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RESEARCH ARTICLE

Spatial scale matters for predicting plant invasions along roads

Dorota Kotowska[1,2,3] | Piotr Skórka[1] | Tomas Pärt[4] | Alistair G. Auffret[4] | Michał Żmihorski[5]

[1]Institute of Nature Conservation, Polish Academy of Sciences, Kraków, Poland

[2]'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary

[3]National Laboratory for Health Security, HUN-REN Centre for Ecological Research, Budapest, Hungary

[4]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[5]Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

Correspondence
Dorota Kotowska
Email: kotowska@iop.krakow.pl

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Abstract

1. Biological invasions threaten global biodiversity and can have severe economic and social impacts. The complexity of this problem challenges effective management of invasive alien species as the contribution of many factors involved in the invasion processes across different spatial scales is not well understood.
2. Here, we identify the most important determinants associated with the occurrence of two invasive alien plants, the North American goldenrods (*Solidago canadensis* and *S. gigantea*), commonly found in agricultural landscapes of Europe. We used Google Street View images to perform a remote, large-scale inventory of goldenrods along 1347 roadside transects across Poland. Using open access geospatial data and machine learning techniques, we investigated the relative role of nearly 50 variables potentially affecting the distribution of studied species at five spatial scales (from within 0.25 to 5 km of the studied locations).
3. We found that the occurrence of goldenrods along roadsides was simultaneously associated with multiple drivers among which those related to human impacts, climate, soil properties and landscape structure were the most important, while local characteristics, such as road parameters or the presence of other alien plants were less influential. However, the relative contribution of different variables in predicting goldenrod distribution changed across spatial scales.
4. *Synthesis*: Mechanisms underlying plant invasions are highly complex and a number of factors can jointly influence the outcomes of this process. However, since different invasion drivers operate at different spatial scales, some important associations may be overlooked when focusing on a single spatial context. Although associations were consistent in direction (positive or negative) across scales, their relative influence on goldenrod occurrence often changed. Socio-economic factors were largely important at local scales, while the effect of landscape factors broadly increased with increasing spatial scale. We highlight that using multi-scale approaches involving a wide range of variables may enable setting priorities for the management of invasive alien plants.

KEYWORDS
anthropogenic pressures, farmland, goldenrods, Google Street View, invasion ecology, roadsides, spatial scale

1 | INTRODUCTION

The phenomenon of biological invasions is a major fingerprint of the Anthropocene, contributing substantially to global human-induced environmental change and threatening both biodiversity and human welfare (IPBES, 2019; Kueffer, 2017; Pyšek et al., 2012). The spread of alien species has been shown to alter the structure and functioning of ecosystems (Hejda, Pyšek, & Jarošík, 2009; Levine et al., 2003), causing extinctions of indigenous fauna and flora (Blackburn et al., 2019) and reducing services that native ecosystems provide for human wellbeing (Kumar Rai & Singh, 2020). These changes are difficult to reverse and have already caused serious economic damage (Diagne et al., 2021). Moreover, the adverse effects of biological invasions are predicted to become exacerbated as the climate, landscape and socio-economic factors are also rapidly changing across the globe (Early et al., 2016; With, 2002). Therefore, an understanding of the different environmental and anthropogenic drivers of invasions is important to deliver guidance on how to manage invasive alien species and prevent new invasion events in the future.

Biological invasions are mainly caused by human activity. For several hundred years, the transfer of plant species outside of their native ranges has been driven by cross-border trade, leading to both intentional and accidental introductions (Hulme, 2009). As such, the main predictor of invasion success has often been found to be the invasion pathway, that is, the method and frequency by which a species has been introduced (Wilson et al., 2009). Human activity is also a strong predictor of invasion processes following the introduction stage, because the establishment and subsequent spread of alien species is commonly associated with anthropogenic habitats (Hejda, Pyšek, Pergl, et al., 2009). Furthermore, it has been recognized that plant invasions are also influenced by landscape structure (Melbourne et al., 2007; With, 2002), including the presence and configuration of human-modified landscape features such as roads, watercourses, built-up areas and abandoned agricultural fields (Kotowska et al., 2021; Lenda et al., 2012). Such land use and landscape characteristics represent not only suitable habitats for alien plants, but also potential source pools and pathways for further invasions (Kotowska et al., 2022; Vilà & Ibáñez, 2011; Warren et al., 2013). In contrast, semi-natural habitats, such as grasslands and woodlands are usually more resistant to establishment of alien plant species (Chytrý et al., 2008).

Climate change is another, growing anthropogenic driver of biological invasions (Diez et al., 2012). Alien plants that have been introduced by humans may become invasive as the climate changes to provide more favourable temperatures, humidity, precipitation or solar radiation (Hulme, 2017). Climate models generally predict invasive species to change their ranges in relation to spatial and temporal changes in climate (Bellard et al., 2018). Still, it is expected that human-mediated long-distance transport and anthropogenic habitat modifications are the major drivers of biological invasions (Hulme, 2017). Also, human population density, income and various other socio-economic indices have been shown to be positively associated with regional numbers of alien plants (Pyšek et al., 2010).

Together, both climate change and human-related land-use alterations lead to modifications in the quality, availability and configuration of habitat resources, and can thus influence plant invasions (Schroeder et al., 2021). Soil properties (e.g. high nitrogen content, acidity) may positively impact invasion of alien plants which, in turn, may also affect nutrient pools in the topsoil and the standing biomass, generally contributing to a homogenization of soil conditions (Dassonville et al., 2008). This 'ecosystem engineering' can then act to facilitate further invasions, although interactions among potentially invasive species can also be an important determinant of whether multiple invasions occur (Lenda et al., 2019). It has been suggested, for instance, that successfully established non-native species may facilitate the establishment of other alien species, thus accelerating the invasion process (the so-called 'invasional meltdown' process; Simberloff & Von Holle, 1999). Moreover, these phenomena may be additionally mediated by soil microorganisms which can influence soil nutrient availability, potentially promoting alien plant invasions (Dawson & Schrama, 2016). However, the relative role of associations among alien plants, environmental drivers and human activity in supporting invasions of alien plants is not clearly understood.

The processes that regulate the introduction, establishment and spread of alien species are clearly highly complex and involve a multitude of factors (Catford et al., 2009). In addition to the many ways in which these different factors affect biological invasions, they also operate at different spatial scales (Czarniecka-Wiera et al., 2020). At large spatial scales (regional level), one expects the effect of climate and human impacts to be most prevalent (Shi et al., 2010). At intermediate (landscape) spatial scales, landscape characteristics may become more important, whereas the impact of local characteristics, such as biotic interactions is likely most pronounced at small, local spatial scales (Catford et al., 2009; Milbau et al., 2009). Hence, depending on the spatial context, the relative importance of different factors enabling/promoting establishment and distribution of invasive alien plants is likely to vary (Ricklefs & Jenkins, 2011). Most empirical studies on the drivers of plant invasions, however, have focused on a single spatial scale (but see: Brown et al., 2008, Kotowska et al., 2022).

Given the number of factors and underlying mechanisms potentially involved in success of invasive alien plants, the pressing issue of predicting their distribution remains a challenge. Dealing with this

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problem requires an integrative approach (Barney & Whitlow, 2008), but many studies are limited by the number of drivers that are covered, and the joint and relative effects of multiple invasion drivers have rarely been examined (but see: Szymura et al., 2018). More comprehensive approaches accounting for the simultaneous role of multiple drivers of invasions across different spatial scales are therefore needed.

Here, we investigate the relative importance of multiple factors associated with occurrence of common invasive alien plants across different spatial scales. We used invasive North American goldenrods (*Solidago* spp.) as model species and collected data on their occurrence along roadside transects in agricultural landscapes of Poland by applying a novel and reliable method based on remote analysis of Google Street View (GSV) images (Kotowska et al., 2021). We tested how local roadside invasion patterns are influenced by multiple characteristics of the environment and its anthropogenic pressures by associating invasive goldenrod occurrences along roads with 49 variables potentially affecting their distribution. These were grouped into seven categories that included human impacts, landscape structure, climate characteristics, soil properties, abundance and diversity of other alien plant species, road characteristics and transect sampling parameters. As the impact of the considered invasion drivers was expected to be scale dependent, we tested their effect on the probability of goldenrod occurrence across different spatial scales, ranging from 0.25 to 5 km of the studied locations.

2 | MATERIALS AND METHODS

2.1 | Model species

Canadian goldenrod (*Solidago canadensis* L.) and giant goldenrod (*S. gigantea* Aiton) are two highly successful plant invaders of North American origin that have colonized a broad range of European landscapes (Weber, 2001). Due to their high competitive ability with efficient seed production, rapid growth, prolific rhizome propagation and capacity to exert allelopathic effects on other plants, they can dominate native vegetation over vast areas forming dense, homogeneous stands (Kabuce & Priede, 2010). Consequently, the spread of these two goldenrod species can lead to a drastic reduction of native plant diversity (Hejda, Pyšek, & Jarošík, 2009; Lenda et al., 2019; Moroń et al., 2009; Pal et al., 2015) and can adversely affect several other species groups, including pollinators (such as bees, hoverflies and butterflies; Lenda et al., 2019, 2021; Moroń et al., 2009, 2021). Goldenrods are found in a wide spectrum of habitats. They occur abundantly both in human-disturbed habitats, such as roadsides, railway embankments, abandoned agricultural lands and ruderal environments associated with built-up areas, as well as in semi-natural grasslands, meadows, forest edges and riverbanks (Kabuce & Priede, 2010; Perera et al., 2021). Since both goldenrod species are similar in morphology and habitat preferences within their secondary range (Perera et al., 2021), we consider them together in this study (and refer to them as 'goldenrods').

2.2 | Study area and transect selection

The study was conducted along roads in agricultural lowland landscapes across the country of Poland (Figure 1). The two goldenrod species are widespread throughout this area with locally high abundances (Lenda et al., 2019; Moroń et al., 2009). For the purpose of roadside transect selection, out of the total of 2478 local administrative units in Poland ('communes', the number represents the total in 2017), we first chose all 1555 rural communes (i.e. those within which there are no cities, as defined by the Central Statistical Office for Poland). Next, to restrict the study area to lowland regions, we excluded 195 communes in which 70% of the commune's area was at an altitude of over 300 m a.s.l., according to the European Digital Elevation Model (available through the Copernicus Land Monitoring Service; https://land.copernicus.eu/). Finally, using GSV imagery via the Google Maps web mapping service, we excluded 13 communes with no GSV coverage. As a result, we selected a total of 1347 communes, in which transects of about 500 m in length were set following the approach described in Kotowska et al. (2021). In each commune, we randomly selected a point along the road network using GIS tools and Open Street Map vector data, and then used it as the location to start a transect. If GSV images were not available for the transect, or more than 50% of the transect length intersected patches of forest, water bodies or urban areas (as identified by the CORINE Land Cover database), it was discarded and the next randomly selected transect in the commune was used instead. The transect was also discarded and replaced when the visibility of roadside vegetation was reduced by, for example, the presence of acoustic barriers. Consequently, the resulting set of 1347 transects established across Poland (mean nearest neighbour distance: 8384 m, range: 990–32,685 m) included roads of different classes (from highways to minor roads), intersecting a range of agricultural habitats. The studied locations were surrounded by farmland landscapes differing greatly in their structure and level of land-use intensity, including large, intensively managed arable fields, pastures and meadows, as well as heterogeneous landscape mosaics composed of small-scale arable fields with different crops, orchards, meadows and low-intensity grazed pastures mixed with patches of other semi-natural and natural open vegetation, marshes, woodlands, wastelands and scattered farmsteads. The selected transects also represented a climatic gradient from suboceanic climate in north-western Poland to continental climate in east and south-eastern part of the country (Kożuchowski, 2011). Spatial data processing was carried out using ArcGIS 10.4.

2.3 | Alien plant species sampling

Large-scale data on distribution of goldenrods and other alien plant species were gathered remotely using Google Street View images. This novel, time- and cost-efficient method for studying roadside vegetation has been proven to be reliable in relation to field inventory data and has been suggested as a tool for

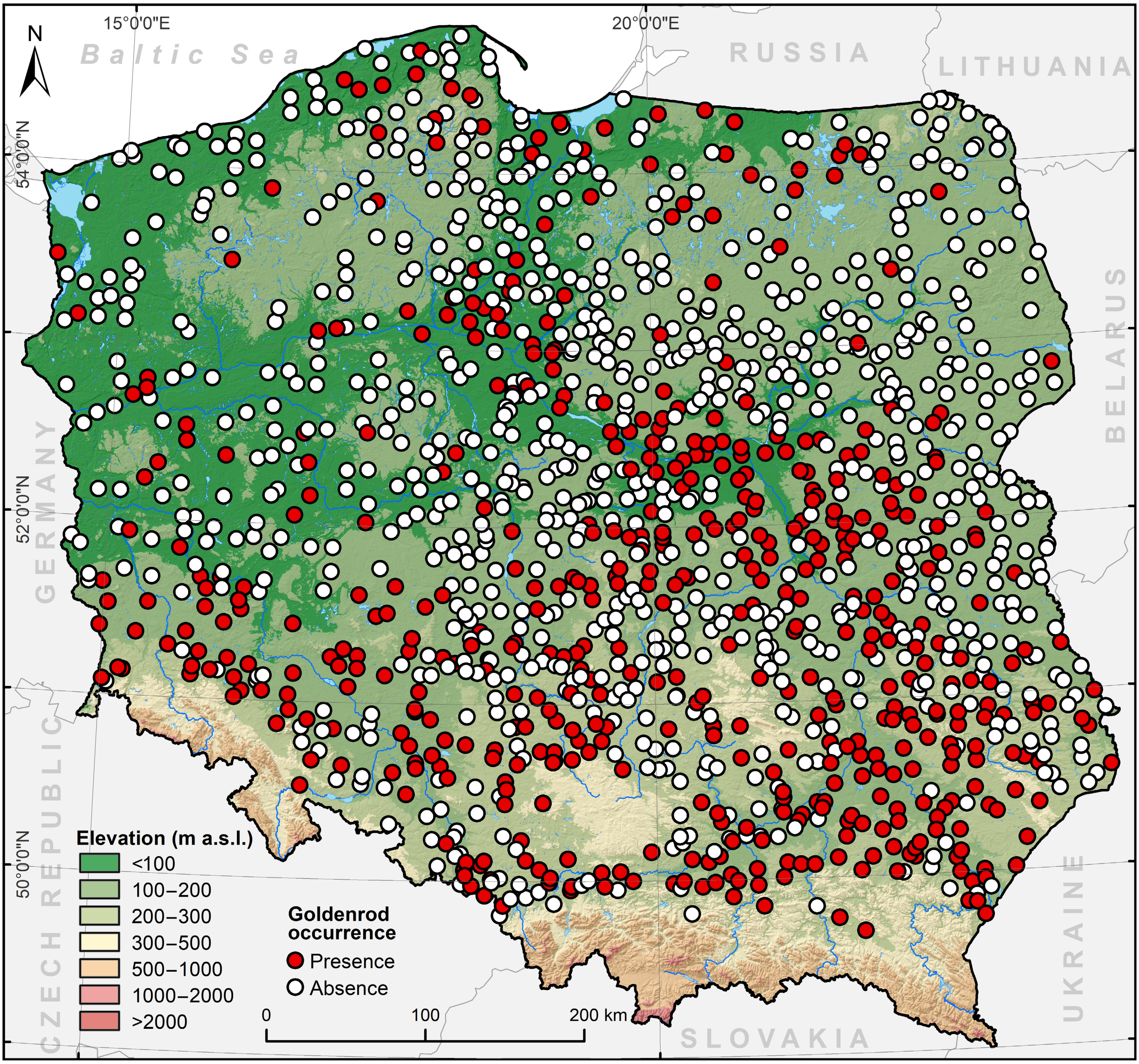

FIGURE 1 Distribution of 1347 transects sampled for goldenrod occurrence in agricultural landscapes across Poland.

detecting invasive alien plants occurrences over large areas (but see Kotowska et al., 2021 for a discussion of its limitations). Each of the 1347 transects was divided into (on average) 25 sections of around 20 m length (Figure 2b). Next, using Google Earth, the transects were sampled for goldenrods and other alien plant species by virtually 'driving' along the road and visually analysing GSV images. The remote data collection was performed based on the panoramic views taken between 2011 and 2018. For each transect section, we determined the occurrence of goldenrods and other identified alien plants (0/1) within 30 m of a transect line. Since the maintenance of roadside vegetation may reduce the probability of plant detection, for each transect section we also assessed the presence of recent road verge mowing (0/1) within 30 m of the road. The 30 m zone was considered mown if the vegetation covering more than 50% of this area had been recently cut, as judged by not yet being fully re-grown in height. The information on road verge mowing along a whole transect was quantified as a proportion of transect sections considered mown. Additionally, for each transect, we noted the date at which GSV pictures were taken and the information on road surface material (asphalt/other). Based on the transect section-scale observations, we determined the goldenrod occurrence (0/1) and the abundance and diversity of other alien plant species that could be detected along a transect (e.g. box elder, black locust, Canadian horseweed; see Appendix S1: Table A.1 for a full species list). Abundance was calculated as the proportion of transect sections occupied by each of the alien plant species.

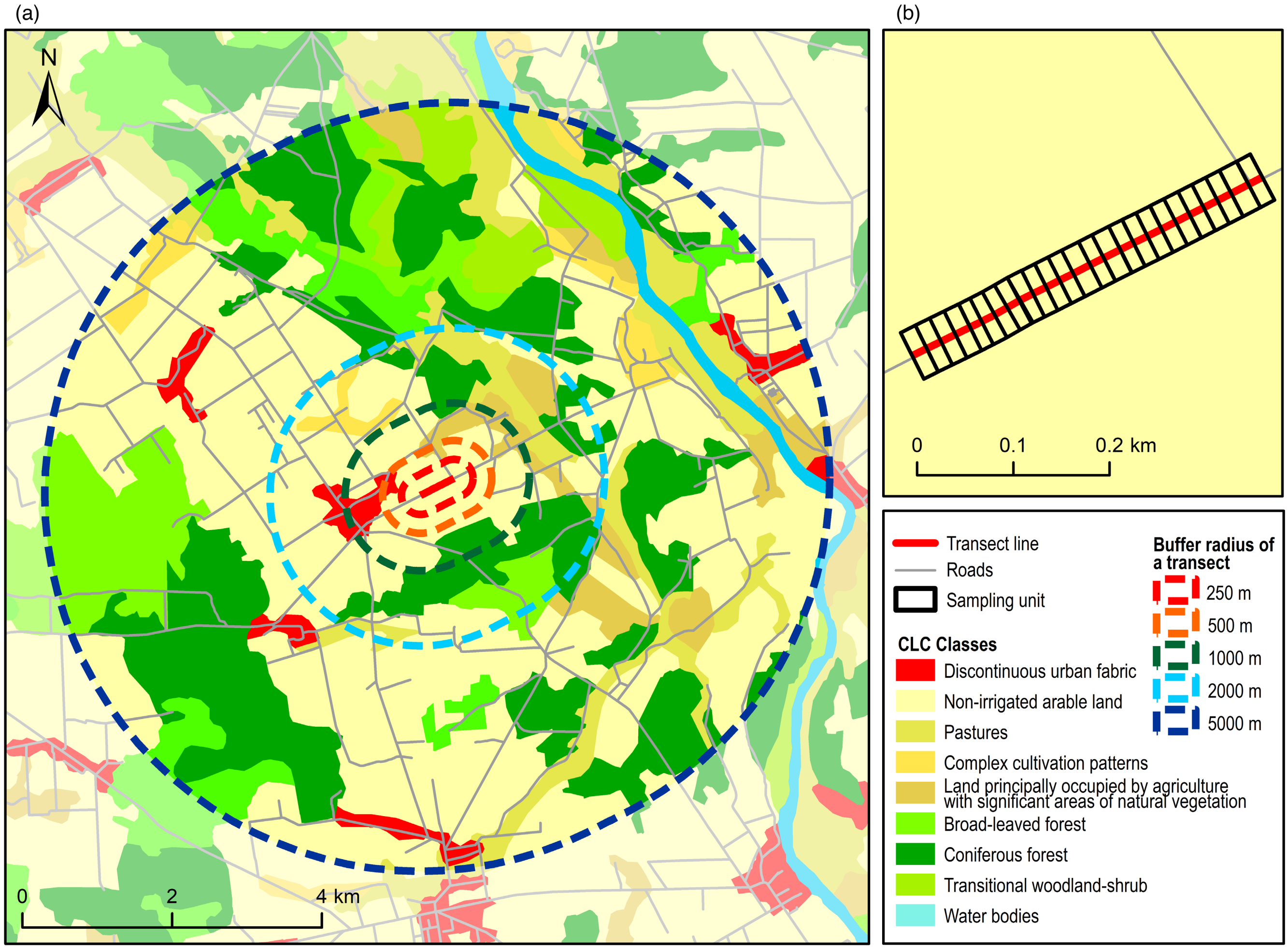

FIGURE 2 An example study location; five spatial scales (i.e. buffer zones of a transect line) at which the plant invasion drivers were analysed (a) and 25 transect sections surveyed for alien plant occurrence within 30 m of a transect line (b).

2.4 | Environmental and human activity-related data

Initially, we considered a set of 62 characteristics grouped into seven categories as explanatory variables potentially explaining goldenrod occurrence along roads in agricultural landscapes of Poland (not all of them were finally used in the analyses; see Section 2.5 for explanations, and Table 1 for a list of variables used in the models and Appendix S1: Table A.1 for a full list of 62 initially considered characteristics). First, variables describing human impacts (i.e. socio-economic indices, Human Footprint Index, agricultural intensity) were included, as the level of goldenrod invasion is generally mediated by human activity. Second, characteristics of landscape structure (e.g. cover of land-use types, landscape heterogeneity indices, distance to watercourses, road density) were used as proxies of the amount of suitable habitat and potential dispersal corridors in the vicinity of the studied transects. Third, topsoil chemical and microbial properties (pH, content of calcium carbonates, phosphorus, potassium and nitrogen, potential microbial basal respiration, microbial biomass) were considered as parameters describing habitat conditions in the areas surrounding transect locations. Fourth, we considered climatic factors (i.e. mean temperature, precipitation, solar radiation and growing season length), as goldenrod occurrence may be more likely in areas characterized by warm temperatures, humid conditions and high solar radiation (Park et al., 2020). Fifth, since biotic interactions among alien plants may intensify their ecosystem impacts and/or promote secondary invasions by other species (Simberloff & Von Holle, 1999), we considered indices describing the abundance and diversity of alien plant species other than goldenrods that were observed along the transects (13 species in total; the number of other alien plant species recorded along a transect ranged between 0 and 5). Sixth, we assumed that the importance of roadsides constituting major dispersal corridors for invasive alien plants (Lázaro-Lobo & Ervin, 2019) may be enhanced by certain road characteristics, for example, those related to high traffic volumes (the number of vehicles passing road section per day) or traffic speed (Joly et al., 2011; Lemke et al., 2019). Thus, we described several parameters of studied roads associated with these characteristics (i.e. road class, road width, road curvature, road direction, road surface). Finally, we also included transect sampling parameters (i.e. month and year when the GSV pictures

TABLE 1 List of variables used in goldenrod occurrence modelling. Full description and data sources are given in Appendix S1: Table A.1.

Category (scale)	Variables
Human impact (within 250, 500, 1000, 2000 and 5000 m of a transect)	Human Footprint Index (HFI), agricultural intensity index, income per capita, population density, citizens >65, proportion of women, higher education rate
Climate (within 250, 500, 1000, 2000 and 5000 m of a transect)	Mean temperature, precipitation, solar radiation, growing season length
Soil (within 250, 500, 1000, 2000 and 5000 m of a transect)	Soil pH, soil $CaCO_3$ content, soil P content, soil K content, soil N content, basal respiration, microbial biomass
Landscape (within 250, 500, 1000, 2000 and 5000 m of a transect)	Landscape composition, landscape configuration, artificial surfaces, arable land, pastures, heterogeneous agricultural areas, forests, semi-natural habitats, wetlands and water bodies, river density, road density, urban areas, grasslands, water and wetness, wastelands, Normalized Difference Vegetation Index (NDVI)
Landscape (distance)	River distance, urban distance
Road (along a transect)	Road width, road curvature, road direction, road class
Transect (within 30 m of a transect)	Mown road verge, transect sections, year of GSV picture, month of GSV picture
Alien species (within 30 m of a transect)	Box elder abundance, black locust abundance, Canadian horseweed abundance, diversity of alien plants (of a total of 13 species)

were taken, number of sections established along a transect line and information on road verge mowing) to account for potential bias arising from remote data collection with GSV panoramas (Kotowska et al., 2021).

These variables were either determined based on the GSV data inspection or calculated using GIS tools based on open geospatial data available for the study area (such as satellite imagery, Open Street Map vector layers, Corine Land Cover database, WorldClim database and other datasets mostly derived from national or European government agencies; see Appendix S1: Table A.1 for the detailed description of variables and data sources). The characteristics that were site specific, that is, abundance and diversity of other alien plant species, road parameters as well as transect sampling parameters, were determined at the transect scale only (i.e. along or within 30 m of the road). Large-scale variables (i.e. human impacts, landscape structure, soil properties and climatic conditions) were measured at five spatial scales, that is, within buffer zones of 250, 500, 1000, 2000 and 5000 m of the studied transects (Figure 2a; except for two distance-based characteristics, see Table 1). The spatial data processing and calculations were performed using ArcGIS 10.4 software, Google Earth Engine platform, and packages: 'raster' (Hijmans, 2022) and 'sf' (Pebesma, 2018) in R (R Core Team, 2020).

2.5 | Statistical analyses

To determine the relative importance of the considered variables for the probability of goldenrod occurrence across different spatial scales we used random forest (RF) models implemented in 'caret' package (Kuhn, 2022) in R. Prior to the analyses, the dataset was filtered to remove near zero variance predictors and highly correlated variables (i.e. those with Pearson's correlation coefficient > 0.9; da Silva et al., 2020). Consequently, out of the total of 62 characteristics, 49 were used in the further analyses (see Table 1). We performed five RF classification models, one for each of the spatial scales at which the large-scale factors were measured. In each model, we used the goldenrod occurrence along a transect (1—presence, 0—absence) as the response variable and each transect as a single data record (1347 in total). In all models, we considered a set of 49 predictor variables which consisted of local factors (four variables describing the abundance and diversity of other alien plant species, four road parameters and four transect sampling parameters), two distance-based variables characterizing landscape structure, and large-scale factors calculated for a given spatial scale (16 characteristics of landscape structure, eight indicators of human impacts, four descriptors of climatic conditions and seven characteristics of soil properties). For each RF model, we set the number of decision trees to 2000. The *mtry* parameter (i.e. the number of randomly selected features to be used at each tree node split) was set to 7, which is the default value calculated as the square root of the total number of variables used in each model (James et al., 2013).

Performance of each of the five RF models was assessed using 10-fold cross-validation, repeated five times. Since the spatial structure in the data can lead to the underestimation of model prediction error, we used spatial blocking to account for this problem while validating our models (Roberts et al., 2017). In this approach, the k-fold cross-validation procedure divides a dataset into k spatially separated folds based on a specified distance (cell size of the blocks; Valavi et al., 2019). Each fold is given an opportunity to be used as a held back test set, while all the remaining folds are used for model fit. The procedure is repeated k times and the mean performance based on k models evaluated on the k hold-out test sets is reported. The size of the blocks for the validation was chosen based on the range of spatial autocorrelation in the model residuals following Roberts et al. (2017). The blocks were constructed using 'blockCV' package (Valavi et al., 2019) in R. As the number of goldenrod presences and absences in our dataset was not equal, at each of the 10 resampling iterations in the cross-validation the prevalent class in training set was randomly sub-sampled, so that the frequencies of goldenrod presence and absence matched. The process was replicated five times to include different sets of random transects in the validation of a model, and results of the replications were averaged. Consequently, 50 different hold-out datasets were used to assess the final model's performance. We used the overall accuracy, kappa coefficient and confusion matrix-based measures (including specificity and sensitivity) as the model performance metrics.

The contribution of each predictor variable in explaining the goldenrod occurrence was measured using the variable importance score, which bases on the decrease in a model accuracy when a single variable is randomly shuffled (Breiman, 2001). To visualize the mean marginal effect of each variable on the probability of goldenrod occurrence, we used partial dependence plots drawn with 'pdp' package (Greenwell, 2017) in R.

To test whether the variable importance scores of different explanatory variables differ across the five spatial scales and seven variable categories, we fitted a generalized additive mixed model (GAMM) with gamma distribution and log link function using 'mgcv' package in R (Wood, 2017). In this model we used the variable importance as a response variable (continuous, ranging from 0.5 to 26.0) and three explanatory variables: spatial scale (categorical with five levels: 250, 500, 1000, 2000 and 5000 m), variable category (categorical with seven levels: human impact, climate, alien species, landscape, road, soil and transect) and interaction of these two. Each variable importance calculated for a given spatial scale was treated independently, thus, the model was performed based on a total of 245 data records and the variable identity was introduced as a random factor (fitted with ridge penalty spline). As our primary interest in this analysis was to test the interaction between the spatial scale and variable category, the performance of this model was compared with a model without the interaction term, basing on the Akaike information criterion (AIC).

Finally, to examine scale dependency in the variable importance scores of all predictor variables, we calculated the Spearman's correlation between the importance score and the spatial scale, independently for all variables. The distribution of these correlation coefficients was then compared to the null model (i.e. distribution of coefficients obtained for correlations between permuted importance scores and spatial scale, repeated 100 times) using 'sm' package (Bowman & Azzalini, 2021) in R.

3 | RESULTS

Goldenrods were recorded in 505 of 1347 sampled transects (37.5%). The species were widespread throughout Poland, with higher concentrations found in the southern part of the country (Figure 1). The performance of RF models explaining goldenrod occurrence was similar across the five considered spatial scales. The models predicted goldenrod occurrence with an overall accuracy of about 68%–70% and achieved corresponding kappa coefficients of about 0.35–0.39, thus indicating moderate model performances. All the models predicted goldenrod absences and presences similarly (ca. 69%–71% and 67%–70% of absences and presences, respectively, were classified correctly; Table 2).

TABLE 2 Performance of five RF models explaining the occurrence of goldenrods at 1357 transects established along roads in Poland in relation to environmental and human activity-related characteristics in five spatial scales.

Scale [m]	Accuracy	Kappa	Sensitivity	Specificity
250	0.6837	0.3500	0.6733	0.6900
500	0.6904	0.3620	0.6752	0.6995
1000	0.7023	0.3855	0.6871	0.7114
2000	0.7008	0.3825	0.6851	0.7102
5000	0.7030	0.3896	0.6990	0.7055

Human impacts, climatic conditions and soil properties were generally most important variable categories for predicting goldenrod occurrences in Polish roadsides at all spatial scales. These were followed by landscape structure, local characteristics of roads, transect sampling parameters and occurrence of other alien plants (Figure 3, Appendix S1: Table A.1). Across all the considered spatial scales, the individual predictor variables: human population density, solar radiation and agricultural intensity were among the most contributing factors in explaining the probability of goldenrod occurrence, while the abundance and diversity of other alien plant species was of relatively low importance (Figure 5, Appendix S1: Figures A.1 and A.2).

The importance of explanatory variables in predicting goldenrod occurrence was, however, scale dependent, as indicated by the GAMM that included an interaction term between the variable category and spatial scale performing better (AIC = 1090.1) than a model without this effect (AIC = 1102.3). This was largely driven by the effect of increasing relative contribution of landscape variables with increasing buffer radius, while no such effect was found for the other categories of variables (Figure 3, Appendix S1: Table A.2).

Scale dependence was also confirmed for several single predictor variables (Figures 4a and 5, Appendix S1: Figures A.1 and A.2). The Spearman correlation coefficients between the spatial scale and the importance of variables in predicting goldenrod occurrence varied from positive, through none to negative (Figure 4a). Broadly speaking, landscape variables, such as landscape composition, coverage of wetlands and water bodies, semi-natural habitats and forests, were again shown to increase in importance with increasing spatial scale (Figures 4a and 5). The influence of some other drivers of goldenrod occurrence decreased with the spatial scale: namely almost all climatic and road variables, some human impacts as well as landscape configuration and potential soil microbial basal respiration (Figures 4a and 5, Appendix S1: Figures A.1 and A.2). On the other hand, the importance of several predictors was not correlated with the buffer radius of a transect, including all the considered variables describing the abundance and diversity of other alien plant species and six of the seven characteristics related to soil properties (Figure 4a, Appendix S1: Figure A.1). The observed pattern in the associations between the spatial scale and variable importance was significantly non-random as indicated by the tests of equity ($p < 0.01$ in each of the 100 runs; Figure 4b). However, the direction

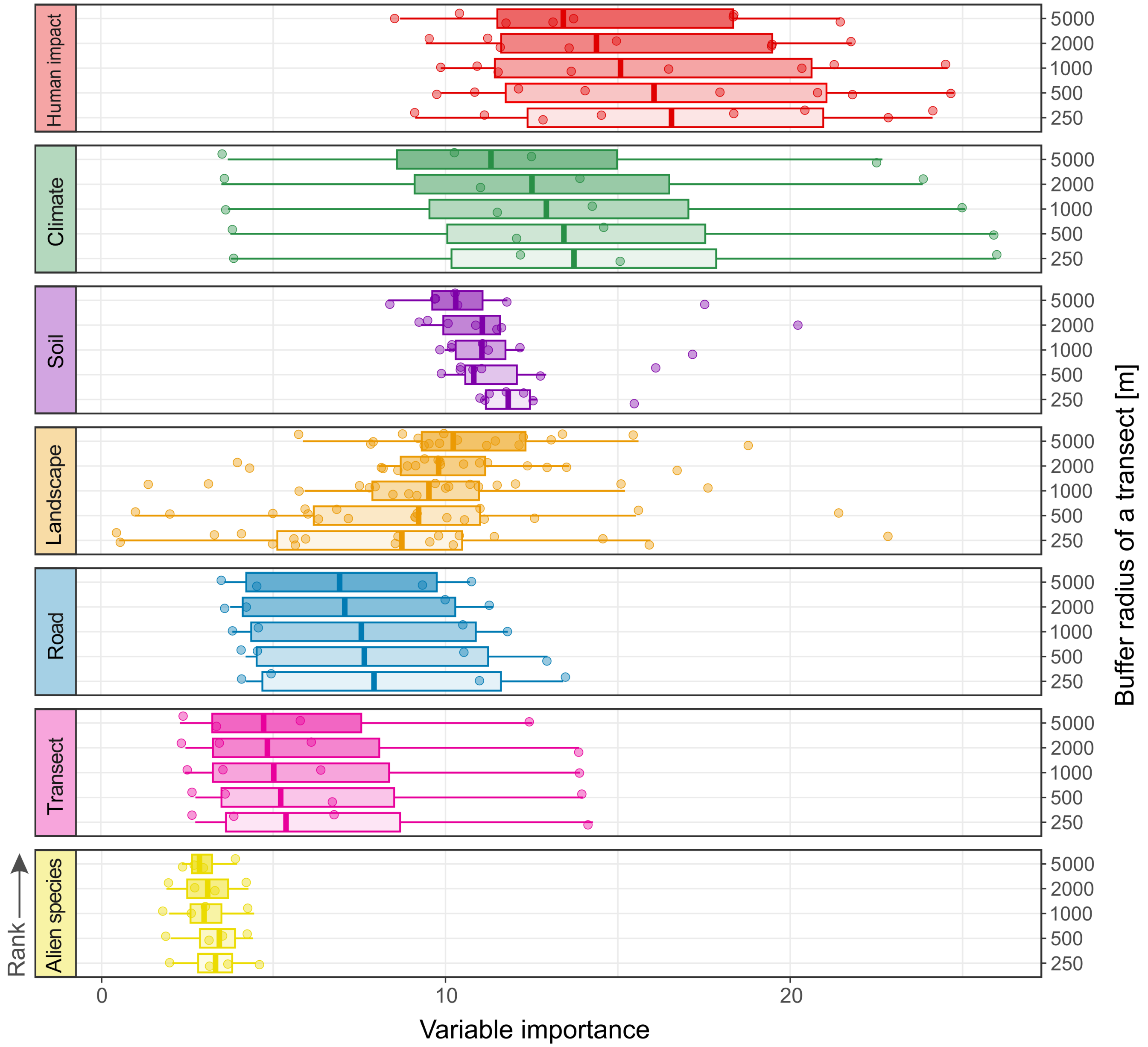

FIGURE 3 Average relative importance of seven variable categories for goldenrod occurrence in five spatial scales based on the RF models.

of relationships between the occurrence of goldenrods and the examined variables was generally similar across the spatial scales as demonstrated by the partial dependence plots (Figure 5, Appendix S1: Figures A.1 and A.2).

4 | DISCUSSION

We found that the occurrence of goldenrods along roadsides is associated with multiple factors, among which those describing human impacts, climatic conditions, soil properties and landscape structure are the most important. However, the relative contribution of these characteristics in predicting goldenrod distribution changed across spatial scales. Thus, our results clearly suggest that the effect of variables driving plant invasions can be dependent on the spatial scale examined. Below we discuss possible explanations of the mechanisms causing the observed patterns and list potential limitations associated with the methods used. Finally, we suggest possible applications of our results for invasive plant management.

4.1 | Importance of environmental and anthropogenic variables

By including a wide range of invasion predictors, we were able to show that plant invasions are influenced by multiple drivers, and that

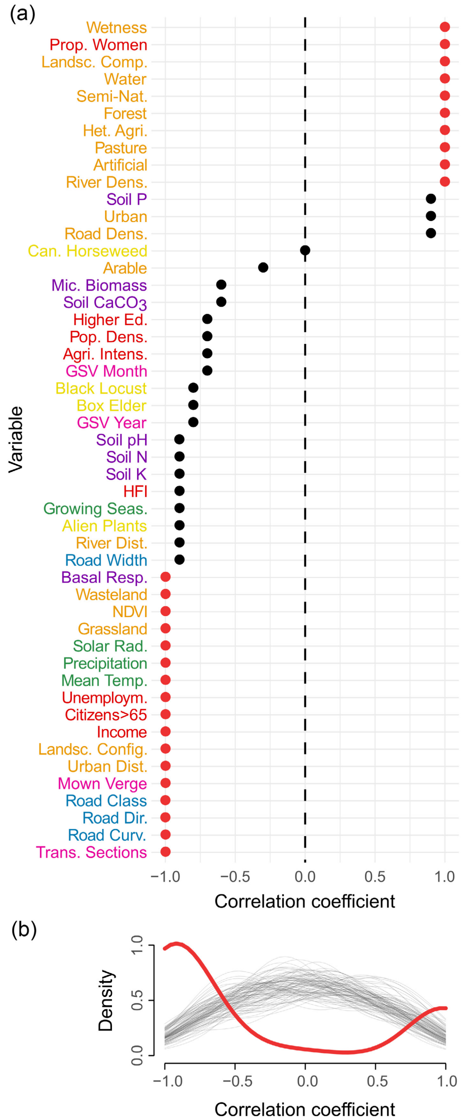

FIGURE 4 The Spearman rank correlation coefficients ($p < 0.05$ in red) between the importance of each variable and increasing spatial scale (a) and the distribution of observed (red curve) and permuted (black curves) correlation coefficients (b). A positive correlation indicates that the relative variable importance increases as the spatial scale increases, a negative correlation means that the relative variable importance decreases with increasing spatial scale. Variable names abbreviations are explained in Table 1 and Appendix S1: Table A.1, variable colour codes are given in Figure 3. Variables are ordered by decreasing correlation coefficient.

their success cannot be described by a single measure. However, some of the considered variables appeared to be more important for the predictions of goldenrod invasion than others. As expected, measures of human activity, such as agricultural intensity, human population density and several other indicators of socio-economic conditions, were among the most influential determinants of goldenrod distribution. This is likely because these characteristics are surrogates of anthropogenic disturbances in natural systems and reflect the level of propagule pressure (Hulme, 2009; Lockwood et al., 2005; Pyšek et al., 2010). It has been suggested that the impact of human activities on species invasions overwhelms the influence of climatic conditions (Dyderski et al., 2022; Pyšek et al., 2010). However, this has not been confirmed in our study as climatic characteristics, mainly thermal conditions (the amount of incoming solar radiation and average annual temperature), were also among the most important variables explaining goldenrod occurrence. These associations are in line with previous research describing the preference of the studied species to well-irradiated areas characterized of relatively warm temperatures (Cao et al., 2018). Furthermore, the occurrence of goldenrods was clearly associated with soil properties, especially phosphorus content. This is consistent with existing studies showing the importance of phosphorus for the goldenrod performance, however, its impact is context dependent. For example, increased phosphorus content can reduce the competitive ability of invasive *Solidago canadensis* under high nitrogen conditions (Wan et al., 2018). On the other hand, depending on the phosphorus form, its availability in the soil can also play a key role in mediating interactions between goldenrods and soil microorganisms such as mycorrhizal fungi, thus enhancing goldenrod invasion (Chen et al., 2023). Soil biota can both drive and respond to plant invasions (Dawson & Schrama, 2016), although existing studies are ambiguous, suggesting that these associations depend on the investigated species and system (e.g. habitat type). Some studies found no link between goldenrod invasion and microbial activity (Klimek et al., 2020; König et al., 2015), whereas others showed either positive or negative relationships (Bobuľská et al., 2019). We found a positive association between microbial activity and goldenrod occurrence. It is therefore possible that contrasting results are due to the analysed component describing soil biota communities. The distribution of goldenrods was also linked with the characteristics of landscape structure, for instance landscape configuration. The general importance of landscape structure for the outcomes of invasion processes has been already highlighted by several studies (Kotowska et al., 2022; Vilà & Ibáñez, 2011). Our results suggest that the dispersal efficiency of alien plants, such as goldenrods, can be positively related to the level of landscape configuration as a high concentration of edge habitats (e.g. ecotones, field margins) may facilitate the movement of invasive plant propagules across the landscape (Warren et al., 2013).

Factors related to road parameters were found to have little impact on the probability of goldenrod invasion. This suggests no substantial differences in goldenrod occurrence among different road types or classes or that the influence of local variables was too low to alleviate the effect of large-scale characteristics (Czarniecka-Wiera et al., 2020). Also, no clear associations between goldenrod presence and other alien plants may suggest that indices measured at the level of a roadside plant community are relatively less important. This is consistent with previous suggestions that the colonization of road verges by invasive alien plants and their further spread can be impacted by processes operating at larger spatial scales than the roadside. For example, invasion probability can be more influenced by the surrounding landscape (Minor et al., 2009; Vilà & Ibáñez, 2011), or it can be a reflection of the increased use of the roads in areas of high population density, which could promote

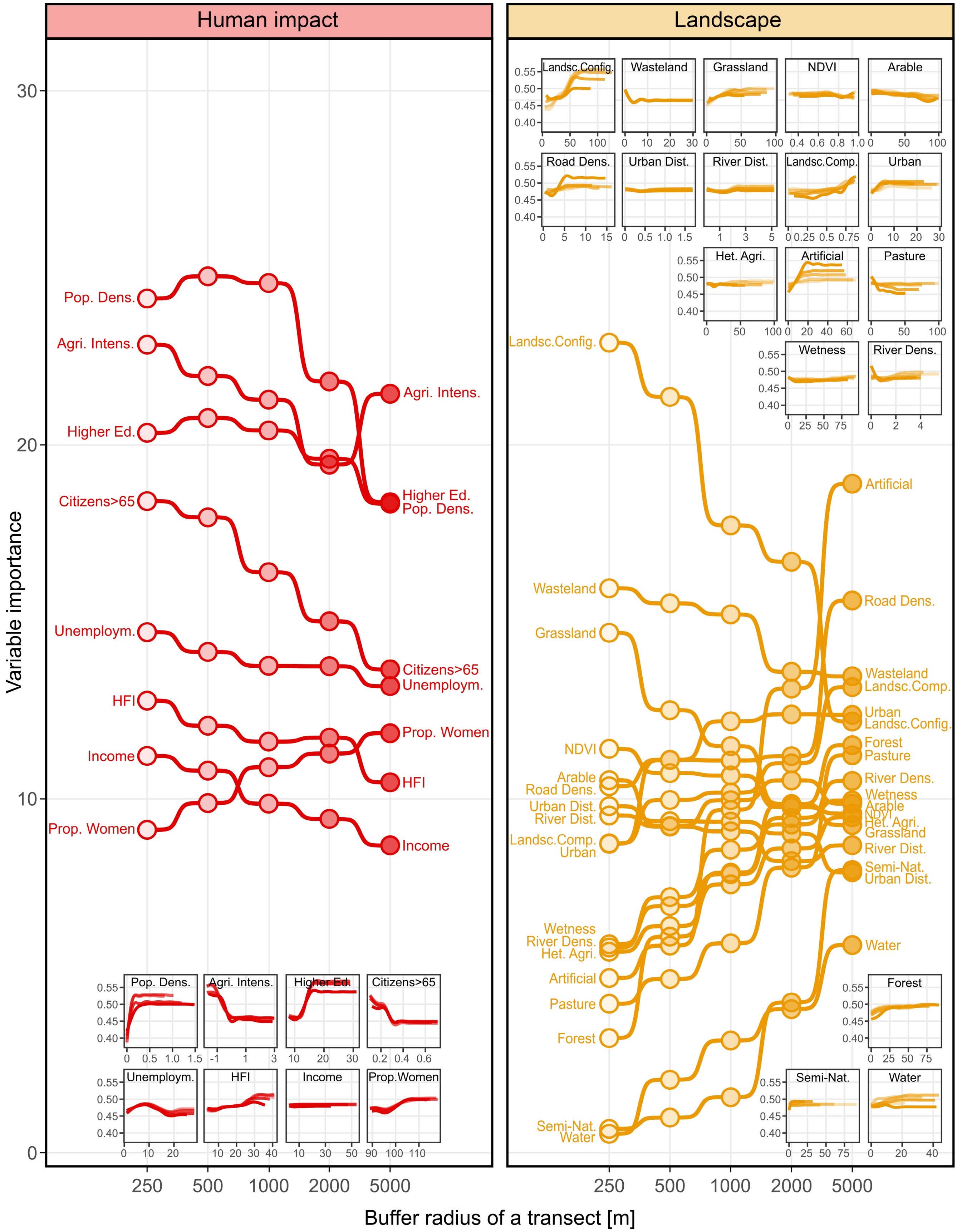

FIGURE 5 Changes in the importance of explanatory variables related to human impacts (left panel) and landscape structure (right panel) for predicting goldenrod occurrence in Polish farmland in five spatial scales based on the RF models. Partial dependence plots showing the mean marginal effect of these variables on the probability of goldenrod occurrence across five spatial scales are given as small inner panels. Each inner plot represents the effect of each variable while holding the other variables constant and different spatial scales are shown with a colour gradient from pale (250 m) to dark (5000 m).

spread of species to roadsides and surrounding habitats (Auffret et al., 2014). On the other hand, the low predictive power of other alien plants for the occurrence of goldenrods might be an indication that these species also relate to the same factors as goldenrods or that possible interactions between alien plants may occur on a very local scale (Lenda et al., 2019), smaller than the scale of the transects used in this study.

We considered a large set of factors potentially affecting goldenrod occurrence in order to capture the high complexity of the invasion process (Catford et al., 2009). While many existing studies concentrate on one specific type of variables, such as landscape structure (e.g. Andrew & Ustin, 2010) or species traits (Van Kleunen et al., 2010), we tried to overcome this potential weakness by covering a variety of different categories that could reasonably be expected to influence invasion success. However, there may, of course, still be important drivers that we did or could not cover in our study. For example, current invasion patterns may be better reflected by historical factors (such as, introduction history, historical land use changes) than contemporary processes (Essl et al., 2011; Mattingly & Orrock, 2013), thus making the predictions about the present situation even more challenging. Moreover, biological invasions are dynamic phenomena, and different drivers are involved in this process at different stages along the invasion pathway (Theoharides & Dukes, 2007). Since the geographic range of goldenrods in the study area is still expanding (Perera et al., 2021), our data likely included observations of the species at different invasion stages. Therefore, some of the considered determinants of goldenrod distribution may have been less informative than expected because their effect could have been site specific. Finally, it would be appropriate to include more invasive plant species with different morphologies and habitat preferences to improve the generality of our conclusions. However, goldenrods are the most common invasive plants in Poland and can be effectively monitored using GSV (Kotowska et al., 2021). Therefore, we focused on the invasion drivers of these species.

4.2 | Effect of spatial scale

We found that the effect of different factors associated with goldenrod occurrence changes across spatial scales, thus corroborating earlier suggestions on the importance of spatial context for understanding patterns in plant invasions (Czarniecka-Wiera et al., 2020; Kotowska et al., 2022; Milbau et al., 2009). Our results indicate that the probability of invasion of alien plants, such as goldenrods, is not only moderated by a multitude of drivers, but also that their role in the invasion process changes depending on the spatial scale considered. For example, the influence of some of the socio-economic characteristics were more prevalent at small spatial scales, suggesting that human activity-related factors may be responsible, for instance, for local introductions and dispersal of the studied plant (Lenda et al., 2014). Simultaneously, the importance of, for example, river density was highest at the largest spatial scale, indicating that watercourses, being the dispersal corridors for goldenrods, may shape their distribution across wider areas. Similarly, the importance of multiple land use types was more pronounced at larger spatial scales, suggesting that the number of habitats available for invasive species may make the landscape more vulnerable (or resistant) to invasions. At the same time, landscape configuration played a more important role for goldenrod distribution at smaller spatial scales, thus following previous conclusions that the scale of effect of habitat fragmentation (i.e. the level of landscape configuration) is smaller than the effect of habitat amount (Kotowska et al., 2022; Miguet et al., 2016). Importantly, the direction of relationships between the occurrence of goldenrods and the examined variables was similar across the spatial scales. This is not surprising as values of a given habitat feature are likely to be positively correlated at different spatial scales, and larger scales contain habitat areas included at smaller scales. Our findings are generally in accordance with earlier suggestions that different invasion drivers operate at different scales (Vicente et al., 2019) and that small-scale patterns may be constrained by larger scale factors (Levin, 1992; Pauchard & Shea, 2006). Although the presented effects may be species specific and may be different depending on the considered range of spatial scales, our results highlight the need for multi-scale approaches in studying the mechanisms driving plant invasions.

Despite our important findings regarding both spatial scale and the effects of a variety of environmental and anthropogenic drivers of invasion, it is still true that the predictive accuracy of our models was not very high. One reason for this is that the considered explanatory variables were measured based on open spatial data acquired from different sources, so their quality varied in terms of accuracy, completeness and reliability. Thus, the performance of our models may have been influenced by some feature noise that could bias the learning process (Zhu & Wu, 2004). Furthermore, we cannot exclude some errors introduced in the reference dataset as a result of remote data collection on goldenrod occurrence with GSV images. The method shows high precision in relation to field inventory data, however, it also has some limitations (e.g. temporal variability in imagery, difficulties in detecting less conspicuous species or individuals) which may reduce the probability of visual plant detection (Kotowska et al., 2021), and thus deteriorate the data quality and, consequently, the model accuracy. Still, given these limitations, which largely only increase the uncertainty in our estimates of goldenrod occurrence–variable relationships, our study using open access environmental data shows the possibilities of investigating species occurrence patterns in relation to multiple possible drivers at different spatial scales.

4.3 | Management implications

Implementing effective measures aiming at preventing, eradicating and controlling plant invasions is strongly limited by the resources (mostly financial) available for their management. Therefore, such efforts require setting priorities to identify invasion hotspots and to target the most important factors driving the success of invasive species (Ziller et al., 2020). However, since the importance of different invasion drivers varies across spatial scales, focusing on a single spatial context can provide incomplete information about patterns of invasive plant species distribution. We therefore suggest that predictions of current and future plant invasions may be more accurate if multiple spatial scales are considered, thus accounting for the small and large-scale biological processes that drive the occurrence of these troublesome species.

Our study highlights how we can benefit from using the huge amounts of freely accessible environmental data and considering different spatial scales to better approach the full complexity of potential mechanisms underlying processes of biological invasions. Such a multiple variable and spatial scale approach opens up for the development of better and more efficient counter-measures to prioritize management attempts to the spatial scale at which the most important factors affecting plant invasions operate. While most strategies for controlling invasive species may focus on the site scale, our results show that local characteristics may be less important for plant invasion patterns as compared to, for example, variables associated with landscape structure. Thus, the development of management initiatives at larger scales, for example, landscape level, may be important for more effective control of invasive plants, such as goldenrods.

AUTHOR CONTRIBUTIONS

Dorota Kotowska, Michał Żmihorski, Piotr Skórka, Tomas Pärt and Alistair G. Auffret conceived the ideas and designed the methodology; Dorota Kotowska collected and analysed the data; Michał Żmihorski and Piotr Skórka contributed ideas to analyses; Dorota Kotowska led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.mw6m9063g (Kotowska et al., 2023).

ORCID

Dorota Kotowska https://orcid.org/0000-0002-0358-3665
Alistair G. Auffret https://orcid.org/0000-0002-4190-4423

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table A.1. Explanatory variables considered as divers of goldenrod occurrence in five RF models.

Table A.2. Summary of generalized additive mixed model (GAMM) explaining the importance of variables for predicting goldenrod occurrence in relation to spatial scale, variable category and their interaction.

Figure A.1. Changes in the importance of explanatory variables related to climatic conditions (left panel) and soil properties (right panel) for predicting goldenrod occurrence in Polish farmland in five spatial scales based on the RF models.

Figure A.2. Changes in the importance of explanatory variables related to road characteristics (left panel), transect sampling parameters (inner panel) and biotic interactions among alien plants (right panel) for predicting goldenrod occurrence in Polish farmland in five spatial scales based on the RF models.

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