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Climatic factors and anthropogenic pressures drive plant invasions in Natura 2000 habitats in Poland

Szymon Święcicki, Natalia Chojnowska, Lukasz Kozub, Iwona Dembicz

Climatic factors and anthropogenic pressures drive plant invasions in Natura 2000 habitats in Poland

Szymon Święcicki (corresponding author), s.swiecicki2@student.uw.edu.pl, Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw

Natalia Chojnowska, na.chojnowsk@student.uw.edu.pl, Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw

Łukasz Kozub PhD, lkozub@uw.edu.pl, Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw

Iwona Dembicz PhD, iwona.dembicz@uw.edu.pl, Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw

Key words

anthropogenic pressure, climate, habitat monitoring, environmental factor, Natura 2000 Ecological Network, invasive species, plant invasion, protected area, statistical model

Abstract

Invasive plants pose an ecological threat around the world. Their influence can also be observed in protected areas such as the European Ecological Network Natura 2000. Although invasional processes can endanger protected habitats, the specific impact of invasive species in such areas and the factors that determine their spread remain understudied. This study aimed to analyse the level of invasiveness and factors correlated with invasions in five selected habitat types protected under the EU Habitats Directive in Natura 2000 areas, based on State Monitoring of Natura 2000 data. A total of 2,096 sites with balanced distribution across the country were analysed, belonging to mesic broadleaf forests, riverine habitats, dry grasslands, mesic wet grasslands and mires. Our study confirmed the presence of 45 invasive species and two potentially invasive species. The most frequently observed species were *Impatiens* *parviflora*, *Prunus serotina*, *Solidago gigantea*, *Erigeron canadensis*, *Solidago canadensis*, and *Bidens frondosa*. We then analysed the correlation between the presence of invasive species in Natura 2000 sites and 38 variables relating to habitat type, land use, human pressure, climatic conditions, migration corridors, and the nature protection status of the surrounding area. The most important variables correlated with invasions were habitat type, temperature seasonality, mean monthly precipitation of the coldest quarter, mean daily minimum near-surface air temperature of the coldest month, distance from rivers and main roads, and mean population density within a 5 km radius. This study demonstrated the effectiveness of the State Monitoring Programme in detecting invasive species and analysing invasional processes. It could be used to inform the planning of future invasion management and prevention strategies.

Introduction

Invasive plants have become an important problem in nature protection around the world (Early et al. 2016). Invasions occur when species are intentionally or accidentally introduced outside their native or historical range and successfully spread into a new environment (Levine 2008). According to the definition of invasive alien species proposed by the Convention on Biological Diversity and International Union for Conservation of Nature (IUCN), these are those species of alien origin that threaten biological diversity and/or the functioning of ecosystems (Tokarska-Guzik et al. 2012). Their number increases globally, and the development of transportation networks and international system of trade allows this process to gain speed (Dobrzycka-Krahel and Medina-Villar 2020). According to calculations from 2008, almost 6,000 plant species have been observed at least once in Europe outside of their native range, and almost 2,000 of them are non-native to the whole European continent. This number has been growing since then, with more than six newly naturalised alien terrestrial plant species observed every year (Lambdon et al. 2008). Invasive plant species transform their newly established habitats in a destructive manner by competing with local plants, lowering biodiversity and changing natural geochemical cycles (Pyšek et al. 2012). Their influence can be observed also in protected areas (PA), even though they often are more resistant to invasions (Hobbs 2000).

European Ecological Network “Natura 2000” is a most recent form of nature protection established in Poland, introduced in 2004. The sites of Natura 2000 are established in all Member States of the European Union, with a main goal of protecting specific types of natural habitats listed in the EU Habitats Directive, and biodiversity (Evans 2012). The Natura 2000 network consists of 26,000 sites and covers 17.5% of the area of Europe, which makes it the biggest such structure in the world (Joint Research Centre 2013).

Each EU country conducts the monitoring of habitats protected under Natura 2000, according to the article 17 of the Habitats Directive (Council of the European Union 1992) and provides reports of their conservation status to assess what is their conservation status (Perzanowska et al. 2019). The conservation status of a habitat depends on many variables, and the invasion of alien species is one of its most important negative drivers as well as one of the most commonly observed ones (Joint Research Centre 2013). Although the general influence of invasive species on the environment is broadly analysed, the studies are lacking in the field of interaction between the natural and alien species in the protected habitats (Foxcroft et al. 2013), especially in Poland (Perzanowska et al. 2019).

Although the data on factors driving invasions of less anthropogenically transformed habitats is scarce, there have been many studies describing facilitators of invasional processes. One of the commonly discussed factors is the intensity of land use and its type, along with human caused disturbances. Strongly transformed and intensively used areas are more susceptible to invasions than natural or close to natural ones (Lembrechts et al. 2016). Additionally, as one of the most important determinants of invasion success is propagule pressure (Lockwood et al. 2005; Simberloff 2009; Johnston et al. 2009; Dyderski et al. 2022), areas where many alien plants are introduced influence the level of invasion in the neighbourhood. Some studies therefore focus on places such as cities (Potgieter et al. 2024) or other densely populated areas (Spear et al. 2013) as invasional hotspots. Introduction of alien plant species depends also on transport corridors such as roads and rivers, which allow plants to reach new territories outside of their natural range (Hansen and Clevenger 2005; Zając et al. 2011; Resasco et al. 2014). Climatic factors are also influencing the intensity of invasional processes. In temperate climate zones, the number of naturalised alien plants is decreasing with growing latitude, which means that in the more severe climate, invasions are hindered (Sax 2001). The shift of plant occurrence ranges is in recent years associated with climate change. Global warming causes plant species to move to higher latitudes, enabling them to invade new territories (Buckley and Csergo 2017; Hulme 2017; Bellard et al. 2018). In our study we aimed to analyse how those factors may influence the invasion processes in the specific conditions of Natura 2000 areas in Poland.

The precise monitoring system of Natura 2000 habitats in Poland guarantees access to specific, up-to-date data about occurrences of alien plant species in habitats protected under the Habitat Directive, extent of their establishment, and their influence on those habitats (Perzanowska et al. 2019). Such information proves to be crucial in management of invasions and protection of natural areas (Baquero et al. 2021), but the data obtained by monitoring systems remains largely unanalysed, therefore the knowledge gap in reference to factors influencing the alien plants pressure and impact on habitats under the Directive is significant. This study aims to fill it in regard to chosen representative types of habitats under protection in the Natura 2000 Network, belonging to five main habitat groups: mesic broadleaf forests, riverine habitats, dry grasslands, mesic and wet grasslands, and mires. Firstly we analysed which invasive plant species occur most commonly in those habitats. Such basic knowledge proves to be crucial in the management of plant invasions. The analysis of correlation between a habitat type and the general level of invasion has already been published by Perzanowska et al. in 2019, therefore our second, and main, aim was to investigate what other, natural and anthropogenic factors at local and landscape scale could influence the establishment of invasive plant species in those habitats irrespectively of the habitat type.

Materials and methods

Monitoring of species and habitats within the Polish State Environmental Monitoring is coordinated by the Chief Inspectorate of Environmental Protection and financed by the National Fund for Environmental Protection and Water Management (GIOŚ, 2006–2018). Among other, monitoring covers all Natura 2000 habitats protected under Natura 2000 network in Poland. Monitoring is repeated every five years, and is done by experts who run observations on the permanent transects measuring typically 10 by 200 meters. In habitats developing typically as smaller patches (such as ephemeral vegetation of muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation) this area may be reduced. Monitored sites are continuous fragments of natural space, located primarily within the Natura 2000 network, but also outside it, in accordance with the requirements of the Habitats Directive (Mróz 2010–2015, GIOŚ 2006–2018, Ciećko 2020).

The information on the presence of not-native species at the sites is gathered during the monitoring at least two levels. Firstly, each habitat type has a specific status indicator where presence and cover of non-native or invasive species is assessed and noted. These indicators may be named differently in different habitat types (“invasive alien species” for open habitats or "geographically alien species in the canopy" and "invasive alien species in the understory and undergrowth" in forests). Secondly, at the level of threats, if the invasive alien species are present on the transect the observer should report a threat “I01 invasive non-native species” and list those species (Mróz 2010–2015). We converted raw data from both of the above levels from the monitoring sites into a long table where the presence of each of the reported species at each of the monitoring sites was one row. Then we removed from these tables all species, which are not regarded as invasive plants in Poland according to Tokarska-Guzik (2012), as observers also often report not-native species that are not regarded as invasive (e.g. archeophytes) or even not native animal species. The resulting table was used in the further analysis (see Suppl. material 3).

Reports for habitats used for the purpose of this study came from the results of the State Environmental Monitoring for the years 2016–2021 (GIOŚ 2006–2024). For each of the monitoring sites we obtained only the results of the last of the monitoring rounds at the time of data acquisition. They were obtained in electronic form from the Chief Inspectorate of Environmental Protection in response to a request for information on the environment and its protection. The obtained reports concerned 15 pre-selected Natura 2000 habitats. Selection included most common habitats types monitored at numerous sites, well spatially dispersed throughout Poland and representing differing broader-habitat groups (Fig. 1.; see also: Suppl. material 5).

In total 2,096 sites of balanced distribution around the country were analysed, each belonging to one of five representative groups of habitats: mesic broadleaf forests (including habitat types: 9130, 9160, 9170) - 726 sites, riverine habitats (including habitat types: 3260, 3270, 6430, 91E0) - 253 sites, dry grasslands (including habitat types: 2330, 6210, 6230) - 329 sites, mesic and wet grasslands (including habitat types: 6410, 6510, 6520) - 531 sites, and mires (including habitat types: 7140, 7230) - 257 sites (Fig. 1; Table 1; see also: Suppl. material 3).

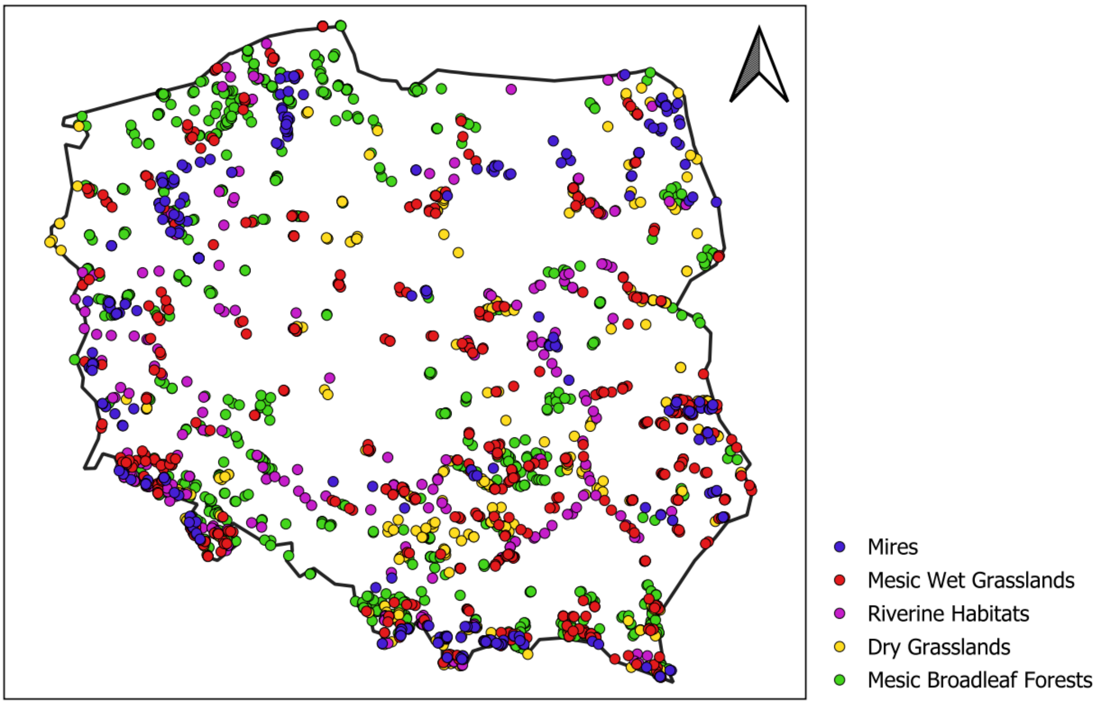

Figure 1. Spatial distribution and types of habitat of analysed sites.

Table 1. Number of sites belonging to different habitats.

Habitat type	Habitat code	Habitat name	Number of sites
Dry grasslands	2330	Inland dunes with open *Corynephorus* and *Agrostis* grasslands	70
	6210	Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)	152
	6230	Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas (and submountain areas in Continental Europe)	107
Riverine habitats	3260	Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation	70
	3270	Rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation	69
	6430	Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	114
	91EO	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)	185
Mesic and wet grasslands	6410	Molinia meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*)	107
	6510	Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*)	308
	6520	Mountain hay meadows	116
Mires	7140	Transition mires and quaking bogs	142

	7230	Alkaline fens	115
Mesic broadleaf forests	9130	*Asperulo-Fagetum* beech forests	279
	9160	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli*	81
	9170	*Galio-Carpinetum* oak-hornbeam forests	181

Of 2,096 analysed sites, the absence of invasive plants *sensu* Tokarska-Guzik (2012) was noted in 1,133, and in 963 invasive species were present. In our analysis we took into account only the presence of invasive species on a site, not their abundance nor the species number. This was due to the fact that the nearly half of the sites were not invaded, and in the nearly half of the invaded ones, only one species was present (553 sites).

For the analysis of factors that might influence the occurrence of invasive plant species in protected areas, we took into consideration following variables, grouped by their character:

1. Habitat type: As mentioned above, to obtain results independent of habitat type, we included it in the model as an independent variable. Such a procedure allowed us to reliably calculate the influence of other factors.

2. Predictors associated with a land use:

- Mean Global Human Modification Index value in the 5 km radius (data obtained from Google Earth Engine, Gorelick et al. 2017). More significant modification of the earth surface may act as a stimulant for alien plants introduction (Kennedy et al. 2019),

- Land cover heterogeneity was calculated on the basis of the data from CORINE Land Cover (2018). It was measured as the number of separate patches of land cover in the 5 km radius. The increase of land cover heterogeneity can create favourable conditions for invasive plant species (Pauchard and Alaback 2004),

- Presence and intensity of disturbances in land cover in the years preceding monitoring of studied sites. The data was obtained from CORINE Land Cover (2018). In the areas where land was disturbed recently, the intensity of invasions would grow (Pretto et al. 2010),

- The share of various land use categories in the 5 km radius. The data was obtained from CORINE Land Cover (2018), and categories analysed were following:

- artificial surfaces (CORINE code "1")
- agriculture (CORINE code "2")
- forests (CORINE codes: "3.1.1", "3.1.2" & "3.1.3")
- other seminatural surfaces (CORINE codes: "3.2-" & "3.3-")
- wetlands (CORINE code "4")
- other water bodies (CORINE codes "5-" except for "5.1.1").

Forests were separated from five general CORINE categories because of their unique qualities in terms of susceptibility for invasions. As mainly natural or seminatural ecosystems, they are more resistant to invasions (Foxcroft et al. 2013). Land use category 5.1.1, water courses, was excluded from the model to avoid double-counting of the same factor - we used distance to the nearest river in another group of predictors.

3. Proxies of human impact:

- Population density (data obtained from worldpop.org, WorldPop 2015) and road density (data obtained from Global Roads Inventory Project, Meijer et al. 2018) in the 5 km radius, which were treated as proxy of anthropogenic pressure potentially facilitating establishment of new alien species (Le et al. 2023).
- Travel time to the nearest city of population over 50,000 (based on the dataset by Weiss et al. 2018). Large cities often act as invasional hotspots, therefore they might become an important propagule source for invasions within protected areas (Kühn et al. 2017).

4. Plant migration corridors:

- Distance from nearest significant road and nearest railway (data obtained from Open Map Service, OpenStreetMap contributors 2015, https://www.openstreetmap.org). As significant, we considered roads classified as "motorway", "trunk" or "primary" in the OSM system. The presence of transportation corridors in the close proximity of the habitat facilitates introduction of alien plant species (Keller et al. 2011),
- Distance from the nearest major river, vector data on major rivers obtained from Map of Poland's Hydrographic Division (MPHP 2019). Rivers are often used by plants as

corridors for migration, therefore they may enhance invasional processes (Zając et al. 2011).

5. Nature protection:

- Share of strictly protected areas in the 5 km radius. By strictly protected areas in Poland we understood National Parks and Nature Reserves (data was obtained from Polish map service geoportal.gov.pl). National Parks and Nature Reserves, as places with high naturality, are generally less susceptible to invasions than areas transformed by humans (Foxcroft et al. 2013),
- Information whether given site lies within the strictly protected areas: nature reserve or national park,
- Information whether given site lies within the Natura 2000 area (located outside nature reserve or national park).

6. Climatic variables: 19 standard CHELSA bioclimatic variables plus average temperature of the coldest (January) and warmest (July) months for the period 1990–2010 (Karger et al. 2017; Karger et al. 2018; Brun et al. 2022).

All the data obtained was unified and organised with the help of QGIS3.40 Bratislava software (QGIS Development Team 2024), which additionally was used for required spatial data calculations. Overview of all of the variables can be found in the Suppl. material 1.

After preparing the database, we conducted our analysis in the R environment (R Core Team 2025). Visual examination of the dataset allowed us to identify data exhibiting a skewed distribution, which was transformed using square root or log transformation according to the type of data and level of skewness. Afterwards a min-max scaling to a range of 0-1 was applied to all variables to remove the differences in gradient lengths. As the independent variable number was 38, we decided to use two-step procedure of variable selection: first, at a level of detection of collinearity among variables, with the help of a random forest approach (Liaw and Wiener 2002) and second with the help of multimodel-inference (Burnham and Anderson 2002). First we calculated the Pearson correlation matrix of all variables to check them for collinearity (Suppl. material 4). Variables exhibiting high correlation (Pearson's $r \geq |0.7|$) were filtered, so that only one of each correlated group remained. We chose the remaining variable on the basis of %IncMSE value (percent increase in mean squared error), calculated with randomForest function (Liaw and Wiener 2002). From the correlated group of variables, only the one with highest %IncMSE (ergo the most important) was kept in the model. Such procedure led to exclusion of following variables: Mean Global Human Modification Index in the 5 km radius, share of forests in the 5 km radius, share of artificial surfaces in 5 km radius, CHELSA bioclimatic variables no.: 2, 3, 5, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, as well as CHELSA tas1 and tas7 (for details see Suppl. material 2). Twenty one remaining variables were included in the preliminary GLM model (family: binomial). At this stage the relative importance of variables was calculated with the use of dredge function from the MuMin package (Bartoń 2025) (Table 2). To limit the risk of overfitting and to save computation time we reduced the maximum allowed number of predictors included in the permuted models to ten. Predictors with the relative importance ≥ 0.5 were considered important (Burnham and Anderson 2002) and included in the final, shortened, GLM model from which the estimates and *p*-values for variables were obtained (Table 2). Those were: habitat type, distance to the nearest river and to the nearest road, mean population density in the 5 km radius, information if the site lies within or outside the nature protection area (Nature Reserve, National Park or Natura 2000) and CHELSA bioclimatic variables no. 4 (temperature seasonality), 6 (mean daily minimum near-surface air temperature of the coldest month) and 19 (mean monthly precipitation of the coldest quarter). For the final model we also calculated theoretical pseudo-R^2 (Nakagawa and Schielzeth 2013) using r.squaredGLMM function from the MuMIn package (Bartoń 2025)

Table 2. Relative importance of variables used as predictors of probability of plant invasion into a habitat. Highlighted are variables with the highest relative importance (≥ 0.5) calculated with multimodel inference.

Variable name	Importance
Habitat Type	**1.00**
Mean Daily Minimum Near-Surface Air Temperature of the Coldest Month	**1.00**
Distance to the nearest river	**1.00**
Temperature Seasonality	**0.99**
Distance to the nearest major road	**0.98**
Population density in 5 km radius	**0.95**
Mean Monthly Precipitation of the Coldest Quarter	**0.72**
Natura 2000	**0.59**
National Park or Nature Reserve	**0.53**

Share of seminatural surfaces in 5 km radius	0.45
Land use change	0.45
Distance to the nearest railway	0.43
Precipitation Seasonality	0.35
Road density in 5 km radius	0.35
Shannon index land cover	0.30
Share ow wetlands in 5 km radius	0.30
Share of protected areas in 5 km radius	0.30
Share of agricultural land in 5 km radius	0.29
Time to the nearest city with population over 50 000	0.27
Mean Diurnal Near-Surface Air Temperature Range	0.27
Share of non-river waterbodies in 5 km radius	0.26

Results

The analysis of the dataset allowed us to determine the presence of 45 invasive and 2 potentially invasive plant species in the sites (Table 3). Their distribution varied between different types of habitats and species (Table 4).

Table 3. List of invasive species observed during the monitoring of analysed sites. Species names used are consistent with the list of Plants of the World Online (POWO 2026).

Species name	Status in the Polish flora	Species name	Status in the Polish flora
Acer negundo	established, invasive	*Lolium multiflorum*	established, invasive
Amelanchier canadensis	established, invasive	*Lupinus polyphyllus*	established, invasive
Bidens frondosa	established, invasive	*Lycium barbarum*	established, invasive
Bunias orientalis	established, invasive	*Oxalis stricta*	established, invasive weed
Clematis vitalba	established, invasive	*Parthenocissus inserta*	established, invasive
Digitalis purpurea	established, invasive	*Prunus serotina*	established, invasive
Echinochloa crus-galli	established, invasive weed	*Quercus rubra*	established, invasive
Echinocystis lobata	established, invasive	*Reynoutria japonica*	established, invasive
Elodea canadensis	established, invasive	*Reynoutria x bohemica*	established, invasive
Epilobium ciliatum	established, invasive	*Rhus typhina*	established, invasive
Eragrostis albensis	established, invasive	*Robinia pseudoacacia*	established, invasive
Erechtites hieraciifolius	established, invasive	*Rosa rugosa*	established, invasive

Species name	Status in the Polish flora	Species name	Status in the Polish flora
Erigeron annuus	established, invasive	*Rudbeckia laciniata*	established, invasive
Erigeron canadensis	established, invasive weed	*Rumex confertus*	established, invasive
Erythranthe guttata	established, invasive	*Setaria pumila*	established, invasive weed
Fraxinus pennsylvanica	established, invasive	*Solidago canadensis*	established, invasive
Galinsoga parviflora	established, invasive weed	*Solidago gigantea*	established, invasive
Galinsoga quadriradiata	established, invasive weed	*Spiraea tomentosa*	established, invasive
Helianthus tuberosus	established, invasive	*Veronica filiformis*	established, invasive
Heracleum sosnowskyi	established, invasive	*Vicia grandiflora*	established, invasive
Impatiens taprobanica	established, invasive	*Xanthium orientale*	established, invasive
Impatiens parviflora	established, invasive	*Asclepias syriaca*	established, potentially invasive
Juglans regia	established, invasive	*Berberis aquifolium*	established, potentially invasive
Juncus tenuis	established, invasive		

The most frequently observed invasive species was *Impatiens parviflora*. It was followed by *Prunus serotina*, *Solidago gigantea*, *Erigeron canadensis*, *Solidago canadensis*, *Bidens frondosa*, and *Quercus rubra* (Table 4).

Table 4. Most frequent invaders, and number of sites invaded by them - total and in different habitat types. Percentages in brackets represent share of sites of given habitat type invaded by species.

Species name	Number of invaded sites	Number of invaded sites in different habitat types				
		Mesic broadleaf forests (out of 726 sites)	Riverine habitats (out of 253 sites)	Dry grasslands (out of 329 sites)	Mesic and wet grasslands (out of 531 sites)	Mires (out of 257 sites)
Impatiens parviflora	**396**	365 (50.5%)	28 (11.1%)	1 (0.3%)	1 (0.2%)	1 (0.4%)
Prunus serotina	**124**	51 (7%)	1 (0.4%)	47 (14.3%)	24 (4.5%)	1 (0.4%)
Solidago gigantea	**121**	35 (4.8%)	34 (13.4%)	19 (5.8%)	31 (5.8%)	2 (0.8%)
Conyza canadensis	**89**	5 (0.7%)	11 (4.3%)	46 (14%)	26 (4.9%)	1 (0.4%)
Solidago canadensis	**66**	4 (0.6%)	12 (4.7%)	18 (5.5%)	32 (6%)	0 (0%)
Bidens frondosa	**58**	20 (2.8%)	5 (2%)	1 (0.3%)	3 (0.6%)	29 (11.3%)
Quercus rubra	**49**	42 (5.8%)	0 (0%)	5 (1.5%)	0 (0%)	2 (0.8%)

Invasive species were present in all analysed types of habitat, however the variation in number of IS observed in different habitat types was significant. Among five analysed types of habitat, the highest share of sites being invaded was observed in riverine habitats, and the lowest - in mires and mesic and wet grasslands (Fig. 2 and Fig. 3).

Table 5. Results of the final GLM showing significant predictors of invasion.

Variable name	P-value	Estimate	Std. error	z value
Habitat Type (Dry grasslands)	-	-	-	-
vs. Mesic broadleaf forests	**<0.001**	0.69	0.15	4.49
vs. Mesic and wet grasslands	**<0.001**	-0.75	0.16	-4.67
vs. Mires	**<0.001**	-2.48	0.29	-8.54
vs. Riverine habitats	**0.018**	0.50	0.21	2.37
Mean Daily Minimum Near-Surface Air Temperature of the Coldest Month	**<0.001**	8.48	0.86	9.83
Distance to the nearest river	**<0.001**	-1.20	0.26	-4.58
Temperature Seasonality	**<0.001**	1.91	0.51	3.70
Distance to the nearest major road	**0.001**	-1.16	0.35	-3.29
Population density in 5 km radius	**<0.001**	1.89	0.43	4.43
Mean Monthly Precipitation of the Coldest Quarter	**0.045**	1.45	0.72	2.00
Natura 2000 site	0.116	-0.23	0.15	-1.57
National Park or Nature Reserve	0.129	-0.19	0.13	-1.52

In the final General Linearised Model we included following variables as predictors of plant invasion into a habitat patch: habitat type, distance to the nearest river, distance to the nearest road, mean population density in the 5 km radius, information if the site lies within or outside the nature protection area (Nature Reserve/National Park or Natura 2000) and three bioclimatic variables: temperature seasonality, mean daily minimum near-surface air temperature of the coldest month and mean monthly precipitation of the coldest quarter. The model explained 46% of the variance (pseudo-R^2 theoretical = 0.457). Results regarding the significance and influence of habitat type proved that the type of habitat has a strong influence on the intensity of invasions. The lowest probability of invasion was noted in mires, which differed significantly (p < 0.0001) from other habitat types. Riverine habitats and mesic broadleaf forests both had high invasion probability levels and did not differ significantly (p = 0.85). Mesic and wet grasslands, as well as dry grasslands stood in the middle, with mesic wet grasslands characterized by significantly lower probability of invasion than riverine habitats and mesic broadleaf forests, but significantly higher than mires (Fig. 4; Table 5).

All climatic variables included in the model were statistically significant, and had influence on invasional success (for the visualisation of the results see Suppl. material 6). The strongest such influence (estimate = +8.48, $p < 0.001$) can be observed in the case of the mean daily minimum near-surface air temperature of the coldest month, which indicates that places with milder temperature minima in the winter are more likely to be invaded. Temperature seasonality also had an influence on the level of invasiveness (estimate = +1.91, $p < 0.001$). The bigger the temperature seasonality, the higher the risk of invasion. The influence of the third bioclimatic variable included in the model is the weakest, but still significant (mean monthly precipitation of the coldest quarter: estimate = +1.45, $p = 0.045$). Its value means that bigger precipitation in the winter slightly raises the susceptibility for invasion.

Another trait of a site that turned out to be important is its accessibility measured by the distance from plant migration corridors such as main roads and major rivers. Both those variables were significant destimulants of invasions - the bigger the distance from roads and rivers, the lower the probability of invasion (roads: estimate = -1.16, $p = 0.001$; rivers: estimate = -1.20, $p < 0.001$). Population density in a 5 km radius proved to be a significant stimulant (estimate = +1.89, $p < 0.001$), which means that with the growth of population density the probability of invasion rises as well. For visualisation of this part of the results, see Suppl. material 6).

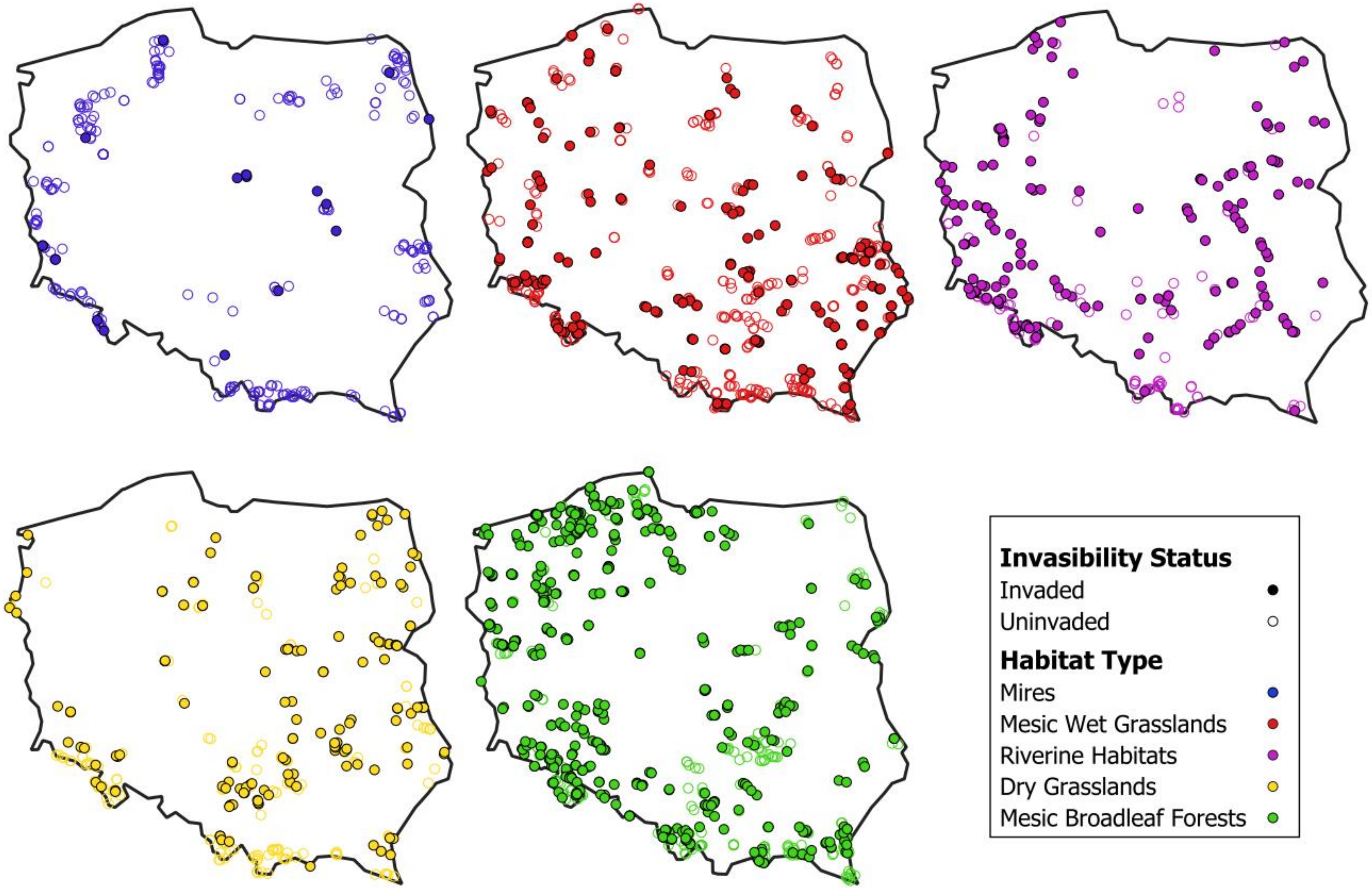

Figure 2. Location of invaded and uninvaded sites in different habitat types.

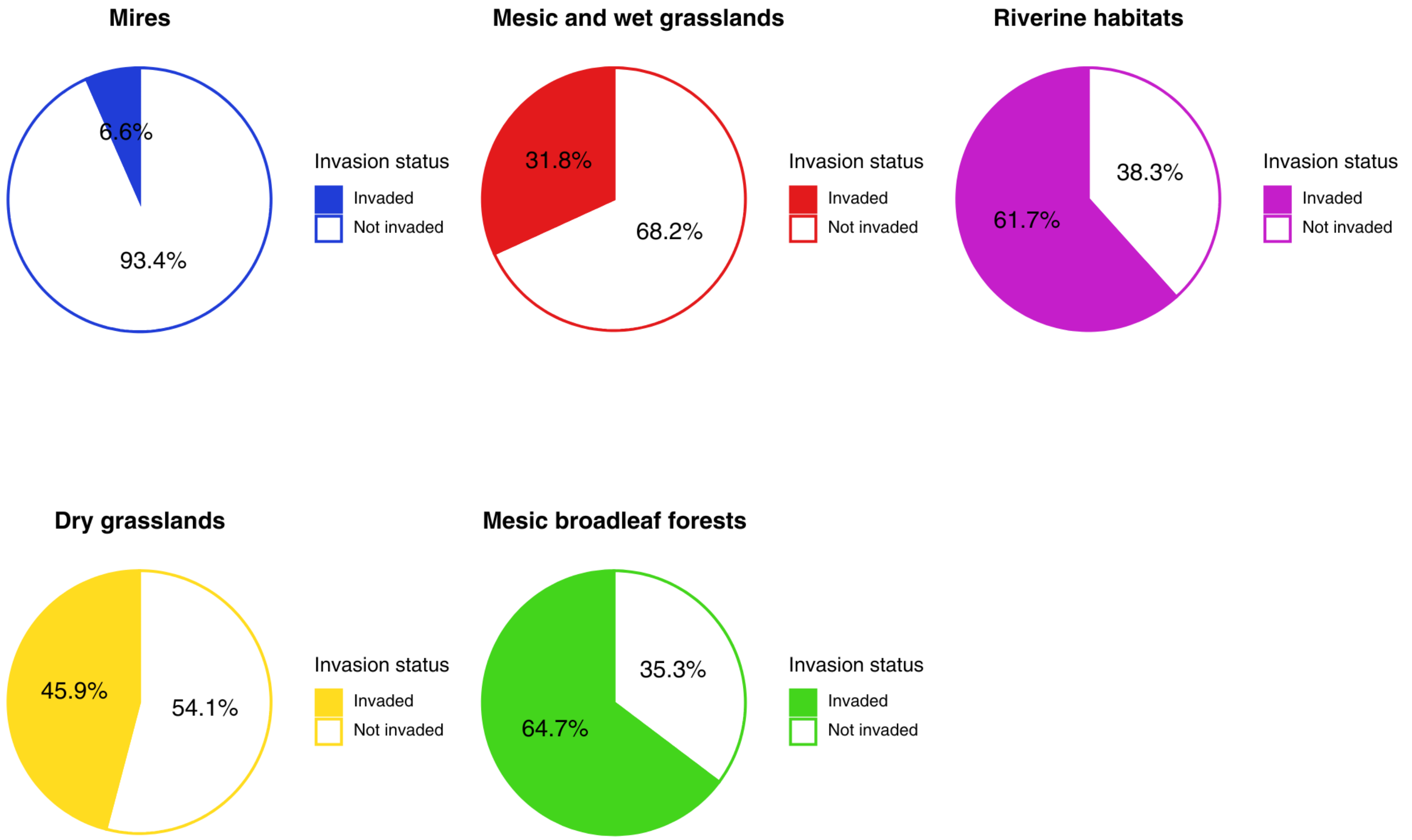

Figure 3. Share of invaded and uninvaded sites in different habitat types.

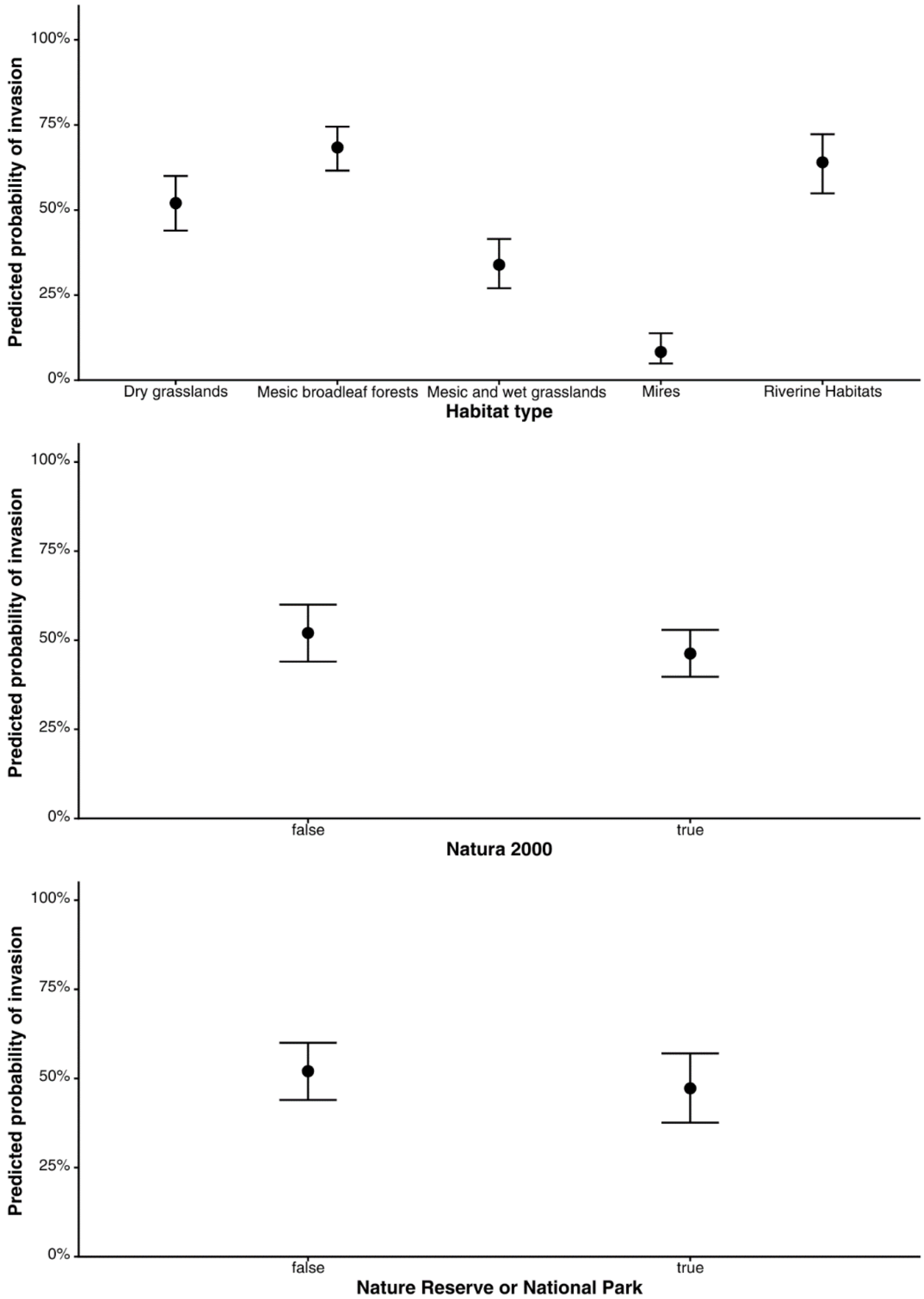

Figure 4. Estimates and standard errors for the categorical variables in the final model.

Nature protection in the place where site is located had a small negative impact on the presence of invasive species according to our model, but it was not statistically significant (sites in Natura 2000 areas: estimate = -0.23, p = 0.116; sites in Nature Reserve or National Park: estimate = -0.19, p = 0.129), therefore the influence cannot be considered certain.

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Discussion

All of the most frequent invaders present in the analysed sites, are known as highly invasive species, many of them observed in most European countries (Kalusová et al. 2024).

Our study confirmed the analysis of Perzanowska (2019) which demonstrated a strong correlation between habitat type and the level of invasion probability in the Natura 2000 areas. According to our model the lowest invasion probability was associated with mire habitats, which is consistent with previous studies on this habitat type susceptibility for invasions (Vilà et al. 2007; Chytrý et al. 2009; González-Moreno et al. 2014). Such correlation can stem from lower propagule pressure on such areas (Pyšek et al. 2002) or be a result of higher competitiveness for resources (Gioria and Osborne 2014), which are less accessible in wetlands, requiring higher specialisation from plant species (Chapin III et al. 1986).

In our model the highest levels of invasions were associated with mesic broadleaf forests and riverine habitats. Such tendency in mesic broadleaf forests might be explained by their character - most of the forests in Poland are highly transformed by humans, and are subject to intensive forest management, which on one hand may strengthen the propagule pressure of invasive species, and on the other - weaken the resilience of such habitats to invasions. Additionally, invasive tree species are one of the most commonly observed invasive plants in Europe (Rejmánek and Richardson 2013) which may result in more frequent invasions in forest ecosystems.

The high invasiveness in riverine habitats may on the other hand be associated with their role as ecological corridors, which serve as transportation channels to many species. It is worth mentioning that in our models distance to a large river was a separate variable, thus the higher invasion level in those communities may stem from the smaller rivers also acting as migration routes or due to the impact of local conditions typical for those habitats. For example river banks are easier to invade because of frequent disturbances caused by flooding events (Pyšek and Prach 1994; Hansen and Clavenger 2005; Zając et al. 2011). High levels of invasions in riverine habitats might also be due to the fact that they demonstrate significant fluctuations in nutrient availability, which was associated with higher vulnerability to invasion (Davis et al. 2000; Perzanowska et al. 2019).

The role of different climatic variables in the establishment and invasions of alien species has been analysed in depth in recent years, and the studies show, that climatic conditions have a strong influence of invasional success of plants (Buckley and Csergo 2017; Bellard et al. 2018; Panda et al. 2018; Osland et al. 2023). Our analysis demonstrated a significant correlation between the level of invasion in Natura 2000 habitats, and three climatic variables: the mean daily minimum near-surface air temperature of the coldest month, the temperature seasonality and the mean monthly precipitation of the coldest quarter. The strongest impact had the temperature in the coldest month. Previous publications on the topic of influence of the temperature of the coldest months on the success of invasions are in line with our results. Higher temperature in winter allows invasive plants or their propagules to survive to the next vegetative season, and therefore enables them to continue their invasion, whereas cold winters usually correlate negatively with invasions (Bradley et al. 2010; Hou et al. 2014; Dai et al. 2022; Osland et al. 2023). Apart from that, the most frequent direction of plant migration nowadays is towards higher latitudes, which means that invasive species establishing themselves in Poland may be generally better adapted to warmer climate conditions (Osland et al. 2023). Correlation discussed here might become even more important in the future, as in Europe climate change is observed most significantly in winter, and the cold temperature extremes are expected to soften (Bednar-Friedl et al. 2022).

Temperature seasonality has been known to influence species composition in ecosystems (Tonkin et al. 2017). Its importance was proven also in reference to invasive plant species (Petitpierre et al. 2016; Gong et al. 2020; Mengistu et al. 2023; Sun et al. 2025). Our calculations revealed a positive correlation between temperature seasonality and the invasiveness, which was in accordance with results obtained in other studies, showing that this factor might be a significant predictor of invasions. Sun et al. (2025) used the data about climate and species occurrences in northern China, to forecast future species distribution in the region, and their results indicated, that the most important predictors are very similar to the ones we obtained: most important was temperature seasonality, and other two significant ones were temperature in the coldest month and the annual precipitation.

In our study the third climatic variable significantly correlated with distribution of invasions was winter precipitation (precipitation in the coldest quarter). According to our model, the higher the precipitation in the winter, the higher the risk of invasion. Such a tendency is not strictly consistent in the literature of the subject. Studies show that changes in precipitation might have both positive and detrimental effects on the success of invasions (Bradley et al. 2010; Dai et al. 2020), therefore the results we obtained might be region specific. Our hypothesis is that higher winter precipitation may mean lower probability of physiological droughts (dry and cold conditions) or may mean more snowfall, which may reduce the impact of severe cold (modify the impact of the most important climatic variable).

The third significant group of predictors obtained from our model was associated with the accessibility of migration corridors, measured by distance from the nearest main road and major river. Our results show that the intensity of invasions in Natura 2000 habitats diminishes with growing distance from nearest main road or major river. As mentioned above in the section describing riverine habitats, linear patches of land such as roads, railways, rivers etc. might act as transportation channels for invasive species, enabling them to reach new areas and facilitating invasional processes (Hulme 2009; Resasco et al. 2014). The role of roads and rivers in relation to invasions in Natura 2000 sites was previously analysed (Szilassi et al. 2021) and similarly to our study, a positive impact of their proximity on the intensity of invasions was observed. Szilassi et al. (2021) observed additionally some differences in the dependency of chosen plants on roads and rivers as migration corridors. Some species were more influenced by the presence of the rivers in the neighbourhood, some by the presence of the roads.

Roads and rivers differ in terms of the main vector being responsible for seed or plant transportation. Rivers are transporting plants themselves (therefore the transportation may be considered unaided), whereas transportation along the roads is more often human driven (aided transportation). That means that plant migration along the roads might be easier to manage, especially considering the fact that rivers support invasions additionally by causing disturbances on the banks (Pyšek and Prach 1994).

The final significant factor in terms of its correlation with invasive plant occurrences, was the human presence and pressure, proxied by population density. Most invasive plants in Poland were introduced by humans, intentionally or accidentally (Tokarska-Guzik 2005), and the success of invasion is also human-dependent, as people transform habitats, change local climatic conditions, native species composition etc. (González-Moreno et al. 2014). The influence of humans on the intensity of invasions was also analysed in the case of nature protection areas (Spear et al. 2013; Early et al. 2016) and specifically Natura 2000 areas (Dimitrakopoulos et al. 2017). Results obtained in those studies correspond to our outcomes - the intensity of invasions grows with the density of population, which in some cases can be a more important predictor than native species richness or accessibility of migration corridors (Spear et al. 2013). In Natura 2000 sites in Greece the influence of population density on occurrences of invasive species was significant only in lower densities (Dimitrakopoulos et al. 2017).

The final model included additionally two variables referring to nature protection: the information whether the analysed site lies within the Natura 2000 area, and whether it is situated within the National Park or Nature Reserve. Despite the fact that the model including those variables turned out to be the best one, neither of them had statistical significance. This may show that even though in general nature protection sites have higher resistance to invasions (Foxcroft et al. 2013), in Poland their effectiveness in the limitation of invasions is negligible.

Some of the variables included in the database were not accounted for in the final model, due to their insignificance or lack of influence on the presence of invasive species. Such a situation concerns for example data referring to shares of land use types in the surrounding of sites. Agricultural areas, as places strongly transformed, and regularly disturbed by humans, are highly susceptible to invasions (Pimentel 1986; Guillemaud et al. 2011; Boscutti et al. 2018). Despite that, our study did not show their influence on plant invasions in the Natura 2000 habitats. Such an outcome may stem from the fact that the relatively low number of studied sites is surrounded mainly by agriculture (only 6 sites with over 50% of agricultural land in the 5 km radius). The dominant land use type in our analysis was forest, which was not included in the final model due to the high correlation of this variable with the habitat type.

Another important omission in the final model is the influence of the cities, which are invasional hotspots (Kühn et al. 2017; Potegier et al. 2025) and were expected to influence invasional processes significantly. Their potential impact on the level of invasions in the analysed sites was intended to be analysed by the use of such variables as the distance from the nearest city with population over 50 thousand, and the share of artificial surfaces in the 5 km radius from the site. Both those variables were characterized by a high correlation with the population density variable, therefore they had to be excluded from the final model in order to avoid circular thinking. Nevertheless, correlation of those variables surpassing 0.7 allows us to interpret them together, and suppose that the influence of cities and their proximity to analysed sites is significant.

Conclusions

The total number as well as severity of plant invasions in Europe is growing, and there is an urgent need for their efficient management. Such management is especially important in nature protection areas, where we aim to sustain natural habitats and original species composition. As our study has shown, the invasional processes have already significantly affected protected habitats in Poland, but many of them still exhibit early stages of invasion or are yet undisturbed by this phenomenon. The EU habitat directive calls for specific protection of chosen valuable habitat types included in the Natura 2000 network, and such is possible only with appropriate knowledge about invasional processes. In our study we showed which factors are the most important predictors of invasions in those habitats. Such knowledge may be used in the preparation of the management strategies and protection actions. Some of the predictors, such as population density and distance from the roads and rivers are important in local management, some of them allow decisionmakers to introduce more general strategies (for example adapted to specific habitat type), and some, such as climatic variables, require a broad, regional approach.

Many authors highlight the need for coordinated EU level management of invasive plants, as in many cases only international efforts in this field might be productive (Pergl et al. 2016; Perzanowska et al. 2019). Such management is already supported by the EU, which introduced The Invasive Alien Species Regulation in 2014 (Regulation (EU) 1143/2014), and The EU Biodiversity Strategy in May 2020. The State Environmental Monitoring, which grants up to date, reliable data, combined with additional research such as ours, might be an important tool to implement such strategies, but still further research on the mechanisms of invasions in the protected areas would be beneficial.

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