mainland Europe have also been shown as not fully resistant to invasion and can be invaded in the future as a result of increasing human activities and climate change (Morgan and Carnegie 2009; Pauchard et al. 2009).

Our analyses showed that mean relative alien species richness as well as the probability of plots being invaded decreases towards higher elevations; however, the decrease is slower in plots located in warm conditions. In temperate Europe, a steady decrease in relative richness of neophytes with elevation has been found in several regions (Becker et al. 2005; Sinisalco et al. 2011; Medvecká et al. 2014). However, in the Macaronesian biogeographical region, particularly in the Canary Islands, previous studies reported a unimodal response with peak alien richness at mid-elevations. Most alien species of Mediterranean origin in the Canary Islands occur at mid-elevations, where conditions are comparable to those in Mediterranean Europe (Alexander et al. 2011; Arévalo et al. 2005; Steinbauer et al. 2016). Mid-elevations also have a long history of human settlements and related introductions of species (Arévalo et al. 2005). At higher elevations, the xero-thermic stress increases, and human influence decreases as land use shifts from agriculture to forestry (Arévalo et al. 2005; Steinbauer et al. 2016). This inconsistency resulting from the combination of climatic and historical factors, is likely reflected in the interaction of elevation and temperature observed in European shrublands. In separate analyses of the plots from the Macaronesian biogeographical region, the level of invasion by non-European neophytes decreased steadily with elevation, while neophytes of European origin showed a sharp decline only at high elevations (approx. > 1600 m).

Effects of temperature and precipitation on levels of invasion

The positive effect of annual mean temperature and the negative effect of annual precipitation on the relative richness of neophytes of European origin can be explained by the Mediterranean origin of many European neophytes. Such species may prefer warm and dry conditions similar to those of their native range when introduced to higher latitudes in Europe, especially in drier lowlands such as those of the Pannonian and Continental biogeographical regions. Non-European neophytes also showed a decrease with annual precipitation and an increase with annual mean temperature, although the latter only had a positive effect on the probability of plots being invaded and not on their relative richness in plots. This indicates that non-European neophytes of various origins prefer European scrub habitats in relatively dry and warm regions such as the Pannonian biogeographical region. However, harsh, dry conditions such as those found in the Mediterranean seem more likely to prevent the invasion of many of these species. The trend toward flora enrichment by non-European neophytes that prefer relatively drier and warmer conditions has already been reported from Switzerland (Scherrer et al. 2022).

Comparison of neophyte invasion in European shrublands with forests and grasslands

The levels of invasion measured in European heathland and scrub habitats as the mean relative neophyte richness in a plot (up to 3.8%) is between values reported for European grasslands (up to 3.6%; Axmanová et al. 2021) and forests (up to 4.7%; Wagner et al. 2017). Riparian forests, the most invaded forest habitats in Europe (Wagner et al. 2017), are more invaded than the most invaded Macaronesian scrub habitats and riparian scrub habitats, but these two scrub habitats are still more invaded than the most invaded grasslands such as continental alluvial pastures and meadows, and coastal sand dune grasslands (Axmanová et al. 2021). However, the total share of neophytes in the whole species pool of European heathland and scrub habitats (4.8%) is lower than for grasslands (6.5%) and forests (7%). Although the pool of neophytes is more limited in scrub habitats, its species occur more frequently across plots: 4.5% of all species occurrences belong to neophytes in scrub habitats and only 0.6% in grasslands and 1% in forests. This indicates greater uniformity in the composition of neophytes, as the same neophytes occur across many invaded plots in heathland and scrub habitats, while the proportion of invaded plots is lower than in grasslands (7.9% vs 11%).

The neophytes with the highest relative richness and higher counts than can be expected in the species pool of European heathlands and scrub, are phanerophytes (Supplementary Information, Table S8), which is a similar pattern to European forests (Wagner et al. 2017). The intentional introduction of many woody species to Europe for commercial forestry and landscaping results in large propagule pressure from tree plantations (Křivánek et al. 2006), which are an important source of neophytes not only for forests but also for shrublands. Moreover, the species pool of native phanerophytes in Europe is generally small due to extinctions during Pleistocene glaciation cycles (Huntley 1993), which is also reflected by the lower counts of native phanerophytes in our data set (marginally significant after the correction). European heathland and scrub habitats and forest habitats share the most successful non-European woody neophytes, including *Prunus serotina*, *Robinia pseudoacacia*, *Quercus rubra*, *Amelanchier lamarckii,* and *Populus x canadensis*, which indicates a significant exchange of neophytes between them (the other successful neophytic phanerophytes can be found in Supplementary Information, Table S8). These species are generally able to establish in a wide range of European heathland and scrub habitats, including coastal, fen and riparian scrub, temperate heathlands and temperate lowland to montane scrub (Supplementary Information, Table S7). The most successful phanerophyte, *Prunus serotina*, was recorded in the highest number of plots, but its occurrence is regionally restricted and concentrated primarily in temperate heathlands (50% of invaded plots) and coastal scrub. This corresponds to its main European range in the lowlands of NW Europe on poor, sandy soils (Starfinger 1997). Neophytic phanerophytes may dominate invaded shrublands and thus have serious impacts, including suppression of native diversity and changes in vegetation dynamics (Langmaier and Lapin 2020). These neophytes with dominance tendencies typically combine various strategies, including competition for resources, prevention of native recruitment through shading, allelopathy, changes in soil properties and nutrient cycling (e.g. Starfinger 1997; Lazzaro et al. 2018). However, the long-term roles of neophytic phanerophytes and their impacts on European vegetation remain poorly understood.

Hemicryptophytes have the second-highest proportion among neophytes of European heathlands and scrub habitats but are less numerous in their species pool than can be expected. They are much less represented among neophytes than among native species, which is also similar to the pattern in European forests (Wagner et al. 2017). This group of neophytes in shrublands includes mainly competitive hemicryptophytes such as *Solidago gigantea*, which is also one of the most successful neophytes in forests and grasslands as well, whereas *Solidago canadensis* is confined to shrublands and grasslands (Wagner et al. 2017; Axmanová et al. 2021). The third group of neophytes that have high proportion in the species pool of European heathlands and scrub are therophytes, although their higher count compared to the expected value in the species pool is only marginally significant after the correction. Those include the non-European species *Impatiens parviflora*, *I. glandulifera*, *Erigeron annuus* and *E. canadensis*. These species are also successful in forest invasions (Wagner et al. 2017), although as a life form, therophytes are relatively more frequent in European grasslands (Axmanová et al. 2021). *Impatiens parviflora* has the advantage of a broad ecological range (Pyšek et al. 2012) and shade tolerance (Tanner 2008), and its spread in forests is strongly promoted by human activities such as timber transport (Eliáš 1999). Although the species occurs in many plots in the data set, it is primarily limited to nutrient-rich and moist conditions in riparian, temperate lowland to montane and fen scrub (Supplementary Information, Table S7). *Impatiens glandulifera* has a similar distribution pattern in shrublands (Supplementary Information, Table S7), and its spread from populations established along watercourses into adjacent forests is facilitated by its broad ecological tolerance, competitiveness under shaded conditions, and efficient transport of seeds by forestry machinery (Čuda et al. 2020). *Impatiens glandulifera* also has the most frequently reported impact on native diversity in invaded habitats compared to other therophytes found in scrub habitats (Hulme and Bremner 2006; Kiełtik and Delimat 2019). *Erigeron canadensis*, and similarly *E. annuus*, are not only common in plots but also widespread across most of the broad scrub habitats and European regions. They are widespread generalists preferring disturbed sites in many habitat types across Europe (e.g. Pyšek et al. 2012; Küzmič and Šilc 2017), and are among the most frequent neophytes in both grasslands and forests in Europe (Wagner et al. 2017; Axmanová et al. 2021). The highest proportions of therophytes generally occur in scrub habitats with open and patchy vegetation, such as semi-desert and saline scrub, where they account for half of all neophytes. They are also common in disturbed coastal and riparian scrub where they can take advantage of sites where vegetation cover is periodically removed (Supplementary Information, Table S9).

In contrast to grasslands and forests, where the proportions of neophytes of non-European and European origin were almost equal in the alien species pool, non-European neophytes prevailed in the alien species pool in European heathlands and scrub habitats. The range of successful non-European neophytes in shrublands also included only two species that have not been mentioned in studies of invasions in European grasslands and forests: *Vaccinium macrocarpon* and *Claytonia perfoliata*. *Vaccinium macrocarpon* is a North American species that occurred in our data set in plots of coastal dune scrub, fen scrub, and temperate heathlands. In Europe, it is cultivated on degraded bogs and naturalized on coastal dunes and in heathlands in Poland, Lithuania, Switzerland and the Netherlands (Gudžinskas et al. 2014). *Claytonia perfoliata* is another North American species that occurs mainly in coastal dune scrub and fen scrub according to our data set. It was previously reported especially from NW Europe (Gudžinskas 2017), where it can dominate the herb layer of disturbed shrublands in spring (Weeda 2010).

Conclusions

We present a continental assessment of patterns of neophyte invasion in European heathland and scrub habitats defined at both fine and coarse resolution. Although shrublands have been less studied as targets of plant invasions, we show that as a whole, they exhibit considerable variability in invasion levels and include habitats important for neophytes. We show that neophytes prefer disturbed shrublands with high or fluctuating resource levels, such as coastal or riparian scrub, and island habitats of Macaronesia. In contrast, shrublands in stressed habitats such as at low elevation of the Mediterranean seem to be less prone to neophyte invasion. Because many neophytes in European shrublands prefer relatively warm conditions, their invasion can accelerate with climate change. Thus, it is likely that nowadays rarely invaded shrublands, such as those at high elevations (Pauchard et al. 2009; Alexander et al. 2016) and northern latitudes (Milbau et al. 2013), may be increasingly more invaded in the future (Pauchard et al. 2009; Alexander et al. 2016). Also, shrubland types that are invaded to different levels in different European biogeographical regions, such as coastal sand dune scrub, are at high invasion risk if human pressures increase. Because political boundaries do not usually act as the barriers to dispersal of alien plants, continental-scale studies with regular updates are needed for successful and up-to-date risk assessments and management measures.

Acknowledgements We thank Ilona Knollová for preparing the EVA output data set, Christian Berg for providing vegetation-plot data from the Austrian Vegetation Database, Jan Divíšek for assistance with geographical stratification of the data set, and Natálie Čeplová for helping us with life forms assignments.

Author contributions VK and MC conceived the study ideas. EA, IB, KE, EG, JCS, MŠ and UŠ contributed the vegetation-plot data and together with EC helped with alien species identification. VK and IA compiled the final list of neophytes and processed the plot data. VK with contribution of IA and KK performed statistical analyses and VK led the writing. MV, IA and VK prepared the maps, and MV prepared environmental variables. All authors read, commented and approved the final manuscript.

Funding Open access publishing supported by the National Technical Library in Prague. V.K., M.C., M.V. and I.A. were supported by the Czech Science Foundation (EXPRO Grant no. 19-28491X). I.B. was funded by the Basque Government (IT1487-22). J-C.S. considers this work a contribution to his VILLUM Investigator project “Biodiversity Dynamics in a Changing World” funded by VILLUM FONDEN (Grant 16549).

Data availability statement The data sets analysed are stored in the European Vegetation Archive http://euroveg.org/eva-database

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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References

Affre L, Suehs CM, Charpentier S, Vilà M, Brundu G, Lambdon P, Traveset A, Hulme PE (2010) Consistency in the habitat degree of invasion for three invasive plant species across Mediterranean islands. Biol Invasions 12:2537–2548. https://doi.org/10.1007/s10530-009-9662-6

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium, Mooney HA (2011) Assembly of nonnative floras along elevation gradients explained by directional ecological filtering. Proc Natl Acad Sci USA 108:656–661. https://doi.org/10.1073/pnas.101313610

Alexander JM, Lembrechts JJ, Cavieres LA, Daehler C, Haider S, Kueffer C, Liu G, McDougall K, Milbau A, Pauchard A, Rew LJ, Seipel T (2016) Plants invasions into mountains and alpine ecosystems: current status and future challenges. Alp Bot 126:89–103. https://doi.org/10.1073/pnas.1013136108

Allan GJ, Francisco-Ortega J, Santos-Guerra A, Boerner E, Zimmer EA (2004) Molecular phylogenetic evidence for the geographic origin and classification of Canary Island *Lotus* (Fabaceae: Loteae). Mol Phylogenet Evol 32:123–138. https://doi.org/10.1016/j.ympev.2003.11.018

Archer SR, Andersen E, Predick KI, Schwinning S, Steidl RJ, Woods SR (2017) Woody plant encroachment: causes and consequences. In: Briske DD (ed) Rangeland systems. Springer, Dordrecht, pp 25–84

Arévalo JR, Delgado JD, Otto R, Naranjo A, Salas M, Férnandez-Palacios JM (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect Plant Ecol Evol Syst 7:185–202. https://doi.org/10.1016/j.ppees.2005.09.003

Axmanová I, Kalusová V, Danihelka J, Dengler J, Pergl P, Pyšek P, Večeřa M, Attore F, Biurrun I, Boch S, Conradi T, Gavilán RG, Jimenéz-Alfaro B, Knollová I, Kuzemko A, Lenoir J, Leostrin A, Medvecká J, Moeslund JE, Obratov-Petkovic D, Svenning J-C, Tsiripidis I, Vassilev K, Chytrý M (2021) Neophyte invasions in European grasslands. J Veg Sci 32:e12994. https://doi.org/10.1111/jvs.12994

Beasley TM, Schumacher RE (1995) Multiple regression approach to analyzing contingency tables: Post hoc and planned comparison procedures. J Exp Educ 64:79–93. https://doi.org/10.1080/00220973.1995.9943797

Becker T, Dietz H, Billeter R, Buschmann H, Edwards PJ (2005) Altitudinal distribution of alien plant species in the Swiss Alps. Perspect Plant Ecol Evol Syst 7:173–183. https://doi.org/10.1016/j.ppees.2005.09.006

Bellard C, Leroy B, Thuiller W, Rysman J-F, Courchamp F (2016) Major drivers of invasion risks throughout the world. Ecography 7:e01241. https://doi.org/10.1002/ecs2.1241

Bivand R (2020) classInt: choose univariate class intervals. Version 0.4-3. https://cran.r-project.org/web/packages/classInt/index.html. Accessed 25 January 2021

Bivand R, Keitt T, Rowlingson B, Pebesma E, Sumner M, Hijmans R, Baston D, Rouault E, Warerdam F, Ooms J, Rundel C (2020) rgdal: bindings for the ’geospatial’ data abstraction library. Version 1.5-12. https://cran.r-project.org/web/packages/rJava/index.html. Accessed 25 January 2021

Boessenkool B (2021) berryFunctions: function collection related to plotting and hydrology. Version 1.19.1. https://cran.r-project.org/web/packages/berryFunctions/index.html. Accessed 25 January 2021

Bramwell D (1976) The endemic flora of the Canary Islands; distribution, relationships and phytogeography. In: Kunkel G (ed) Biogeography and ecology in the Canary Islands. Monographiae Biologicae, vol 30. Springer, Dordrecht, pp 207–242

Campos JA, Herrera M, Biurrun I, Loidi J (2004) The role of alien plants in the natural coastal vegetation in central northern Spain. Biodivers Conserv 13:2275–2293. https://doi.org/10.1023/B:BIOC.0000047902.27442.92

Campos JA, Biurrun I, García-Mijangos I, Loidi J, Herrera M (2013) Assessing the level of plant invasion: a multi-scale approach based on vegetation plots. Plant Biosyst 147:1148–1162. https://doi.org/10.1080/11263504.2013.861538

Cao Pinna L, Axmanová I, Chytrý M, Malavasi M, Acosta ATR, Giulio S, Attore F, Bergmeier E, Biurrun I, Campos JA, Font X, Küzmič F, Landucci F, Marcenò C, Rodrígez-Rojo MP, Carboni, (2021) The biogeography of alien plant invasions in the Mediterranean Basin. J Veg Sci 32:e12980. https://doi.org/10.1111/jvs.12980

Carboni M, Livingstone SW, Isaac ME, Cadotte MW (2021) Invasion drives plant diversity loss through competition and ecosystem modification. J Ecol 109:3587–3601. https://doi.org/10.1111/1365-2745.13739

Castro SA, Daehler CC, Silva L, Torres-Santana CW, Reyes-Bentacort JA, Atkinson R, Jaramillo P, Guezou A, Jaksic FM (2010) Floristic homogenization as a teleconnected trend in oceanic islands. Divers Distrib 16:902–910. https://doi.org/10.1111/j.1472-4642.2010.00695.x

Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Glob Chang Biol 18:44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x

Celesti-Grapow L, Blasi C (1998) A comparison of the urban flora of different phytoclimatic regions in Italy. Glob Ecol Biogeogr Lett 7:367–378. https://doi.org/10.1046/j.1466-822x.1998.00304.x

Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77:339–354

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008a) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008b) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553. https://doi.org/10.1890/07-0682.1

Chytrý M, Pyšek P, Wild J, Pino J, Maskell LC, Vilà M (2009) European map of alien plant invasions based on the quantitative assessment across habitats. Divers Distrib 15:98–107. https://doi.org/10.1111/j.1472-4642.2008.00515.x

Chytrý M, Hennekens SM, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F, Landucci F, Schaminée JHJ, Aćić S, Agrillo E, Ambarli D, Angelini P, Apostolova I, Attore F, Berg C, Bergmeier E, Biurrun I, Botta-Dukát Z, Brisse H, Campos JA, Carlón L, Čarni A, Casella L, Csiky J, Ćušterevska R, Dajić Stevanović Z, Danihelka J, De Bie E, de Ruffay P, De Sanctis M, Dickoré WB, Dimopoulos P, Dubyna D, Dziuba T, Ejrnæs R, Ermakov N, Ewald J, Fanelli G, Fernández-González F, FitzPatrick Ú, Font X, García-Mijangos I, Gavilán RG, Golub V, Guarino R, Haveman R, Indreica A, Işık Gürsoy D, Jandt U, Janssen JAM, Jiroušek M, Kącki Z, Kavgacı A, Kleikamp M, Kolomiychuk V, Krstivojević Ćuk M, Krstonošić D, Kuzemko A, Lenoir J, Lysenko T, Marcenò K, Martynenko V, Michalcová D, Moeslund JE, Onyshchenko V, Pedashenko H, Pérez-Haase A, Peterka T, Prokhorov V, Rašomavičius V, Rodríguez Rojo MP, Rodwell JS, Rogova T, Ruprecht E, Rūsiņa S, Seidler G, Šibík J, Šilc U, Škvorc Ž, Sopotlieva D, Stančić Z, Svenning J-C, Swacha G, Tsiripidis I, Turtureanu PD, Uğurlu E, Uogintas D, Valachovič M, Vashenyak Y, Vassilev K, Venanzoni R, Virtanen R, Weekes L, Willner W, Wolgemuth T, Yamalov S (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Appl Veg Sci 19:173–180. https://doi.org/10.1111/avsc.12191

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò K, Landucci F, Danihelka J, Hájek M, Dengler J, Novák P, Zukal D, Jiménez-Alfaro B, Mucina L, Abdulhak S, Aćić S, Agrillo E, Attore F, Bergmeier E, Biurrun I, Boch S, Bölöni J, Bonari G, Braslavskaya T, Bruelheide H, Campos JA, Čarni A, Casella L, Ćuk M, Ćušterevska R, De Bie E, Delbosc P, Demina O, Didukh Y, Dítě D, Dziuba T, Ewald R, Gavilán RG, Gégout J-C, Giusso del Galdo GP, Golub V, Goncharova N, Goral F, Graf U, Indreica A, Isermann M, Jandt U, Jansen F, Jansen J, Jašková A, Jiroušek M, Kącki Z, Kalníková V, Kavgacı A, Khanina L, Korolyuk AY, Kozhevnikova M, Kuzemko A, Küzmič F, Kuznetsov OL, Laiviņš M, Lavrinenko I, Lavrinenko

O, Lebedeva M, Lososová Z, Lysenko T, Maciejewski L, Mardari C, Marinšek A, Napreenko MG, Onyshchenko V, Pérez-Haase A, Pielech R, Prokhorov V, Rašomavičius V, Rodríguez Rojo MP, Rūsiņa S, Schrautzer J, Šibík J, Šilc U, Škvorc Ž, Smagin VA, Stančić Z, Stanisci A, Tikhonova E, Tonteri T, Uogintas D, Valachovič M, Vassilev K, Vynokurov D, Willner W, Yamalov S, Evans D, Pallitzsch Lund M, Spyropoulou R, Tryfon E, Schaminée JHJ (2020) EUNIS habitat classification: expert system, characteristic species combinations and distribution maps of European habitats. Appl Veg Sci 23:648–675. https://doi.org/10.1111/avsc.12519

Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: specific problems and possible solutions. Trends Ecol Evol 32:13–22. https://doi.org/10.1016/j.tree.2016.11.001

García Criado M, Meyers-Smith IH, Bjorkman AD, Lehmann CER, Stevens N (2019) Woody plant encroachment intensifies under climate change across tundra and savanna biomes. Glob Ecol Biogeogr 29:925–943. https://doi.org/10.1111/geb.13072

Čuda J, Skálová H, Pyšek P (2020) Spread of *Impatiens glandulifera* from riparian habitats to forests and its associated impacts: insights from a new invasion. Weed Res 60:8–15. https://doi.org/10.1111/wre.12400

DAISIE (2009) Handbook of alien species in Europe. Springer, Dordrecht

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Deng Y, Li X, Shi F, Hu X (2021) Woody plant encroachment enhanced global vegetation greening and ecosystem water-use efficiency. Glob Ecol Biogeogr 30:2337–2353. https://doi.org/10.1111/geb.13386

Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592:571–576. https://doi.org/10.1038/s41586-021-03405-6

Di Castri F (1989) History of biological invasions with special emphasis on the Old World. In: Drake JA, Mooney HA, DiCastri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds) Biological invasions. A global perspective. SCOPE 37. Wiley, Chichester, pp 1–30

Dickens SJM, Allen EB (2014) Exotic plant invasion alters chaparral ecosystem resistance and resilience pre- and post-wildfire. Biol Invasions 16:1119–1130. https://doi.org/10.1007/s10530-013-0566-0

Divíšek J, Chytrý M (2018) High-resolution and large-extent mapping of plant species richness using vegetation-plot databases. Ecol Indic 89:840–851. https://doi.org/10.1016/j.ecolind.2017.11.005

Dobson AJ (1990) An introduction to generalized linear models. Chapman and Hall, London

Douma JC, Weedon JT (2019) Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. Methods Ecol Evol 10:1412–1430. https://doi.org/10.1111/2041-210X.13234

EEA (2016) Biogeographical regions in Europe. Copenhagen: European Environment Agency. https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3. Accessed 27 September 2021

Eliáš P (1999) Biological and ecological causes of invasion of *Impatiens parviflora* DC. into forest communities in central Europe. Acta Hortic Regioc 1:1–3

Elven R, Murray DF, Razzhivin VY, Yurtsev BA (2011) Checklist of the Panarctic flora (PAF). http://nhm2.uio.no/paf/. Accessed 20 March 2022

ESRI (2011) ArcGIS Desktop. Environmental Systems Research Institute, Redlands

Euro+Med PlantBase (2021) Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/. Accessed 15 September 2021

Evans JS, Murphy MA & Ram K (2021) spatialEco: spatial analysis and modelling utilities. Version 1.3-2. https://cran.rproject.org/web/packages/spatialEco/index.html. Accessed 25 January 2021

Expósito AB, Siverio A, Bermejo LA, Sobrino-Vesperinas E (2018) Checklist of alien plant species in a natural protected area: Anaga Rural Park (Tenerife, Canary Islands); effect of human infrastructure on their abundance. Plant Ecol Evol 151:142–152. https://doi.org/10.5091/plecevo.2018.1330

Fischer HS (2015) On the combination of species cover values from different vegetation layers. Appl Veg Sci 18:169–170. https://doi.org/10.1111/avsc.12130

Fridley JD, Sax DF (2014) The imbalance of nature: revisiting a Darwinian framework for invasion biology. Glob Ecol Biogeogr 23:1157–1166. https://doi.org/10.1111/geb.12221

Gallardo B, Bacher S, Bradley B, Comín FA, Gallien L, Jeschke JM, Sorte CJ, Vilà M (2019) InvasiBES: Understanding and managing the impacts of invasive alien species on biodiversity and ecosystem services. NeoBiota 50:109–122. https://doi.org/10.3897/neobiota.50.35466

Giulio S, Acosta ATR, Carboni M, Campos JA, Chytrý M, Loidi J, Pergl J, Pyšek P, Isermann M, Janssen JAM, Rodwell JS, Schaminée JHJ, Marcenò C (2020) Alien flora across European coastal dunes. Appl Veg Sci 23:317–327. https://doi.org/10.1111/avsc.12490

Goldstein LJ, Suding KN (2014) Applying competition theory to invasion: Resource impacts indicate invasion mechanisms in California shrublands. Biol Invasions 16:191–203. https://doi.org/10.1007/s10530-013-0513-0

Guarino R, Chytrý M, Attorre F, Landucci F, Marcenò C (2021) Alien plant invasions in Mediterranean habitats: an assessment for Sicily. Biol Invasions 23:3091–3107. https://doi.org/10.1007/s10530-021-02561-0

Gudžinskas Z (2017) Alien herbaceous plants new to Lithuania. Bot Lith 23:33–42. https://doi.org/10.1515/botlit-2017-0003

Gudžinskas Z, Petrulaitis L, Arlikevičiūtė L (2014) *Vaccinium macrocarpon* – a new alien species in Lithuania. Bot Lith 20:41–45. https://doi.org/10.2478/botlit-2014-0005

Guo Q, Fei S, Dukes JS, Oswalt CM, Iannone BV III, Potter KM (2015) A unified approach for quantifying invasibility and degree of invasion. Ecology 10:2613–2621. https://doi.org/10.1890/14-2172.1

Hijmans RJ, van Etten J, Sumner M, Cheng J, Baston D, Bevan A, Bivan R, Busetto L, Canty M, Fasoli B, Forrest D, Ghosh A, Golicher D, Gray J, Greenberg JA, Hiemstra P, Hingee K, Ilich A, Institute for Mathematics Applied Geosciences, Karney C, Mattiuzzi M, Mosher S, Naimi B, Nowosad J, Pebesma E, Lamigueiro OP, Racine EB, Rowlingson B, Shortidge A, Venables B, Wueest R (2021) raster: Geographic data analysis and modeling. Version 3.3-13. https://cran.r-project.org/web/packages/raster/index.html. Accessed 25 January 2021

Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J Appl Ecol 43:43–50. https://doi.org/10.1111/j.1365-2664.2005.01102.x

Huntley B (1993) Species-richness in north-temperate zone forests. J Biogeogr 20:163–180. https://doi.org/10.2307/2845669

Hughes J (2020) Reghelper: helper functions for regression analysis. R package version 0.3.5. https://cran.r-project.org/web/packages/reghelper/reghelper.pdf. Accessed 25 January 2021

Hulme PE (2004) Islands, invasions and impacts: a Mediterranean perspective. In: Fernández-Palacios JM, Morici C (eds) Ecología insular/Island ecology, Asociación Española de Ecología Terrestre (AEET), Cabildo Insular de la Palma, pp 359–383

Isermann M (2008) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Brock H, Brundu G, Child L, Daehler CC, Pyšek P (eds) Plant Invasions: human perception, ecological impacts and management. Backhuys Publishers, Leiden, pp 289–306

Janssen JAM (2016) European red list of habitats - heathlands habitat group. F8.1 Canarian xerophytic scrub. https://forum.eionet.europa.eu/european-red-list-habitats/library/terrestrial-habitats/f.-heathland-and-scrub/f8.1-canarian-xerophytic-scrub. Accessed 22 March 2022

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled SRTM for the globe. Version 4, available from the CGIAR-CSI SRTM 90m Database. http://srtm.csi.cgiar.org. Accessed 25 January 2021

Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D (2009) Standards for associations and alliances of the US National Vegetation Classification. Ecol Monogr 79:173–199. https://doi.org/10.1890/07-1804.1

Kalusová V, Chytrý M, Peet RK, Wentworth TR (2014) Alien species pool influences the level of habitat invasion in the intercontinental exchange of alien plants. Glob Ecol Biogeogr 23:1366–1375. https://doi.org/10.1111/geb.12209

Kalusová V, Chytrý M, Peet RK, Wentworth TR (2015) Intercontinental comparison of habitat levels of invasion between temperate North America and Europe. Ecology 96:3363–3373. https://doi.org/10.1890/15-0021.1

Kalusová V, Chytrý M, van Kleunen M, Mucina L, Dawson W, Essl F, Kreft H, Pergl J, Weigelt P, Winter M, Pyšek P (2017) Naturalization of European plants on other continents: The role of donor habitats. Proc Natl Acad Sci USA 114:13756–13761. https://doi.org/10.1073/pnas.1705487114

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder P, Kessler M (2017) Climatologies at high resolution for the Earth land surface areas. Sci Data. 4:170122. https://doi.org/10.1038/sdata.2017.122

Kassambara A (2021) Rstatix: pipe-friendly framework for basic statistical tests. R package version 0.7.0. https://cloud.r-project.org/package=rstatix. Accessed 20 July 2021

Kiełtik P, Delimat A (2019) Impact of the alien plant *Impatiens glandulifera* on species diversity of invaded vegetation in the northern foothills of the Tatra Mountains, central Europe. Plant Ecol 220:1–12. https://doi.org/10.1007/s11258-018-0898-z

Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv Biol 5:1487–1498. https://doi.org/10.1111/j.1523-1739.2006.00477.x

Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, Veer G, Vilà M, Nentwig W (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. J Appl Ecol 52:552–561. https://doi.org/10.1111/1365-2664.12427

Küzmič F, Šilc U (2017) Alien species in different habitat types of Slovenia: analysis of vegetation database. Period Biol 119:199–208. https://doi.org/10.18054/pb.v119i3.5183

Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Kokkoris Y, Kühn I, Marchante H, Perglová I, Pino J, Vilà M, Zikos A, Roy D, Hulme PE (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80:101–149

Landi S, Tordoni E, Amici V, Bacaro G, Carboni M, Filibeck G, Scoppola A, Bagella S (2020) Contrasting patterns of native and non-native plants in a network of protected areas across spatial scales. Biodiv Conserv 29:2035–2053. https://doi.org/10.1007/s10531-020-01958-y

Langmaier M, Lapin K (2020) A systematic review of the impact of invasive alien plants on forest regeneration in European temperate forests. Front Plant Sci 11:524969. https://doi.org/10.3389/fpls.2020.524969

Lazzaro L, Mazza G, d'Ericco G, Fabiani A, Giuliani C, Inghilesi AF, Lagomarsino A, Landi S, Lastrucci L, Pastorelli R, Rovesi PF, Torrini G, Tricario E, Foggi B (2018) How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. Sci Total Environ 622–623:1509–1518. https://doi.org/10.1016/j.scitotenv.2017.10.017

Liendo D, Biurrun I, Campos JA, García-Mijangos I, Pearman PB (2021) Effects of disturbance and alien plants on the phylogenetic structure of riverine communities. J Veg Sci 32:e12933. https://doi.org/10.1111/jvs.12933

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536. https://doi.org/10.2307/176544

McDougall KL, Khuroo AA, Loope LL, Parks CG, Pauchard A, Reshi ZA, Rushworth I, Kueffer C (2011) Plant invasions in mountains: global lessons for better management. Mt Res Dev 31:380–387. https://doi.org/10.1659/MRD-JOURNAL-D-11-00082.1

Medvecká J, Jarolímek I, Senko D, Svitok M (2014) Fifty years of plant invasion dynamics in Slovakia along a 2500 m altitudinal gradient. Biol Invasions 16:1627–1638. https://doi.org/10.1007/s10530-013-0596-7

Milbau A, Shevtsova A, Osler N, Mooshammer M, Graae BJ (2013) Plant community type and small-scale disturbances, but not altitude, influences the invisibility in subarctic ecosystems. New Phytol 197:1002–1011. https://doi.org/10.1111/nph.12054

Ming N, Deane DC, Li S, Wu S, Sui X, Xu H, Chu Ch, He F, Fang S (2021) Invasion success and impacts depend on different characteristics in non-native plants. Divers Distrib 27:1194–1207. https://doi.org/10.1111/ddi.13267

Morgan JW, Carnegie V (2009) Backcountry huts as introduction points for invasion by non-native species into alpine vegetation. Arct Antarc Alp Res 41:238–245. https://doi.org/10.1657/1938-4246-41.2.238

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, Gavilán García R, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniëls FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachovič M, Schaminée JHJ, Lysenko T, Didukh YP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM, Tichý M (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl Veg Sci 19(Suppl_1):3–264. https://doi.org/10.1111/avsc.12257

Myśliwy M (2014) Plant invasions across different habitat types at floristic survey. Appl Ecol Environ 12:193–207. https://doi.org/10.15666/aeer/1201_193207

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1002/ecy.2542

Novoa A, Moodley D, Catford JA, Golivets M, Bufford J, Essl F, Lenzner B, Pattison Z, Pyšek P (2021) Global costs of plant invasions must not be underestimated. NeoBiota 69:75–78. https://doi.org/10.3897/neobiota.69.74121

Pauchard A, Kuefler C, Dietz H, Daehler CC, Alexander J, Edward J, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall K, Millaer CI, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: plant invasions reaching new elevations. Front Ecol Environ 7:479–486. https://doi.org/10.1890/080072

Pino J, Font X, Carbó J, Jové M, Pallarés L (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). Biol Conserv 122:339–350. https://doi.org/10.1016/j.biocon.2004.08.006

POWO (2021) Plants of the world online. Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/. Accessed 10 November 2021

Pyšek P (1998) Alien and native species in central European urban floras: a quantitative comparison. J Biogeogr 25:155–163. https://doi.org/10.1046/j.1365-2699.1998.251177.x

Pyšek P, Chytrý M (2014) Habitat invasion research: where vegetation science and invasion ecology meet. J Veg Sci 25:1811–1187. https://doi.org/10.1111/jvs.12146

Pyšek P, Jarošík V, Kučera T (2002) Patterns of invasion in temperate nature reserves. Biol Cons 104:13–24. https://doi.org/10.1016/S0006-3207(01)00150-1

Pyšek P, Chytrý M, Jarošík V (2009) Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In: Perrings C, Mooney H, Williamson M (eds) Bioinvasions and globalization: ecology, economics, management, and policy. Press, Oxford, Oxford Uni, pp 66–79

Pyšek P, Chytrý M, Pergl J, Sádlo J, Wild J (2012) Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. Preslia 84:575–629

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reyes-Betancort JA, Santos Guerra A, Rosana Guma I, Humphries CJ, Carine MA (2008) Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. Anales Jard Bot Madrid 65:25–45. https://doi.org/10.3989/ajbm.2008.v65.i1.244

Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers Distrib 13:126–139. https://doi.org/10.1111/j.1366-9516.2006.00314.x

Rodwell JS (2016) European Red List of Habitats. F3.1b Temperate *Rubus* scrub. https://forum.eionet.europa.eu/european-red-list-habitats/library/terrestrial-habitats/f.-heathland-and-scrub/f3.1b-temperate-rubus-scrub. Accessed 20 March 2022

Riera M, Pino J, Melero Y (2021) Impact of introduction pathways on the spread and geographical distribution of alien species: Implications for preventive management in Mediterranean ecosystems. Divers Distrib 27:1019–1034. https://doi.org/10.1111/ddi.13251

Sandvik H, Dolmen D, Elven R, Falkenhaug T, Forsgren E, Hansen H, Hassel K, Husa V, Kjærstad G, Ødegaard F, Pedersen HC, Solheim H, Stokke BG, Åsen PA, Åström S, Brandrud T-E, Elven H, Endrestøl A, Finstad A, Fredriksen S, Gammelmo Ø, Gjershaug JO, Gulliksen B, Hamnes I, Hatteland AB, Hegre H, Hesthagen T, Jelmert A, Jensen TC, Johnsen SI, Karlsbakk E, Magnusson C, Nedreaas K, Nordén B, Oug E, Pedersen O, Pedersen PA, Sjøtun K, Skei JK, Solstad H, Sundheim L, Swenson JE, Syvertsen PO, Talgø V, Vandvik V, Westergaard KB, Wienerrother R, Yetrehus B, Hilmo O, Henriksen S, Gederaas L (2019) Alien plants, animals, fungi and algae in Norway: an inventory of neobiota.

Biol Invasions 21:2997–3012. https://doi.org/10.1007/s10530-019-02058-x

Scherrer D, Bürgi M, Gessler A, Kessler M, Nobis MP, Wohlgemuth T (2022) Abundance changes of neophytes and native species indicate a thermophilisation and eutrophisation of the Swiss flora during the 20th century. Ecol Indic 135:e108558. https://doi.org/10.1016/j.ecolind.2022.108558

Silva L, Land EO, Luengo JLR (eds) (2008) Invasive terrestrial flora and fauna of Macaronesia. TOP 100 in Azores, Madeira and Canaries. ARENA, Ponta Delgada

Simberloff D (1995) Why do introduced species appear to devastate islands more than mainland areas? Pac Sci 49:87–97

Siniscalco C, Barni E, Bacaro G (2011) Non-native species distribution along elevation gradient in the western Italian Alps. Plant Biosyst 145:150–158. https://doi.org/10.1080/11263504.2010.540786

Sîrbu C, Oprea A, Samuil C, Tănase C (2012) Neophyte Invasion in Moldavia (Eastern Romania) in different habitat types. Folia Geobot Phytotaxon 47:215–229. https://doi.org/10.1007/s12224-011-9112-y

Sol D (2000) Are islands more susceptible to be invaded than continents? Birds say no. Ecography 23:687–692. https://doi.org/10.1111/j.1600-0587.2000.tb00312.x

Starfinger U (1997) Introduction and naturalization of *Prunus serotina* in central Europe. In: Brock JH, Wade M, Pyšek P, Green D (eds) Plant invasions: studies from North America and Europe. Backhuys Publishers, Leiden, pp 161–171

Steers RJ, Fritzke SL, Rogers JJ, Cartan J, Hacker K (2013) Invasive pine tree effects on northern coastal scrub structure and composition. Invasive Plant Sci Manag 6:231–242. https://doi.org/10.1614/IPSM-D-12-00044.1

Steinbauer MJ, Irl SDH, González-Mancebo JM, Breiner FT, Hernández-Hernández R, Hopfenmüller S, Kidane Y, Jentsch A, Beierkuhnlein C (2016) Plant invasion and speciation along elevational gradients on the oceanic island La Palma, Canary Islands. Ecol Evol 7:771–779. https://doi.org/10.1002/ece3.2640

Stierstorfer C, von Gaisberg M (2005) Annotated checklist and distribution of the vascular plants of El Hierro, Canary Islands, Spain. Englera 27:3–221. https://doi.org/10.2307/20358176

Tanner R (2008) Datasheets: *Impatiens parviflora* (small balsam). CAB Europe, Egham, Surrey , UK. http://www.cabi.org, date. Accessed 20 March 2022

Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11:2234–2250. https://doi.org/10.1111/j.1365-2486.2005.01018.x

TPL (2013) The plant list, Version 1.1. Available at: http://www.theplantlist.org/. Accessed 15 March 2021

van Kleunen M, Pyšek P, Dawson W, Essl F, Kreft H, Pergl J, Weigelt P, Stein A, Dullinger S, König C, Lenzner B, Maurel N, Moser D, Seebens H, Kartesz J, Nishino M, Aleksyan A, Ansong M, Antonova AL, Barcelona JF, Breckle SW, Brundu G, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Conn B, de Sá DM, Dufour-Dror J-M, Ebel AL, Figueiredo E, Fragman-Sapir O, Fuentes N, Groom QJ, Henderson L, Indejit JN, Krestov P, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Nickrent D, Nowak A, Patzelt A, Pelser PB, Shu W, Thomas J, Uludag T, Velayos M, Verkhosina A, Villaseñor JL, Weber E, Wieringa JJ, Yazlik A, Zeddam A, Zykova E, Winter M (2019) The Global Naturalized Alien Floras (GloNAF) database. Ecology 100:e02542. https://doi.org/10.1002/ecy.2542

van Rensburg BJ, Hugo S, Levin N, Kark S (2013) Are environmental transitions more prone to biological invasions? Divers Distrib 19:341–351. https://doi.org/10.1111/ddi.12026

Vilà M, Hulme PE (2016) Impact of biological invasions on ecosystem services. Springer, Cham

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veg Sci 18:35–42. https://doi.org/10.1111/j.1654-1103.2007.tb02513.x

Vilà M, Pino J, Montero A, Font X (2010) Are island plant communities more invaded than their mainland counterparts? J Veg Sci 21:438–446. https://doi.org/10.1111/j.1654-1103.2009.01166.x

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J-C, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Divers Distrib 23:969–981. https://doi.org/10.1111/ddi.12592

Wagner V, Večeřa M, Jiménez-Alfaro B, Pergl J, Lenoir J, Svenning J-C, Pyšek P, Agrillo E, Biurrun I, Campos JA, Ewald J, Fernández-González F, Jandt U, Rašomavičius V, Šilc U, Škvorc Ž, Vassilev K, Wohlgemuth T, Chytrý M (2021) Alien plant invasion hotspots and invasion debt in European woodlands. J Veg Sci 32:e13014. https://doi.org/10.1111/jvs.13014

Ware C, Bergstrom DM, Muller E, Alsos IG (2012) Humans introduce viable seeds to the arctic on footwear. Biol Invasions 14:567–577. https://doi.org/10.1007/s10530-011-0098-4

Wasowitz P, Przedpelska-Wasowitz EM, Kristinsson H (2016) Alien vascular plants in Iceland: diversity, spatial trends, temporal trends, and the impact of climate change. Flora 208:648–673. https://doi.org/10.1016/j.flora.2013.09.009

Weeda EJ (2010) The role of archaeophytes and neophytes in the Dutch coastal dunes. J Coast Conserv 14:75–79. https://doi.org/10.1007/s11852-009-0079-2

Wiser SK, Hurst JM, Wright EF, Allen RB (2011) New Zealand's forests and shrubland communities: a quantitative classification based on nationally representative plot network. Appl Veg Sci 14:506–523. https://doi.org/10.1111/j.1654-109X.2011.01146.x

Zefferman E, Stevens JT, Charles GK, Dunbar-Irwin M, Emam T, Fick S, Morales LV, Wolf KM, Young DN, Young TP (2015) Plant communities in harsh sites are less invaded:

a summary of observations and proposed explanations. AoB Plants 7:056. https://doi.org/10.1093/aobpla/plv056

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