

Alien plant invasion hotspots and invasion debt in European woodlands

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Abstract

Questions: European woodlands harbor at least 386 alien plant species but the factors driving local invasions remain unknown. By using a large vegetation-plot database, we asked how local richness and abundance of alien species vary by regions, elevation, climate, soil properties, human disturbance, and habitat types.

Location: Western, central and southern Europe.

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Methods: We linked consolidated data from the European Vegetation Archive (16,211 plots) to a habitat classification scheme, climate, soil properties and human disturbance variables. In addition, we used 250 km × 250 km regional grid cells to test whether local patterns differ among regions. We used generalized additive models (GAMs) and quantile GAMs to explore how relative alien species richness and the sum of alien species covers per plot relate to predictors. Random Forest analyses (RFs) were employed to assess the importance of individual predictors that were not multicollinear.

Results: Relative alien species richness and the sum of alien species covers varied across regions and habitat types, with effects being more pronounced at the maximum rather than average responses. Both response variables declined with increasing elevation and distance to the nearest road or railroad and increased with the amount of sealed soil. Maxima in fitted functions matched plots from regional invasion hotspots in northwestern and central Europe. RFs accounted for 39.6% and 20.9% of the total variation in relative alien species richness and the sum of alien species covers, respectively, with region and habitat being the most important variables.

Conclusions: The importance of maximum response quantiles and the prevalence of regional hotspots point to invasion debt in European woodlands. As alien plants expand further, their species richness and abundance in woodlands will be likely driven by the shared effects of the introduction and planting history, differences in the invaded habitat types, and dispersal corridors.

KEYWORDS

alien plants, biological invasions, Europe, European Vegetation Archive, exotic plants, forest, habitat type, invasibility, neophytes, non-native plants

1 | INTRODUCTION

At least 386 alien plant species have been introduced to European woodlands deliberately or accidentally after the year 1500 (Wagner et al., 2017). While most alien species reach only low abundances and frequencies, some can become invasive by spreading fast. Some species can even become transformative by changing plant species composition, suppressing native tree regeneration (Langmaier & Lapin, 2020), and altering ecosystem functioning (e.g., Aerts et al., 2017). For example, black locust (*Robinia pseudoacacia*) can homogenize woodland understorey composition (Šibíková et al., 2019; Vítková et al., 2020) and trigger soil acidification and nitrification (Lazzaro et al., 2018). Similarly, black cherry (*Prunus serotina*) can change nitrogen, phosphorus, and carbon cycles to its advantage, potentially altering the photosynthetic capacity of the long-lived native broad-leaved species (Aerts et al., 2017).

To decrease possible detrimental effects, the European Union has outlined strategies for the prevention and management of invasive alien species (European Parliament, 2014). However, designing efficient strategies depends on understanding the drivers of local alien plant invasions across European regions. Such knowledge is particularly important for woodlands because they cover a

third of the continent's territory and provide essential ecosystem services, including carbon sequestration, water retention, timber production, and biodiversity conservation (Forest Europe, 2015). However, the factors that drive alien plant invasions in European woodlands are not well understood. A recent Europe-wide study has shown that in general, macroclimate is an important abiotic predictor of local plant species richness in woodlands, in congruence with a northwest to southeast continentality gradient (Večeřa et al., 2019). However, it is not clear whether the same patterns hold true specifically for local alien plant species richness. Macroclimate was not an essential predictor of local alien plant species richness in deciduous woodlands of Catalonia (Gassó et al., 2011) and was just one of several predictors of local alien plant species richness in woodlands of the Czech Republic (Divíšek & Chytrý, 2018). This indicates that other predictors could be more important. For instance, there is strong evidence that the level of invasion generally decreases with elevation, partly due to a drop in human activities and alien plant propagule pressure, which are usually confounded (Alexander et al., 2011; Pyšek et al., 2011). By comparison, the role of abiotic soil conditions in structuring alien plant invasions is less clear. Alien plant invasions are often favored at sites with increased soil nutrient availability (Davis et al., 2000;

Gurevitch et al., 2008), yet many alien species can grow in low-nutrient ecosystems, likely because of their higher resource-use efficiency compared to native species (Funk & Vitousek, 2007). Soil pH explains some variation in local plant species richness in European woodlands (e.g. Večeřa et al., 2019) but its importance specifically for local alien plant richness is unknown. Human presence and disturbance at the landscape scale can accelerate alien plant invasions by enhancing propagule pressure and facilitating habitat edge effects (Vilà & Ibáñez, 2011; Conedera et al., 2018). Levels of invasion have been found to increase with landscape fragmentation (Ohlemüller et al., 2006), proportion of urban and industrial land (Chytrý et al., 2008a; Liendo et al., 2016), proximity to roads (González-Moreno et al., 2013), and human population density (Pyšek et al., 2010b; Spear et al., 2013; but see Carboni et al., 2010).

Many studies have revealed marked differences in the level of invasion across habitat types (e.g., Chytrý et al., 2005, 2008b; Campos et al., 2013; González-Moreno et al., 2014; Wagner et al., 2017; Giulio et al., 2020). Habitat types explained more variation (18%) in levels of invasion by neophytes (alien species that arrived in Europe after 1500 AD) than propagule pressure (3.1%) and climate (5.9%) in a study from the Czech Republic (Chytrý et al., 2008a). Habitat type was also the strongest predictor of alien plant invasions in Iberian vegetation (González-Moreno et al., 2014). This signal could reflect the integrating role of habitat type as a surrogate capturing the effects of both abiotic and biotic filters but might also reflect a confounding effect of the environmental variables that underlie habitat typologies, like elevation, landscape configuration, soil properties, or biotic interactions.

Identifying the main factors driving alien plant invasions is complex because invasions are dynamic processes and alien species pools are not fully saturated due to dispersal limitation (Brown & Peet, 2003). This could lead to invasion debt, i.e., a time lag between the introduction and spread of alien species (Essl et al., 2011, 2012). At a large scale, this could translate into hotspots of invasion among regions where introduction and spread have been frequent, and invasion debt among regions that are lagging in this respect (Ronk et al., 2017). Hence, an analysis of alien species richness and abundance using quantiles closer to the maximum could provide better insights than the more conventional analysis of the mean response (Brown & Peet, 2003).

Here, we are building on our previous work on alien plant invasions in European woodlands (Wagner et al., 2017) by analyzing a large data set of woodland vegetation-plot data stored in the European Vegetation Archive (Chytrý et al., 2016). Whereas our previous study focused on characterizing the alien species pool, this study aims to understand the possible drivers of alien plant invasion in European woodlands. Specifically, we asked: (a) How do relative alien species richness and sum of alien species covers change across regions, habitat types, environmental conditions, and human disturbance? (b) What is the importance of these predictors for explaining variation in alien plant invasions?

2 | METHODS

2.1 | Vegetation data

We extracted vegetation-plot data from the European Vegetation Archive (EVA, version 13 January 2016, see Appendix S1, Methods supplement, in Supplementary Information and Wagner et al., 2017 for details on data preparation). This data set contained plots from western, central and southern Europe, as well as Lithuania (Figure 1). For each vascular plant species in a plot, we assigned information on its status in the respective country (native, alien, or uncertain), with alien species defined as those that have been introduced after the year 1500 (i.e., neophytes sensu Thellung, 1915) and Raunkiær's life-form (e.g., hemicryptophytes, phanerophytes, therophytes). The data set encompassed data for plots surveyed in and after the year 1970 (53% collected after 2000) and was restricted to plots with an area ranging from 100 to 1,000 m² (or lacking plot size information, assuming that most of these plots were within this range; 77% of plots had a size of 100–500 m²). We assigned plots to European Nature Information System (EUNIS) woodland habitat types via a custom cross-walk (see Wagner et al., 2017 for details). The used version of the EUNIS habitat classification corresponds to that published in the European Red List of Habitats (Janssen et al., 2016). A cross-walk to the recently revised EUNIS version is provided by Chytrý et al. (2020). Only plots unambiguously assigned to a habitat type were included in the analysis.

Our study focused on the spontaneously established alien vascular plants rather than outcomes of deliberate planting. Hence, we excluded plots with alien tree and shrub species mostly known from planted populations (e.g., *Abies alba* in Belgium, *Pinus strobus* in Slovenia). We also removed plots with alien tree species that are naturalized but widely planted if they covered more than 20% in the tree layer or an unidentified vegetation layer. In addition, we also filtered out plots in which taxa with an uncertain status (native vs alien) had more than 20% cover (for details, see Wagner et al., 2017).

2.2 | Response variables

For each vegetation plot, we calculated two measures of the level of invasion: (a) relative alien species richness, defined as the percentage of the number of alien vascular plant species among all vascular plant species in a plot, and (b) absolute sum of alien species covers (in %) in a plot (see Appendix S1, Figure S1.1, in Supplementary Information for the frequency distribution of response variables). We chose relative alien species richness instead of the total number of alien species per plot because our data set included different plot sizes. If an alien species occurred in different vegetation layers, we included its absolute sum of covers across layers (alien species occurred in different layers only in

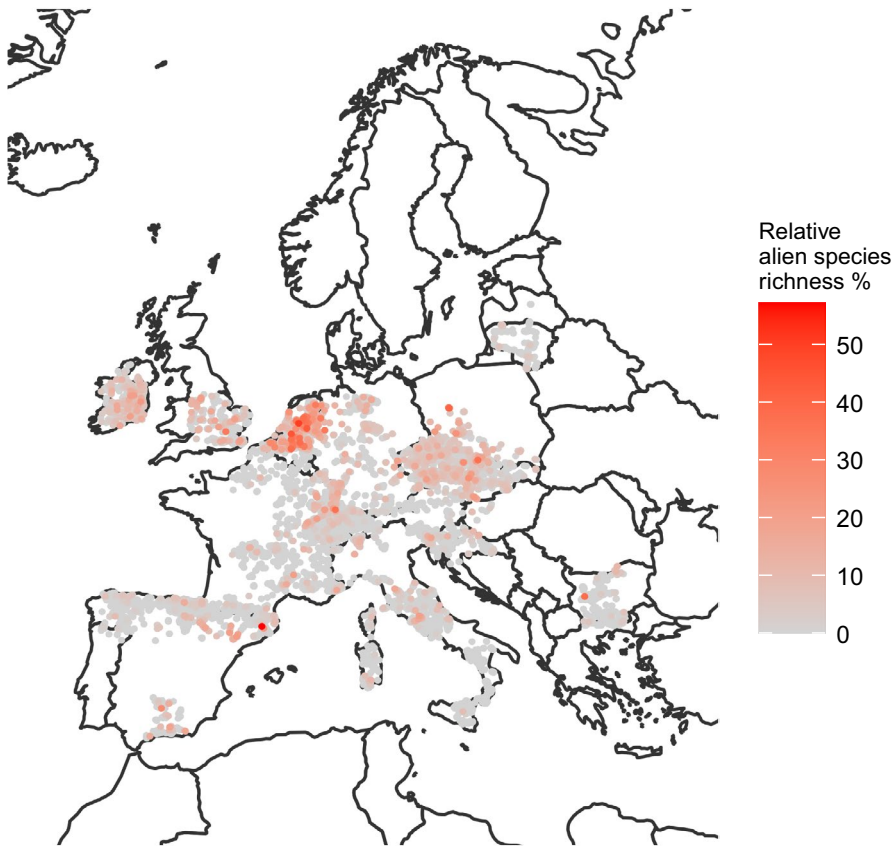


FIGURE 1 Location and relative alien species richness of vegetation plots included in the final data set ($n = 16,211$ plots)

16% of plots). We also considered the presence/absence of any alien species in a plot as a metric but dropped it since subsequent statistical models performed poorly, likely due to the overabundance of absences. In addition, we computed response metrics for five alien species groups: (a) all species; (b) all species except *Impatiens parviflora*; (c) phanerophytes; (d) hemicryptophytes; and (e) therophytes (including *Impatiens parviflora*). We removed *Impatiens parviflora* from one subset since it has a much higher frequency in European woodlands than any other alien species (Wagner et al., 2017) and could dominate the results. We focused on phanerophytes, hemicryptophytes, and therophytes because they represent the three most frequent life forms among alien vascular plant species in European woodlands (Wagner et al., 2017).

2.3 | Predictor variables

We considered 75 predictor variables for our analysis: habitat type, region, elevation, six climate variables and two Principal Component (PC) axes based on a PC analysis (PCA) of climate variables, four soil variables and two PC axes based on a PCA of these soil variables, and 50 human disturbance variables (including variables extracted for different spatial buffers) and eight PC axes based on PCAs of these human disturbance variables (two axes for each buffer category of 200 m, 500 m, 1,000 m and 2,000 m; Table 1). We hypothesized that patterns in our data could vary by region, possibly due to regional differences in alien plant introduction and planting history. To

test this hypothesis, we assigned plots to a grid of 250 km \times 250 km, with grid cell ID as a predictor factor with 41 levels. We chose this specific resolution because it was a compromise between capturing regional effects and limiting the total number of levels in this variable. Information on elevation was derived from the original records or, if missing, extracted with the *raster* package (Hijmans, 2019) in R (R Core Team, 2020) following Jarvis et al. (2008). We extracted climate variables that could potentially affect alien plant species distribution and abundance (BIO1: Mean annual temperature; BIO4: Temperature seasonality; BIO6: Minimum temperature of the coldest month; BIO10: Mean temperature of the warmest quarter; BIO12: Annual precipitation sum; BIO15: Precipitation seasonality) from the CHELSA data set, which has a resolution of 30 arc seconds (~ 1 km \times 1 km at the equator; Karger et al., 2017). Topsoil properties (pH and fraction of sand, organic carbon, and gravel) were retrieved from the Harmonized World Soil Database, which offers data at a 0.05° resolution (~ 5.5 km \times 3.9 km at the equator; Wieder et al., 2014).

We extracted several measures to capture human disturbance. Imperviousness (the percentage of sealed soil, including roads, buildings, parking lots and industry areas) was prepared from a raster data set of the Copernicus satellite program, which is based on an automatic derivation of calibrated Normalized Difference Vegetation Index (NDVI) in the year 2006 (European Environment Agency, 2013; 100 m \times 100 m resolution). Estimates of human population density were retrieved from a data set of the GEOSTAT initiative of the European Union (Eurostat, 2012), based on a

**TABLE 1** Overview of predictor variables

	Source	Data type
Habitat type (Appendix S1, Table S1.1)	Custom assignment based on Schaminée et al. (2014) and Janssen et al. (2016), see Wagner et al. (2017) for details	Categorical, 15 levels
Region (regional grid cells)	Custom calculation	Categorical, 41 levels (250 km × 250 km cells)
Environmental variables		
Elevation (m)	Original plot data, Jarvis et al. (2008)	Continuous, original entry or extracted from a raster of 90 m × 90 m resolution ^a)
BIO1: Mean annual temperature × 10 (°C)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
BIO4: Temperature seasonality (SD × 100)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
BIO6: Min. temperature of coldest month × 10 (°C)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
BIO10: Mean temperature of warmest quarter × 10 (°C)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
BIO12: Annual precipitation sum (mm)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
BIO15: Precipitation seasonality (CV)	Karger et al. (2017)	Continuous, extracted from a raster of 30 arcsec (~1 km × 1 km ^a) resolution
Topsoil pH	Wieder et al. (2014)	Continuous, extracted from a raster of 0.05° (~5.5 km × 5.5 km ^a) resolution
Topsoil sand fraction (% weight)	Wieder et al. (2014)	Percentage, extracted from a raster of 0.05° resolution
Topsoil organic carbon (% weight)	Wieder et al. (2014)	Percentage, extracted from a raster of 0.05° resolution
Topsoil gravel fraction (% weight)	Wieder et al. (2014)	Percentage, extracted from a raster of 0.05° resolution
Degree of human disturbance		
Imperviousness (%) (year 2006) = percentage of sealed soil	Copernicus (Geoland-2), EEA (2013)	Percentage, extracted from a raster of 100 m × 100 m resolution (mean, max. in buffer ^b)
Human population density (year 2011)	Eurostat 2012	Count, extracted from grid polygons of 1 km × 1 km ^b resolution (mean, max. in buffer ^b)
Degree of woodland fragmentation (m)	Custom calculation based on Copernicus (EEA, 2016)	Continuous, extracted from a raster of 20 m × 20 m (mean in buffer ^b)
Woodland edge complexity	Custom calculation based on Copernicus (EEA, 2016)	Continuous, extracted from a raster of 20 m × 20 m resolution (mean in buffer ^b)
Distance to the nearest road (km)	OpenStreetMap Contributors (2019)	Polyline vector
Distance to the nearest railroad (km)	OpenStreetMap Contributors (2019)	Polyline vector
Road density	Meijer et al. (2018)	Continuous, extracted from a raster of 5 arc minutes (~9 × 9 km ^a) resolution (mean, max. in buffer ^b)
Cover of human-dominated land-cover types (%), four different variables (Appendix S1, Table S1.1)	Aggregated CORINE land-cover types; Bossard et al. (2000)	Continuous, extracted from a raster of 500 m × 500 m ^b resolution (mean in buffer ^b)

Note: See Appendix S1, Methods supplement, for more details on data extractions.

Abbreviations: CV, coefficient of variation; EEA, European Environment Agency; Min., Minimum; Max., Maximum; SD, standard deviation.

^aAt equator.

^bExtracted within 200-m, 500-m, 1,000-m and 2,000-m buffer circles around plots.

1 km × 1 km grid for the year 2011. We calculated the level of woodland fragmentation and woodland edge complexity based on Copernicus satellite products (European Environment Agency, 2016; original resolution: 20 m × 20 m). To quantify fragmentation,

we used the area-weighted average patch size index (S_a ; Turner et al., 2001), computed as $S_a = \sum (S_k^2) / \sum (S_k)$, where S_k is the size of the k -th woodland patch within a spatial buffer. The larger the index, the larger the patch sizes within a buffer and the less

fragmentation. The complexity of woodland edges was quantified using Patton's diversity index (Patton, 1975), calculated as the perimeter of an individual woodland patch divided by the perimeter of a circle covering the same area as that of the focal patch. Values >1 indicate more complex patch edges and less interior woodland environment compared to the circular patch area. We estimated the proximity to the next propagule dispersal corridor by calculating the distance between plots and the closest road or railroad, respectively, in OpenStreetMap (OpenStreetMap Contributors, 2019). We considered all roads (motorways, trunks, primary, secondary, tertiary roads, residential streets) and all railroads (regular railroads, light rails, monorails, narrow gauges, racks, tram lines). Road density was extracted from global road density raster data (9 km \times 9 km resolution; Meijer et al., 2018). We estimated the cover of human-altered landscapes based on CORINE land-cover types (Bossard et al., 2000), which we aggregated into four groups: (a) intensive agricultural land cover; (b) artificial land-cover types I: artificial land cover potentially related to the spread of alien species; (c) artificial land-cover types II: theoretically the highest affinity to spread of alien species; and (d) all human-dominated land-cover types combined (see Appendix S1, Table S1.1 for more details). We hypothesized that human disturbance has an effect at the landscape level by influencing the area surrounding a plot. Hence, we used spatial buffers of 200 m, 500 m, 1,000 m, and 2,000 m when extracting mean values for human population density, imperviousness and road density (using QGIS; QGIS Development Team, 2019), and woodland fragmentation, woodland edge complexity, and the cover of human-dominated land-cover types (using ArgGIS; ESRI, 2011). For comparison purposes, we also extracted maximum values for imperviousness, human population density, and road density within the buffers in QGIS.

In addition, we constructed simplified and uncorrelated variables for three predictor groups (climate, soil, human disturbance) by calculating two ordination axes using PCA in the *vegan* package (Oksanen et al., 2018) in R (R Core Team, 2020; see details in Appendix S1). These single predictor variables and the PC axes were subsequently used as predictor variables in our bivariate analyses.

2.4 | Data filtering

After preparing our response and predictor variables, we took several data filtering steps. First, we included only plots with geographic coordinates and a location uncertainty of $\leq 1,000$ m (44% of plots in the final data set had an uncertainty of ≤ 500 m). However, plots that lacked information on location uncertainty but were surveyed after the year 2000 were included (33%), assuming that by that time, global positioning system (GPS) devices or accurate georeferencing were used to record plot locations. We reduced spatial clustering and sampling bias at the landscape and regional scales by randomly resampling up to 10 plots within a combination of 10 km \times 10 km grid cell and habitat type. Next, to balance out regional unevenness, we randomly selected up to 200 plots

for a combination of 250 km \times 250 km grid cell and habitat type. Regional grid cells with <100 plots were excluded from the analysis. *Fagus* woodlands on non-acid soils were much more common than other habitat types. To balance out this overrepresentation, we randomly resampled up to 200 plots of this habitat type per country. We finally excluded rare habitat types with <400 plots in the whole data set after resampling and deleted outliers (see Appendix S1). The final data set included 16,211 plots (Figure 1) and encompassed 15 EUNIS habitat types (see Appendix S1, Tables S1.2, S1.3 and S1.4 for an overview of databases, regions and habitats represented in the final data set).

2.5 | Bivariate relationships

We fitted standard generalized additive models (GAMs; Wood, 2011) and quantile GAMs (qGAMs; Fasiolo et al., 2017) to bivariate relationships between each of the two studied response variables on the one hand, and predictor variables on the other hand (both model types were run with a Gaussian error family). GAMs and qGAMs allowed us to explore trends using the original, untransformed variables. We used GAMs to inspect trends in average response rate and qGAMs to analyze values closer to the maximum response rates ($\tau = 0.90$ and 0.99). We included the qGAMs approach because our data were zero-inflated (alien plants were present only in 17% of plots), and we hypothesized that signals could be fitted better at higher quantiles rather than as averages. We ran GAMs and qGAMs using the R packages *mgcv* (Wood, 2011) and *qgam* (Fasiolo et al., 2017), respectively. Smoothing parameters were constructed using cubic regression splines with $k = 10$ dimensions and estimated with restricted maximum likelihood estimation.

2.6 | Variable importance

We used Random Forest (RF) analyses in the *randomForest* package (Liaw & Wiener, 2002) in R to assess the importance of predictor variables for structuring relative alien species richness and the sum of alien species covers. RF analysis is a machine-learning algorithm that averages predictions over several recursively partitioned decision trees based on bootstrapped data ("bagging"), creating a higher accuracy than decision trees. It uses a random subset of predictors for each tree to assess predictor importance in the presence of multicollinearity (Breiman, 2001). Nonetheless, collinearity was present when we included all predictor variables, as suggested by generalized variance inflation factors (GVIF, Appendix S1, Table S1.6), which could bias RF results (Dormann et al., 2013). Hence, we considered all predictor variables but only included those with a GVIF ≤ 2 in the RFs.

Each RF was based on 10,000 grown trees, with four randomly chosen predictors considered at each split, minimum node sizes of 40 plots, and randomization of cases without replacement. Variable importance was assessed based on out of bag (OOB) data, as the

average increase in squared OOB residuals when a variable in the OOB data is permuted (%IncMSE). The latter metric is unbiased compared to the increase in node purity, another metric reported by the package (Grömping, 2009 and references therein). To compare the importance of predictor variables for our two response variables, we normalized %IncMSE values across predictors to sum to 100% (Grömping, 2009).

3 | RESULTS

3.1 | Bivariate relationships

Both the relative alien species richness and the sum of alien species covers differed by habitat type (Figure 2). Differences were apparent in GAM estimates but amplified when using qGAMs at the maximum response rates ($\tau = 0.90$ and 0.99). According to GAM estimates, relative alien species richness was highest in temperate and boreal mountain *Betula* and *Populus tremula* woodland on mineral soils (G1.9a), acidophilous *Quercus* woodland (G1.8), *Fagus* woodland on acid soils (G1.6b), and temperate and boreal softwood riparian woodland (G1.1; Figure 2a). In general, habitats with low relative alien species richness had also low sum of alien species covers. However, the ranking based on the sum of covers was more nuanced for habitats with higher relative alien species richness, with temperate and boreal softwood riparian woodland (G1.1) having the highest sum of alien species covers (Figure 2b). In general, woodland habitat types at temperate latitudes, such as those listed above, had higher levels of invasion than Mediterranean or montane habitat types like Mediterranean

evergreen *Quercus* woodland (G2.1) and temperate and submediterranean montane *Pinus sylvestris*–*Pinus nigra* woodland (G3.4b).

The relative alien species richness and the sum of alien species covers differed across regional grid cells (Figure 3). In general, it was higher in northern than in southern regions and peaked in northwestern and central Europe. These regional patterns were consistent for relative alien species richness and the sum of alien species covers and for responses at the mean and $\tau = 0.99$ quantiles (Figure 3).

Relative alien species richness and the sum of alien species covers declined with increasing elevation, distance to the nearest road, and distance to the nearest railroad, and increased with maximum imperviousness (percentage of sealed soil cover) in 2,000-m buffers (Figure 4). However, these relationships were only pronounced when values closer to the maximum were analyzed ($\tau = 0.90$ and 0.99). None or only weak relationships were found in the analysis of average trends ($\tau = 0.5$; Figure 4). With respect to elevation, relative alien species richness declined at elevations of 0–750 m, whereas the sum of alien species covers showed a slight increase and then a decrease in this elevation range (Figure 4). Neither the relative alien species richness nor the sum of alien species covers showed a clear trend with climate and soil variables but displayed only local maxima along these gradients (Appendix S1, Figures S1.2 and S1.3).

A closer inspection of bivariate relationships between relative alien species richness and the sum of alien species covers on the one hand and elevation, distance to the nearest road, distance to the nearest railroad, and the mean annual temperature on the other, revealed that peaks were driven by regional signals. For all of these predictor variables, most plots that matched the maxima in relative alien species richness at $\tau = 0.90$ and 0.99 quantiles were from the



FIGURE 2 Differences in (a) the relative alien species richness and (b) the sum of alien species covers among EUNIS habitat types of European woodlands. Colored symbols are group estimates as fitted by generalized additive models (GAMs) and quantile GAMs (qGAMs) for quantiles $\tau = 0.90$ and 0.99 . In both figures, the habitat types are sorted in decreasing order according to coefficient estimates from qGAMs of relative alien species richness at $\tau = 0.99$ (panel figure a)

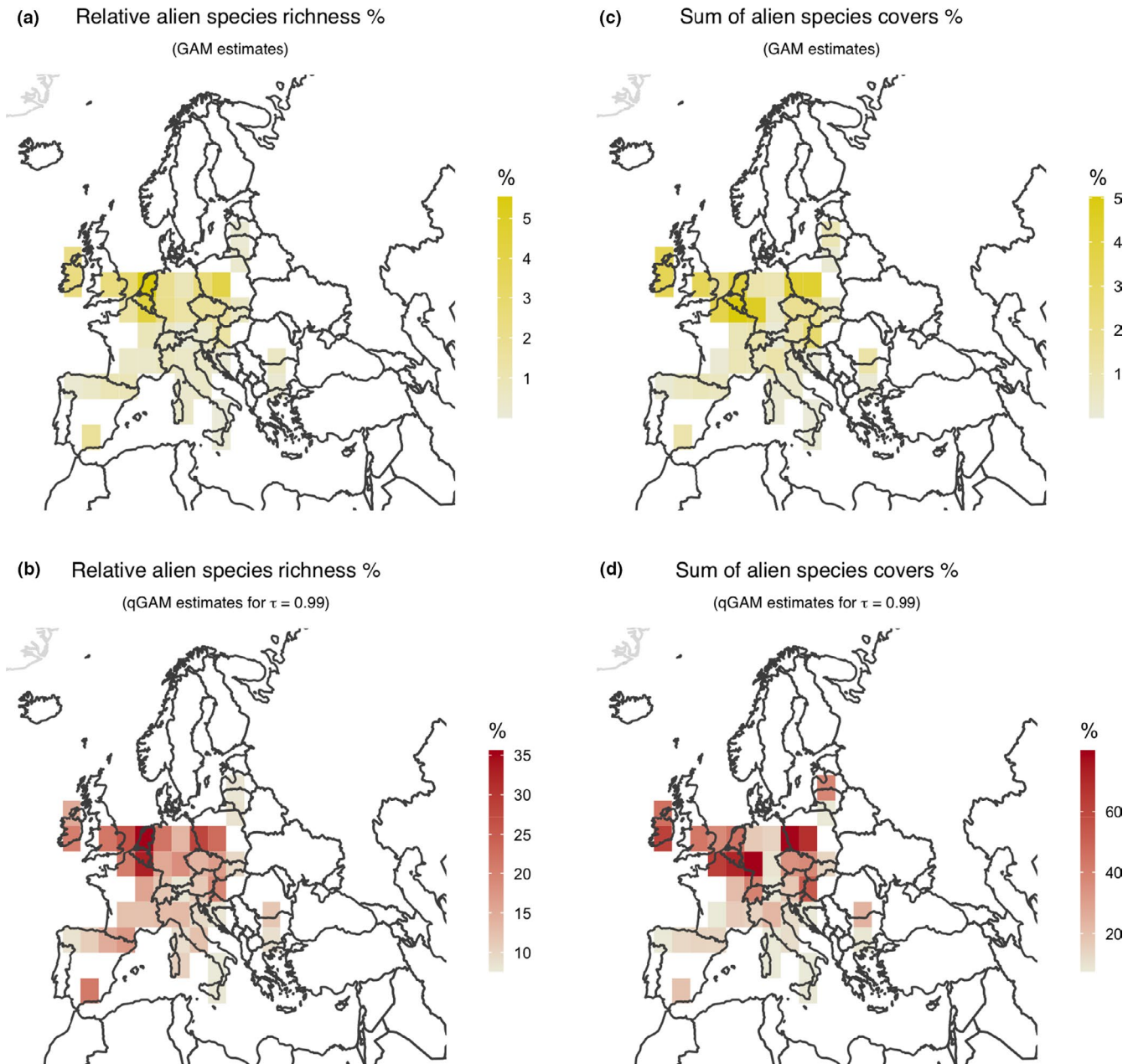


FIGURE 3 Differences in relative alien species richness (a, b) and the sum of alien species covers (c, d) among regional grid cells. Colored cells are estimates fitted by quantile generalized additive models (qGAMs) at quantile $\tau = 0.99$ with the factor variable “region” ($n = 41$ levels) used as the only predictor variable. Areas in white were not included due to insufficient data availability. Results for qGAMs at quantile $\tau = 0.90$ are not displayed since models failed to converge

Netherlands, Belgium, Poland and the Czech Republic (Table 2). Plots that were associated with maxima in the sum of alien species covers at these quantiles were from the Czech Republic, the Netherlands, and France (Table 3).

3.2 | Variable importance

The variables that we considered in our RFs models explained together 39.6% of the total variation in relative alien species richness.

By comparison, the total amount of variation explained for the sum of alien species covers was only 20.9% (Figure 5a, b). Habitat type and regional grid cells were the most important predictors ($> 10\%$) for both response variables. Variable importance and percentage of explained variation changed little when we removed *Impatiens parviflora* ($n = 15,214$ plots; Appendix S1, Figure S1.4a, b) or inspected patterns only among alien phanerophytes (Figure S1.4c, d). By contrast, when we analyzed only alien hemicryptophytes (Figure S1.4e, f) or alien therophytes (Figure S1.4g, h), the percentage of explained variation decreased.

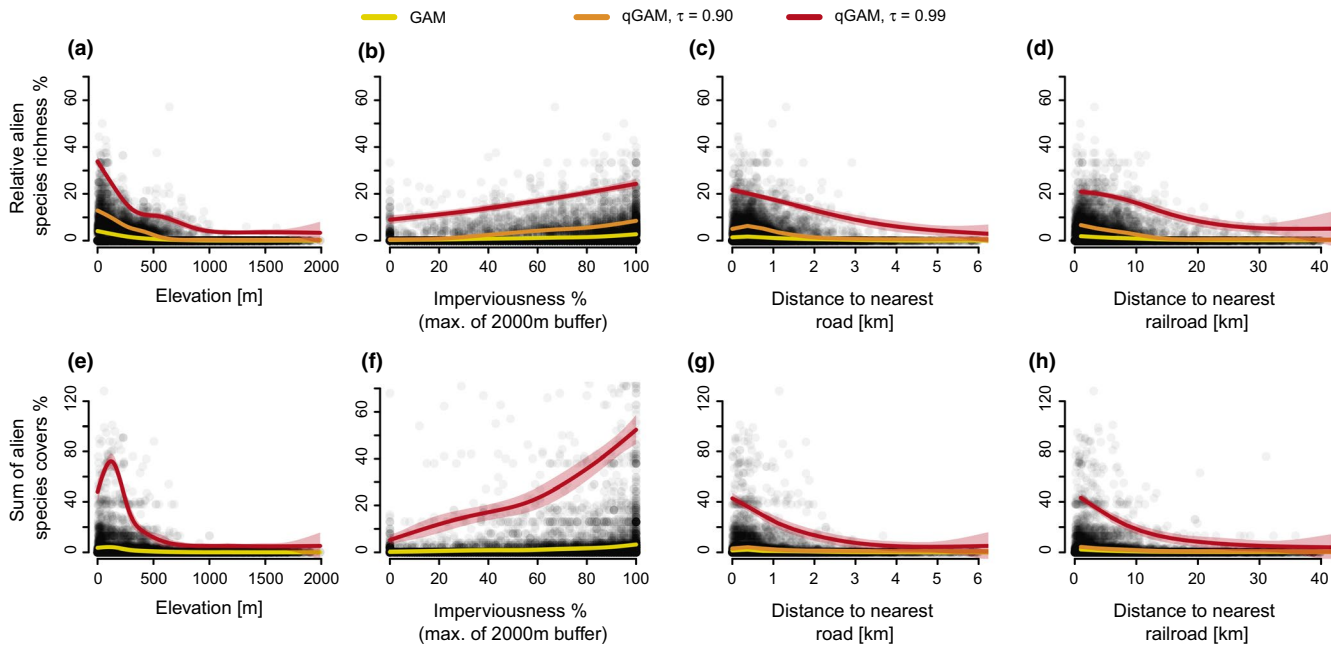


FIGURE 4 Bivariate relationships between (a–d) relative alien species richness and (e–h) sum of alien species covers with elevation, imperviousness (max. of 2,000 m buffer), distance to the nearest road, and distance to the nearest railroad. Lines were fitted using generalized additive models (GAMs) and quantile generalized additive models (qGAMs), with a 95% confidence interval. Only fits of converged models are shown. See Appendix S1, Figures S1.2 and S1.3 for relationships with all continuous predictors

4 | DISCUSSION

Several key findings suggest that European woodlands display regional hotspots of local alien plant invasion and that woodlands in some regions might not be fully saturated with alien species but rather experience invasion debt (Brown & Peet, 2003; Essl et al., 2012). First, although macroclimate is an important predictor of local plant species richness in European woodlands (Večeřa et al., 2019), it did not emerge as a significant driver of local relative alien species richness across European woodlands. Second, local levels of alien plant invasions differed strongly by region, with regional hotspots in northwestern and central Europe. Third, for continuous predictors that showed relationships with relative alien species richness and the sum of alien species covers (i.e., elevation, distance to the nearest road or nearest railroad, imperviousness), effects were only pronounced at higher quantiles and non-detectable at the average response of our response variables. When we looked closer at peaks in these relationships, the signal at the maximum quantiles was driven by vegetation plots located within regional invasion hotspots.

Interestingly, the regional hotspots that we detected broadly match hotspots of regional alien species richness described by Ronk et al. (2017). In contrast to our work, this study assessed richness at a coarser spatial resolution, based on species lists for 50 km × 50 km grid cells in Europe. This may imply that the magnitude of alien plant invasions at the local scale in European woodlands is influenced by regional differences in alien species pool size. In theory, the high estimates for the Czech Republic and France could be due to more intense sampling in these regions (% of plots in the final data set: 15.1%, 12.1%, respectively). Plots in the Netherlands and Belgium

made up only 5.9% and 2.2% of the final data set, respectively (Appendix S1, Table S1.3), albeit these countries are also smaller. Here, the high levels of invasion could also reflect the region's legacy as an invasion hub, especially the long history of international trade at its seaports and high density of traffic corridors (Eurostat, 2018). Another explanation is the lower richness in the native woodland flora in northwestern Europe (Večeřa et al., 2019). Since we used a relative measure of alien species richness (to account for different plot sizes), calculated as the number of alien species divided by all species in a plot, naturally species-poor forests could appear to be relatively more invaded. The lower magnitude of alien plant invasions in southern Europe is in line with patterns observed by Ronk et al. (2017) at a coarser spatial scale. The prevalence of summer drought in this region could make its woodlands more resistant to invasion. Alternatively, given the high rates of alien plant invasions in other regions with summer drought, like California (van Kleunen et al., 2015), our results could also imply that invasion debt is more prominent in southern European woodlands (Rouget et al., 2016). These hypotheses deserve more attention by researchers in the future. Furthermore, our study did not cover all of Europe and might have missed other regional patterns of local alien plant invasions in European woodlands.

Our results also join an increasing number of studies that found habitat type to be an important predictor of the magnitude of invasions (Chytrý et al., 2008a; Pyšek et al., 2010a; Pyšek & Chytrý, 2014; Dyderski & Jagodziński, 2019). Our study encompassed a smaller set of habitat types than Wagner et al. (2017) due to stronger data filtering. However, the trends in mean relative alien species richness among habitat types were broadly similar. For instance, the

TABLE 2 Regional origin of plots associated with peaks in $\tau = 0.90$ and 0.99 quantiles of relative alien species richness along selected predictor variables; peaks were defined as plots falling into the range of a predictor variable and the response quantile, as inspected for a bivariate relationship; n = no. of plots and % = percentage of plots in the peak; displayed are only the three regions with the highest plot numbers

≥0.90 quantile			≥0.99 quantile		
Region	<i>n</i>	%	Region	<i>n</i>	%
<i>Elevation: 0–500 m</i>			<i>Elevation: 0–500 m</i>		
Netherlands	344	22.2	Netherlands	72	42.6
Czech Republic	269	17.4	Belgium	45	26.6
Belgium	165	10.6	Poland	13	7.7
<i>Distance to nearest road: 0–2 km</i>			<i>Distance to nearest road: 0–2 km</i>		
Netherlands	338	25.3	Netherlands	70	40.5
Czech Republic	290	18.0	Belgium	45	26.0
Belgium	165	10.2	Poland	13	7.5
<i>Distance to nearest railroad: 0–10 km</i>			<i>Distance to nearest railroad: 0–10 km</i>		
Netherlands	329	21.4	Netherlands	70	41.4
Czech Republic	290	18.8	Belgium	42	24.9
Belgium	159	10.3	Poland	13	7.7
<i>Mean annual temperature: 8–12°C</i>			<i>Mean annual temperature: 8–12°C</i>		
Netherlands	344	24.7	Netherlands	72	43.6
Czech Republic	259	18.6	Belgium	45	27.3
Belgium	165	11.8	Poland	13	7.9

three highest-ranked habitats according to the mean (G1.1, G1.8, G1.9a), as shown by GAMs, were among the five highest-ranked habitat types in Wagner et al. (2017). The high levels of invasion in temperate and boreal softwood riparian woodlands are well known (Schnitzler et al., 2007). They can be linked to several habitat characteristics, including a high propagule pressure at low elevations, their role as dispersal corridors and intersections by roads and railroads, and their exposure to nutrient pulses, frequent disturbance, and light gaps due to flooding. The high rankings for acidophilous *Quercus* woodland and temperate and boreal mountain *Betula* and *Populus tremula* woodland on mineral soils are more surprising. In theory, they could be explained by native species richness per plot, which tends to be low in these habitat types (Wagner et al., 2017, their Appendix S5). However, in general, we did not find a significant correlation between mean alien species richness and mean native species richness per habitat type (Pearson's $r = -0.41$, $df = 13$, $P = 0.126$; calculated for the most frequent plot size of 100 m^2). In addition, the high levels of invasion in these habitat types may be due to their relatively open canopy cover, occurrence in regional invasion hotspots, higher local disturbance through management, and

TABLE 3 Regional origin of plots associated with peaks in $\tau = 0.90$ and 0.99% quantiles of the sum of alien species covers along selected predictor variables; peaks were defined as plots falling into the range of a predictor variable and the response quantile; n = no. of plots and % = percentage of plots; displayed are only the three regions with the highest plot numbers

≥0.90 quantile			≥0.99 quantile		
Region	<i>n</i>	%	Region	<i>n</i>	%
<i>Elevation: 0–500 m</i>			<i>Elevation: 0–500 m</i>		
Czech Republic	341	16.8	France	32	20.4
Netherlands	322	15.3	Belgium	25	15.9
France	152	14.6	Czech Republic	23	14.6
<i>Distance to nearest: 0–2 km</i>			<i>Distance to nearest: 0–2 km</i>		
Czech Republic	365	22.1	France	32	19.5
Netherlands	317	20.8	Czech Republic	28	17.1
France	159	11.2	Belgium	25	15.2
<i>Distance to nearest railroad: 0–10 km</i>			<i>Distance to nearest railroad: 0–10 km</i>		
Czech Republic	367	23.6	France	31	19.9
Netherlands	312	20.0	Czech Republic	27	17.3
France	156	10.0	Belgium	25	16.0
<i>Mean annual temperature: 8–12°C</i>			<i>Mean annual temperature: 8–12°C</i>		
Czech Republic	329	23.6	France	30	20.3
Netherlands	322	23.1	Belgium	25	16.9
France	147	10.5	Czech Republic	24	16.2

the ability of frequent alien species to colonize acidic soils and forest gaps, as displayed for example by *Prunus serotina* (Godefroid et al., 2005) or *Impatiens parviflora* (Chmura et al., 2007).

The magnitude of alien plant invasions in European woodlands decreased with increasing elevation. Similar signals at the local scale have been explained by declining propagule pressure or directional filtering. The latter process refers to an overrepresentation of taxa with a niche optimum at lower elevations within the species pool (e.g., Alexander et al., 2011; Pyšek et al., 2011). However, in our study, the decline of the levels of alien plant invasions with elevation could also be partly due to the confounding effect of region, with maxima reported from regional hotspots at low elevations, like the Netherlands.

Distances to the nearest road and railroad and cover of impervious surfaces were the only clear indicators of human-induced disturbance associated with the magnitude of alien plant invasions in European woodlands. In general, the decline of alien species richness and cover with increasing distances from these corridors supports the role of road and railroad traffic as a pathway for alien plant invasions (von der Lippe & Kowarik, 2008). Imperviousness showed a positive relationship with our response variable, but only when we extracted maximum imperviousness values in a 2,000-m buffer around the plot. This could reflect the importance of urban areas as propagule sources and as dispersal corridors (Klotz & Kühn, 2010) in the wider perimeter of woodlands. In our study, the effect of distances to the nearest road and railroad, and imperviousness, may

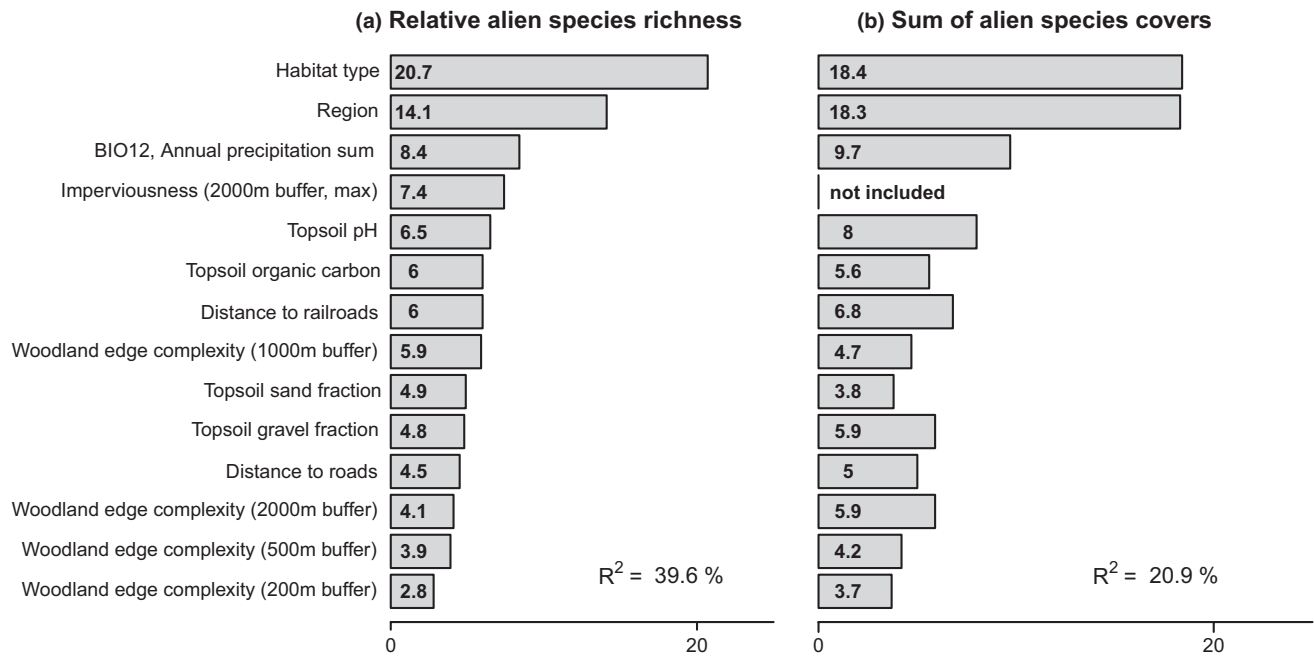


FIGURE 5 Importance of predictors for explaining (a) relative alien species richness and (b) sum of alien species covers when all aliens are included, assessed by Random Forest analyses. Bars show an average increase in the mean standard error (MSE), normalized across predictors to sum to 100%. Only predictors with a generalized variance inflation factor ≤ 2 were included to avoid multicollinearity. See Appendix S1, Figure S1.4 for importance values for other alien groups

also reflect a confounding effect with region. Northwestern Europe, where the magnitude of invasion was particularly high, has one of the highest road and imperviousness densities in Europe (Eurostat, 2018; European Environment Agency, 2021).

Surprisingly, our study did not detect a link between alien plant invasions and other human disturbance predictors, including population density, woodland fragmentation and edge complexity, and the cover of human-dominated land. We hypothesize that other factors, like introduction and planting history, could override the importance of human disturbance at the landscape scale. For instance, given that trees and shrubs are over-represented in the European alien woodland flora compared to natives (Wagner et al., 2017), our finding could echo the large-scale planting of this group in the mid-18th to early 20th century (Bucharova & van Kleunen, 2009; Nyssen et al., 2016). Well-known examples are the planting of *Prunus serotina* (Schrader & Starfinger, 2009; Nyssen et al., 2016) and *Robinia pseudoacacia* (Vítková et al., 2017) in northwestern and central Europe. This hypothesis is supported by Bucharova and van Kleunen (2009) and Pyšek et al. (2009), who found planting frequency to be the most important predictor of the success of alien trees in Europe. Planting could have removed landscape filters and facilitated the spread of alien phanerophytes into European woodlands. Furthermore, our proxies of human disturbance at the continental scale were available only at the turn of the 21st century, roughly when 50% of our vegetation plots had been sampled. However, invasions may be the result of much earlier human disturbance activities. Linking our data to historic disturbance and planting data could have explained more variation, but such data are more difficult to gather at the European extent.

Soil properties explained only a small amount of variation in our data. It is possible that their spatial resolution ($\sim 5.5 \text{ km} \times 3.9 \text{ km}$) was too coarse to detect any signal in the data. Linking our data to soil information at a finer spatial resolution might have improved models, but such data were not available and are generally underrepresented or recorded inconsistently in vegetation databases. Future studies that couple vegetation surveys with detailed analyses of soil abiotic and biotic properties could shed more light in this respect.

RFs predicted 39.6% and 20.9% of the variation in relative alien species richness and the sum of alien species covers, respectively. The lower variance explained in the latter response variable is likely due to a higher imprecision in cover estimates compared to species richness estimates, and to a stronger influence of effects not captured in our models, such as local disturbance (Chabrierie et al., 2008). In addition, we considered only single effects in driving alien plant invasions. However, invasion patterns are driven by interactions of multiple effects (Thuiller et al., 2006; Pyšek et al., 2015). An analysis of interactions between habitat type and human disturbance, in particular, could reveal whether some habitat types are more prone to invasions under increased human disturbance.

5 | CONCLUSIONS

Alien plant invasions in European woodlands display regional hotspots and signs of regional invasion debt. Their magnitude depends on the woodland habitat type and is linked to transportation corridors and the extent of urban areas in the region. Looking into the future, our results imply that alien plant invasions will continue to

expand in European woodlands, likely driven by the complex effects of regional introduction history, factors associated with differences between habitat types, and the prevalence of dispersal corridors and urban areas. A challenge for future research is to clarify the role of local and historic factors as drivers of alien plant invasions. Avoidance strategies, such as regulations of alien plant introductions and plantings (Brundu & Richardson, 2017; Pötzelsberger et al., 2020), must be key components for the protection of European woodlands from future invasions. Given that alien plant invasions are dynamic processes and will likely proceed further, we advocate for continuous surveys in European woodlands at the local and regional scales.

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AUTHOR CONTRIBUTIONS

VW and MC conceived the idea and developed the study design. VW and MV prepared the data. VW carried out the statistical analysis, with feedback from co-authors, and led the writing. All co-authors supplied data, contributed information on species status and life-form assignments, and helped develop the manuscript.

DATA AVAILABILITY STATEMENT

Vegetation-plot data used in this study are stored in the European Vegetation Archive with reference to project no. 1 (2014-05-31). Accompanying data and R scripts can be accessed at https://figshare.com/articles/dataset/R_scripts_and_data_files/13697329.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Methods supplement, supplementary tables and figures.

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