

Drivers of *Solidago* species invasion in Central Europe—Case study in the landscape of the Carpathian Mountains and their foreground

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Abstract

Abstract Aim: The invasion process is a complex, context-dependent phenomenon; nevertheless, it can be described using the PAB framework. This framework encompasses the joint effect of propagule pressure (P), abiotic characteristics of the environment (A), and biotic characteristics of both the invader and recipient vegetation (B). We analyzed the effectiveness of proxies of PAB factors to explain the spatial pattern of *Solidago canadensis* and *S. gigantea* invasion using invasive species distribution models. **Location:** Carpathian Mountains and their foreground, Central Europe. **Methods:** The data on species presence or absence were from an atlas of neophyte distribution based on a 2×2 km grid, covering approximately 31,200 km² (7752 grid cells). Proxies of PAB factors, along with data on historical distribution of invaders were used as explanatory variables in Boosted Regression Trees models to explain the distribution of invasive *Solidago*. The areas with potentially lower sampling effort were excluded from analysis based on a target species approach. **Results:** Proxies of the PAB factors helped to explain the distribution of both *S. canadensis* and *S. gigantea*. Distributions of both species were limited climatically because a mountain climate is not conducive to their growth; however, the *S. canadensis* distribution pattern was correlated with proxies of human pressure, whereas *S. gigantea* distribution was connected with environmental characteristics. The varied responses of species with regard to distance from their historical distribution sites indicated differences in their invasion drivers. **Main conclusions:** Proxies of PAB are helpful in the choice of explanatory variables as well as the ecological interpretation of species distribution models. The results underline that human activity can cause variation in the invasion of ecologically similar species.

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Keywords: alien plants, biological invasion, Boosted Regression Trees, drivers of invasion, PAB framework, *Solidago canadensis*,

Solidago gigantea

1 INTRODUCTION

Biodiversity and the function of ecosystems are threatened by global change drivers such as changes in land use and climate, as well as biological invasions (Linders et al., 2019; Sala et al., 2000). Invasive species alter a wide range of ecosystem services, including provisioning, regulation, and cultural and supporting functions, and they are particularly hazardous for biodiversity maintenance, human welfare, and the economy (Charles & Dukes, 2007; Chytrý et al., 2009; Hejda, Pyšek, & Jarošík, 2009; Pejchar & Mooney, 2009; Vilà & Ibáñez, 2011). Globalization (e.g., international trade and travel) and climate change (e.g., global warming, droughts,

and floods) can interact, which can in turn increase the level of biological invasions (Catford, Jansson, & Nilsson, 2009; Le Maitre, Richardson, & Chapman, 2004; Pino, Font, Carbó, Jové, & Pallarès, 2005; Seebens et al., 2015). As the total number of invasive species increases, some sites may host several alien species (Kuebbing & Nuñez, 2015).

The invasion process is a complex phenomenon, driven by numerous interacting processes, and the effect of this interaction is highly contingent on the context (Chamberlain, Bronstein, & Rudgers, 2014; Frost et al., 2019). Consequently, drivers of plant invasion can vary depending on the specific region and habitat (Taylor et al., 2016). Nevertheless, invasions have a common pattern, which can be summarized as the joint effect of propagule pressure, abiotic characteristics of the environment, and biotic characteristics of both the invader and recipient vegetation (Catford et al., 2009), the so-called PAB framework. Propagule pressure (P) includes dispersal and geographical constraints, while abiotic characteristics (A) comprise environmental and habitat constraints and biotic characteristics (B) describe the internal dynamics of the vegetation and community interactions (Catford et al., 2009). All these factors operate at different spatial scales (Czarniecka-Wiera, Szymura, & Kącki, 2020; Milbau, Stout, Graae, & Nijs, 2009) and are influenced by human activity (Essl et al., 2011). In practice, different indices can be applied as proxies of propagule pressure and abiotic and biotic conditions in modelling plant invasion process (Bazzichetto et al., 2018; Beaury, Finn, Corbin, Barr, & Bradley, 2020; Chytrý et al., 2008; Szymura, Szymura, Zając, & Zając, 2018).

Related to the propagule pressure, the biological invasion correlates with many anthropogenic factors, such as density of the communication network, percentage of urban areas, gardening, and the fragmentation of natural habitats. Such factors can serve as a proxy of propagule pressure (Foxcroft, Pickett, & Cadenasso, 2011; Pollnac, Seipel, Repath, & Rew, 2012; Štajerová, Šmilauer, Bruna, & Pyšek, 2017; Szymura et al., 2018; Vilà & Ibáñez, 2011). In addition, economic and demographic variables reflect the intensity of human activities; therefore, socioeconomic factors such as gross domestic production and human population density can be important in predicting the invasion level (Essl et al., 2011; Hulme, 2017; Pino et al., 2005; Pyšek & Richardson, 2010) because they correlate with trade intensity and communication network density (Hulme, 2009). Among the abiotic interactions with the greatest impact on a large spatial scale (continental, regional), climate is considered the most critical in limiting the geographic distribution of species (Hulme, 2017; Thuiller, Richardson, & Midgley, 2007). In terms of resource availability, invasive species usually prefer productive habitats where they are able to achieve competitive dominance (Czarniecka-Wiera et al., 2020; Peltzer, Kurokawa, & Wardle, 2016; Perkins, Leger, & Nowak, 2011). In addition, environments with high variability in resource availability, resulting from periodic external supply (e.g., surface runoff) or destruction of local vegetation that previously used the resources (e.g., human disturbances, abandonment of agricultural crops), are more susceptible to invasions than habitats with stable availability of resources (Davis, Grime, & Thompson, 2000; Kulmatiski, Beard, & Stark, 2006; Rejmánek, 1989). Given the biotic characteristics of the invader and recipient communities, the limiting similarity hypothesis proposes that the invasion by alien species will be successful if the native species of the recipient community differ from the invader in terms of functional traits and resource requirements (MacArthur & Levins, 1967), which decreases competition for resources (Funk, Cleland, Suding, & Zavaleta, 2008). Thus the functional traits of the invader should not overlap with traits of native plants occurring in the invaded community, which will allow it to occupy an empty niche and successfully invade the community (Funk et al., 2008; Hejda & de Bello, 2013). Because some sites can be invaded by several species simultaneously, determining the interaction between invaders is critical for understanding their distribution (Kuebbing & Nuñez, 2015). For example, the local species assemblage can be driven by a priority effect, and the effect is particularly strong when interacting species have similar use of resources (Vannette & Fukami, 2014). In practice, the abundance and composition of invasive species are also related to landscape characteristics (e.g., habitat fragmentation, patch size, shape, and connections), habitat type, landuse, and the composition of the surrounding landscape because these factors correlate with propagule pressure and habitat quality and availability (Basnou, Iguzquiza, & Pino, 2015; Chytrý et al., 2009; González-Moreno et al., 2013; Štajerová et al., 2017; Szymura, Szymura, & Świercz, 2016).

Because of the complexity of biological invasion, better understanding of the underlying factors and their

management is challenging. As tools for obtaining reliable and repeatable information for biological analyses as well as nature conservation and management of the invaders, invasive species distribution models (iSDMs) are considered useful (Lozano et al., 2020; Zurell et al., 2020). Modelling species' environmental requirements and mapping their distributions through space and time help to identify the main introduction pathways and secondary spread and the areas and landuse types that are more prone to invasion. These various threads could be woven into a strategy of prevention and elimination of invasive plant species on a regional scale (Lozano et al., 2020). The iSDMs are especially useful in the face of accelerating global changes and data deficiencies, as well as limited research funding (Yates et al., 2018). The PAB approach, despite its obvious advantages for selection of explanatory variables and model results interpretation, has rarely been used within an invasive species distribution modelling framework (but see Bazzichetto et al., 2018; Czarniecka-Wiera et al., 2020; Lozano et al., 2020).

Goldenrod species from North America represent successful invaders in Europe, Asia, Australia, and New Zealand (Gusev, 2015; Szymura & Szymura, 2013; Ye, Yan, Wu, & Yu, 2019; Zhang & Wan, 2017). In Central Europe, two invasive *Solidago* species occur, *S. gigantea* Aiton (giant goldenrod) and *S. canadensis* L. (Canadian goldenrod). Due to their high environmental impact, wide range of distribution, and locally high abundance, invasive *Solidago* species have to be controlled in Europe (Fenesi et al., 2015; Sheppard, Shaw, & Sforza, 2006; Skórka, Lenda, & Tryjanowski, 2010). They have been proposed for addition to the list of hazardous alien species that threaten ecosystems, habitats, or other species in European Union countries (CABI, 2018; EPPO, 2020; Tokarska-Guzik et al., 2015). Unfortunately, the eradication of widely established invasive plant species, such as *Solidago*, is not feasible. The management strategies need to integrate different options that account for the distribution and abundance of the invader, its environmental niche, and the areas that are likely to experience high impacts (Nagy et al., 2020; Shiferaw et al., 2019; Woodford et al., 2016). Management needs to consider intrinsic factors related to the biology and ecology of the invader, as well as extrinsic environmental factors, such as dispersal vectors and invasion pathways (Shiferaw et al., 2019).

Solidago canadensis and *S. gigantea* differ with regard to ecological niche in their native range and the time of introduction into Europe. However, previous studies suggest that these two species do not differ regarding their habitat preferences in Central Europe, and observed differences in their spatial distribution patterns emerge from historical contingency and limitation in long-range dispersal. The two *Solidago* species occupy different areas and rarely form mixed-species stands (Szymura & Szymura, 2016). In this study, we aimed to find the main drivers of *Solidago* species' invasion at a regional scale, using a species distribution model and applying PAB framework for selection of adequate explanatory variables and for ecological interpretation of the models. The distribution models can be used for mapping of invasion probability at a regional level to facilitate invasion control at a macroecological scale.

2 METHODS

2.1 Studied species

Goldenrod species are hemicryptophytes (shoots are annual and newly sprout each spring) with rhizomes; they are insect pollinated and self-incompatible, with inflorescences forming at the top of each shoot which can produce up to 10 000–20 000 wind-dispersed seeds per one ramet (Bielecka, Królak, & Biardzka, 2017; Guzikowa & Maycock, 1986; Moran, Reid, & Levine, 2017; Schmid, Puttick, Burgess, & Bazzaz, 1988). The seeds of *S. canadensis* and *S. gigantea* have a high germination percentage (Weber, 2000; Weber & Jakobs, 2005), but in dense, well-established *Solidago* stands, seed germination and seedling emergence are exceptional. The clone size increases via horizontal rhizomes, and the death of an established genet is a rare event (Meyer & Schmid, 1999a,b).

The native habitats of *S. canadensis* are tall-grass prairies, infrequently grazed pastures, abandoned farmlands, roadsides, and waste areas in North America (Johnson, 1995; Werner, Bradbury, & Grossi, 1980). *Solidago gigantea* prefers moist habitats, such as woods, stream edges, and woodland borders (Johnson, 1995). In Europe, *S. gigantea* and *S. canadensis* occupy similar habitats and prefer fallow lands and ruderal

habitats on moist to mesic sites, such as abandoned farmlands, scrub, roadsides, forest edges, grasslands, wetlands, and riversides (Szymura & Szymura, 2013; Szymura & Szymura, 2016). Invasive goldenrods are highly competitive for nutrients, water, and space, and they release allelopathic compounds that inhibit growth of other plants (Gusev, 2015; Ledger et al., 2015; Werner et al., 1980; Zhang & Wan, 2017). Due to prolific vegetative propagation, they form dense stands and decrease the biodiversity of plants (Chmura et al., 2016; Ye et al., 2019; Zhang & Wan, 2017); arthropods (de Groot, Kleijn, & Jogan, 2007), including pollinators (e.g. wild bees, hoverflies and butterflies) (Moroń et al., 2009; Moroń, Marjańska, Skórka, Lenda, & Woyciechowski, 2021; Lenda et al., 2020) and ants (Kajzer-Bonk, Szpiłyk, & Woyciechowski, 2016; Lenda, Witek, Skórka, Moroń, & Woyciechowski, 2013); and birds (Skórka et al., 2010).

Solidago canadensis was the first alien *Solidago* species recorded in Europe, in 1648, while *S. gigantea* was first recorded in 1758. The species were found in the territory of Poland about 100 years later, *S. gigantea* in 1853 and *S. canadensis* in 1872 (Tokarska-Guzik, 2005). After *S. canadensis* and *S. gigantea* were introduced into botanical gardens, they were distributed among gardeners. The plants were attractive and easy to grow as ornamental plants, and they were useful for beekeepers (Guzikowa & Maycock, 1986; Roháčová & Drozd, 2009; Weber, 1997; Zihare & Blumberga, 2017). Recently *Solidago* species have become widely distributed throughout Poland. According to the stages of invasion (Blackburn et al., 2011), *S. canadensis* and *S. gigantea* are now fully invasive species, with individuals dispersing, surviving, and reproducing at multiple sites in a wide variation of habitats over an extensive spatial area (E category).

2.2 Study area and species distribution data

The study area comprises approximately 31 200 km² in the southeast part of Poland, which extends from latitude 50.2° to 49°N and longitude from 19° to 23°E (Figure 1). This area is diversified due to environmental conditions mostly shaped by the altitude ranging from 160 to 2503 m a.s.l. Additional factors underlying diversity are correlated with climate, land use systems, land relief, and human population density. In the northern part, the lowland areas are used for agriculture and the foothills are dominated by forests, and the southern part has high mountains with alpine vegetation. In addition to the north–south altitudinal gradient, there is also a climatic gradient of continentality, with higher temperature range in the eastern part of the study region (Szabo-Takacs, Farda, Zahradníček, & Štěpánek, 2015) which, in the studied region, correlated strongly with decreasing eastward precipitation (Appendix, Tab S.3.). The study area includes a densely populated industrial landscape (Silesia), urban agglomerations (largest city Kraków), and moderately populated agricultural areas, as well as sparsely populated areas in the mountains. The detailed characteristics of the study area (climate, topography, land use structure, and human population density) were previously described by Szymura et al. (2018).

FIGURE 1 The study region location (green) on a background of land relief (a), and distribution of communication network and settlements on the background of altitude within the study region (b).

The data on distribution of the studied *Solidago* species were obtained from the atlas Distribution of Neophytes in the Polish Carpathians and their Foreland (Zajac & Zajac, 2015), which shows maps of species presence or absence in a 2 × 2 km grid in the Polish part of the Carpathian Mountains and their foreland, Central Europe. The fieldwork designed for the purpose of compiling the atlas was based on a survey of flora in particular regions (e.g., mountain ranges, particular towns and surrounding areas) and exploration focused exclusively on neophytes in given regions. These observations were supplemented with additional data from phytosociological relevés, herbarium records, and published materials. The fieldwork was carried out by several dozen professional botanists as well as graduate students, focusing on a predefined 2 × 2 km grid for sampling (Zajac A., personal information). This work represents a ‘survey’ type of data, according to Elith et al. (2020) nomenclature. Such data, with true absence records, enable species distribution models to be less biased and to perform better, compared with presence-only records, the ‘collection’ data type (Barbet-Massin et al., 2012; Elith et al., 2020). This distinction is of particular importance for examination of wide-ranging and tolerant species (Brotons, Thuiller, Araújo, & Hirzel, 2004). To reduce the possible effect of lower sampling effort in some regions (Bailey, Boyd, Hjort, Lavers, & Field, 2017; Yang, Ma, & Kreft, 2013), the potentially undersampled squares were excluded from modelling. For this purpose, we used

a ‘target group approach’ (Chapman, Pescott, Roy, & Tanner, 2019; Phillips et al., 2009) and a previously established model which explains neophyte richness (the ‘target group’ in this case) as a function of environmental and socio-economic variables in the studied region (Szymura et al., 2018). We assumed that the squares with the highest negative model residuals (i.e., squares where recorded neophyte richness was much lower than predicted by the model) indicated potentially undersampled regions. After preliminary testing, we decided to exclude from modelling 25% of squares (1950 squares) with the highest negative residual values and simultaneously without any invasive *Solidago* records (for details of this calculation see Appendix 1).

2.3 Explanatory variables and statistical analysis

We prepared a data set of environmental variables that can be considered as proxies of propagule pressure, abiotic environment, and biotic characteristics, based on the PAB framework (Catford et al., 2009; Table 1). These proxies were chosen based on the results of previous study on *Solidago* (Szymura et al., 2016) and the most influential drivers of neophytes in the region (Szymura et al., 2018).

TABLE 1 Explanatory variables selected for modelling invasive *Solidago* distribution. Variables indicated by italic were excluded from further analysis due to collinearity.

Explanatory variable	Abbreviation
Communication routes (railways and roads) density	Communication
Shannon’s diversity index of landscape	SHDI
<i>Urban area percentage</i>	<i>Urban</i>
Cropland area percentage	Cropland
<i>Forest area percentage</i>	<i>Forest</i>
Human population density	Density
Income per capita	Income
<i>Topographic roughness index</i>	<i>TRI</i>
Topographic position index	TPI
Average annual temperature	Temperature
Topographic wetness index	TWI
Temperature seasonality	Ts
<i>Annual sum of precipitation</i>	<i>Precipitation</i>
CaCO ₃ content	Ca
K content	K
<i>N content</i>	<i>N</i>
<i>P content</i>	<i>P</i>
pH in H ₂ O	pH
Distance to nearest introduction site <i>S.canadensis</i>	distance_S.can
Distance to nearest introduction site <i>S.gigantea</i>	distance_S.gig
Presence of competing <i>Solidago</i> species*	Competitor

* Presence of one invasive *Solidago* species in the same 2 × 2 km square was considered as an explanatory variable for the other; that is, in model for *S. canadensis*, its presence explained the presence of *S. gigantea* and vice versa.

The anthropogenic variables were derived from CORINE 2012 database (urban), the Central Statistical Office of Poland (income), and Statistics Poland (density). The length of communication routes (communication) was obtained from the Polish Geographical Objects Database (BDOO). The other data were calculated from the CORINE 2012 database (cropland, forest, SHDI). A Digital Elevation Model for Europe (EU-DEM) was used to calculate the topographic metrics (TPI and TWI). Maps prepared by Ballabio et al. (2019) using data from Land Use and Cover Area frame Survey (LUCAS) were used to calculate soil characteristics (content of N, P, K, and soil pH). The climate data (precipitation, temperature) were derived from a climatic model

developed by Hijmans, Cameron, Parra, Jones, & Jarvis (2005). Before the analyses, the Pearson correlations between each pair of explanatory variables were checked. If the coefficient exceeded 0.7, the variable with the weaker ecological meaning was eliminated to avoid collinearity (Dormann et al., 2013). For details see Appendix Table S2. The average values of the variables were calculated for each 2×2 km grid cell acquired from Zajac and Zajac (2015), and the landscape diversity (SHDI) was expressed by Shannon's diversity index.

Maps showing the distribution of goldenrods before their spreading phase (Tokarska-Guzik, 2005) were used to calculate the distances from a focal 2×2 km square to the nearest site of goldenrod occurrence in the 1950s (distance, for details see Appendix, Map S2.). To check whether the presence of one *Solidago* species in a 2×2 km square explained the presence of the second species (possible priority effect), the data on distribution of the potential competitor were used as an explanatory variable (competitor). All the calculations and map handlings were done using QGIS, SAGA GIS, and FRAGSTAT software.

Goldenrod species spatial pattern of distribution was modelled using a boosted regression trees (BRT) technique (De'Ath, 2007; De'Ath & Fabricius, 2000) employing packages gbm, dismo, and Biomod2 in the R environment. After initial examinations, the BRT settings were applied: tree complexity, 5; bag fraction, 0.5; learning rate, 0.001; and cross-validation, 10 fold. The optimal number of trees was 3900 for *S. canadensis* and 3850 for *S. gigantea*. Models for each species were constructed using all explanatory variables, and then simplified to obtain the parsimonious model. The BRT modelling and simplification of models were done based on Elith, Leathwick, & Hastie (2008) suggestions. Then, the modeling, using the tuned model parameters and a minimal set of explanatory variables, was performed in Biomod2 package with spatially blocked cross-validation (Valavi, Elith, Lahoz-Monfort, & Guillera-Aroita, 2019). We applied 5-fold cross-validation, using spatial blocks constructed based on 10×10 km squares for *S. canadensis* and 20×20 km squares for *S. gigantea*. The sizes of the squares were chosen based on spatial autocorrelation of raw distribution data (Roberts et al., 2017), and the blocks were constructed using BlockCV package within the R environment (Valavi et al., 2019). For details of this approach see the Appendix. The performance of the models was evaluated using area under the receiver-operating characteristic curve (AUC). The ecological interpretation of the model relied on the relative influences of explanatory variables and drawing response curves for each explanatory variable (Elith, Ferrier, Huettmann, & Leathwick, 2005). Eventually, maps of projected *S. canadensis* and *S. gigantea* probability of occurrence were drawn (Figure 6). The probability of species presence in a given 2×2 km square was modelled for particular spatially blocked cross-validation runs and averaged.

3 RESULTS

Goldenrod species were observed in 60.5% of the squares (in 3544 out of 5850 finally examined squares). *Solidago gigantea* was the most frequent species (53.1%, 3107 squares) followed by *S. canadensis* (21.4%, 1255 squares).

Solidago gigantea localities were widespread throughout almost the entire area, aside from the higher altitudes in the southern part of the study region. The *S. canadensis* was concentrated in the western part of the study area, while being sporadically dispersed in the eastern part and also avoiding the southern fragment with higher altitudes (Figure 2).

The average value of AUC was 0.836 for *S. canadensis* and 0.786 for *S. gigantea*. Despite some differences in model evaluations of particular spatially blocked folds (Figure 3), the models for *S. canadensis* generally performed better than those for *S. gigantea*. The parsimonious (simplified) model for *S. canadensis* relied on a higher number of explanatory variables than those for *S. gigantea*.

FIGURE 2. Distribution of invasive *Solidago* species (orange color) in studied region. The light gray color show distribution of squares with confirmed *Solidago* absence. Squares excluded from analysis, are not shown (left blank).

FIGURE 3. The values of area under curve (AUC) for simplified models of *S. canadensis* and *S. gigantea*

distributions, with spatially blocked, 5-fold cross-validation.

Both species reacted to climatic conditions, expressed by the annual average temperature (Tam) and temperature seasonality (Ts), as well as the distance from the initial introduction sites (Figure 4). Moreover, the spatial pattern of distribution of *S. canadensis* was also explained by anthropogenic factors, such as population density as well as the percentage of agricultural lands (cropland). The full list of all variables included in the final models, along with their relative influence, is shown in Figure 4.

FIGURE 4. Variables importance for each variable involved in the simplified models. The whiskers denote the standard deviation calculated basing on spatially blocked cross-validation.

The modelled response of species on particular variables is shown in Figure 5. The distribution of both species was climatically limited, with the species being unlikely to occur in regions with an average annual temperature below 5.5degC. The probability of *S. canadensis* occurrence increased with human population density (Figure 5), as well as distance from its introduction site, with squares placed 100 km distant from the initial sites of introduction having the highest probability. The distribution of *S. gigantea* was also correlated with the pattern of its initial introduction, and the probability of its occurrence generally decreased with the distance (Figure 5), reaching the lowest value at about 40 km and fluctuating above it.

FIGURE 5 The modeled responses of *Solidago* species for particular environmental variables. The shape of the response was modelled using the evaluation strips method (Elith et al., 2005), with spatially blocked, 5-fold cross-validation. The graphs are sorted according decreasing value of variables' importance, upper panel for *S. canadensis* , lower – for *S. gigantea* .

Finally, the projection of the modelled probability of the presence of the invasive *Solidago* species was performed, employing the 'projection' function in the Biomod2 package. The projection was performed five times, for each spatially blocked fold in cross-validation, and then averaged. The results of the projections are presented on Figure 6. The average cutoff values, calculated basing on the AUC values, were 0.205 for *S. canadensis* and 0.539 for *S. gigantea* .

FIGURE 6 The projected probability of presence of the invasive *Solidago* species. The optimal cutoff value was 0.205 for *S. canadensis* and 0.539 for *S. gigantea* .

4 DISCUSSION

The model's performance in interpreting the AUC values (Šimundić, 2009) should be considered as good for *S. gigantea* and very good for *S. canadensis* , despite the relatively limited number of explanatory variables retained after the model's simplification. Moreover, in the case of species with broad environmental tolerance, such as the studied *Solidago* , the model's performance is usually lower than it is in comparing with specialist species, both plants and animals (Guisan et al., 2007; Regos, Gagne, Alcaraz-Segura, Honrado, & Domínguez, 2019). The model's performance is improved by variables that can be interpreted as proxies of P, A, B factors (see discussion below); however, the importance of the variables differed considerably between particular P, A, and B factors, as well as species studied.

Ecological interpretation of the models

Propagule pressure

The recent distributions of examined species were correlated with initial patterns of their introductions, in 1950s. Quite surprisingly, the two species revealed an opposite relationship to these historical patterns. In the case of *S. gigantea* , the pattern was rather simple and intuitive: the probability was highest in squares closer to the sites of initial distribution. However, *S. canadensis* quite surprisingly was the most likely to occur in squares 100 km from the initial sites of introduction. These results suggest different mechanisms of long-range dispersals. Recently, *S. canadensis* was considered to have a higher ornamental value (because of larger size, bigger inflorescences, and clump occurrence) than *S. gigantea* . As a result, it is offered by garden shops, but *S. gigantea* is not (Szymura M. personal observations, data from internet shops offering ornamental plants). A similar pattern of trade has been described in Estonia, Central Europe, where only *S.*

canadensis is offered in markets (Ööpik, Bunce, & Tischler, 2013). Moreover, the honey from *S. canadensis* has recently been promoted on social media, without supporting scientific data, as a ‘superfood’ with healing properties. This claim could encourage beekeepers to produce goldenrod honey, which would lead to further spread of *S. canadensis* and exacerbate its existing negative environmental impact. (Lenda et al., 2020).

The distribution of *S. canadensis* is positively correlated with human population density. This straightforward correlation breaks if the population density exceeds 5000/km². This happened in a few of the most densely inhabited squares, representing strict city centres. It was generally found that the plant species richness in areas with moderate levels of urbanisation (e.g., suburban areas) exceeded the richness recorded in non-urbanised areas as well as in central, urban core areas (McKinney, 2008). The lack of a further increase in alien species richness in strict city centres, despite the high propagule pressure, was explained by the loss of suitable areas for plants (McKinney, 2008). Such generally limited neophytes’ richness caused by population density has previously been shown for this region (Szymura et al., 2018).

The results of the modelling support the assumption that recent *S. gigantea* dispersal has occurred mostly spontaneously without any human aid, while *S. canadensis* dispersal is still related to human presence and, additionally, intentional transport over longer distances via, for example, internet commerce (Lenda et al., 2014).

Abiotic factors

The variables representing abiotic environment (A) are the most important for model performance for both species; however, the impact of these variables was more pronounced in the case of *S. gigantea*, compared with *S. canadensis*.

The distribution of both species was restricted climatically, and their presence was unlikely in areas with an average yearly temperature below approximately 5.5°C. The temperature corresponds with the altitudinal zonation of vegetation in the studied region and relates to a lower limit of the montane zone, starting from an altitude of approximately 600–850 m a.s.l. in the studied region. The negative effect of cold climate on the distribution of both *Solidago* species studied is in accordance with studies examining their potential distribution in Europe, which indicated that northern Europe as a region is outside their climatic requirements (Weber, 2001). Although both species can be observed sporadically at higher altitudes, their typical upper limit is 1200 m a.s.l. (Moran et al., 2017; Weber & Jakobs, 2005). In the case of *S. gigantea*, positive correlations have been found between the mean temperature and growth parameters, and high spring temperatures (above 24 °C) are advantageous for germination (for review, see Weber & Jakobs, 2005). *Solidago canadensis* plants are taller at lower altitudes, and at higher altitudes, they are not able to develop seeds because of the limited length of the vegetation period (Moran et al., 2017). It should be noted that the data referred to here regarding altitude come from the central Alps, while the climate in the Carpathian Mountains is more severe; therefore, the upper limits of the vegetation zones are at lower altitudes in the Carpathian Mountains comparing with the Alps (Ellenberg, 1988; Pawłowski, 1972).

The species distributions were also correlated with temperature seasonality, which in the studied region is also related to the precipitation pattern (Appendix, Table S.3.). *Solidago canadensis* is more abundant in the western part of the study region, which has lower temperature seasonality and higher precipitation, while *S. gigantea* avoids the southern part of the region with higher precipitation and also lower temperature seasonality. Previous studies examining the potential range of this species in Europe (Weber, 2001) suggested that these aspects (continentality gradient and precipitation) did not restrict their distribution in this part of Europe. Therefore, the extent to which the observed relation is causal is not clear, and the possibility exists that it reflects a peculiarity of the distribution in the studied region.

The models did not indicate that soil properties and landrelief features are among the crucial factors explaining the distributions of the invaders. Both species are known to have rather broad tolerance to soils (Szymura & Szymura 2016; Weber & Jakobs, 2005; Werner et al., 1980), which could explain why soil properties were not relevant in studied region. Observations from early phase of invasion on studied region, up to 1989s, underlined the role of river valleys, as a main route of invasion (Tokarska-Guzik, 2005). The results obtained

here show that the species are broadly widespread and their invasion is no longer related to watercourses.

Biotic factors

Because character of the data (observation for 2x2 km grid), we had no detailed information regarding invaded habitats. However the data still allowed testing the hypothesis regarding species co-occurrence at landscape scale and the effect of dominant land cover/land use forms. Results from other region of Central Europe revealed existence of large areas dominated by a single invasive *Solidago* species, where presence of another was unlikely. This spatial pattern results, most likely, from priority effect (Szymura & Szymura 2016). In the studied region we had no evidences for such phenomenon: the presence of one species did not explain the absence of the other. The species rarely formed mixed stands (Szymura & Szymura, 2016), but considering grain size used in this examination (square 2×2 km) it can be assumed that they could co-occurred in the same landscape. We also found that the presence of *S. canadensis* is rather unlikely in a landscape dominated by agricultural areas. It could be linked to high use of herbicides and a small amount of available area for invasive goldenrod habitats (e.g., abandon fields, meadow, pastures) in lands with intense, large-scale agriculture (Szymura et al., 2016; Szymura & Szymura, 2016).

The relatively low importance of variables that can be related to biotic interactions does not necessarily mean that biotic interactions did not shape invasion pattern. It is more likely related to the grid size in this study (2×2 km), while the biotic interactions occur mostly in the closest vicinity of the studied individuals. Such data can potentially be derived from other sources of information, namely phytosociological relevés, which document species composition and abundance in small plots (~ 25 m² for herbal vegetation).

4.5 Conservation implications

The two species differed regarding prominent constrains: both were limited climatically, avoiding cold, mountain climate, but *S. canadensis* with a still limited range was also related to proxies of human pressure. Based on the results, it can be hypothesized that recent dispersal of *S. gigantea* in the studied region has happened mostly spontaneously, while the spread of *S. canadensis* could be related to trade and intentional introductions. Given the wide range of distribution of both species, their successful eradication in the region seems unlikely. However, local eradication in mountains, above 600–850 m a.s.l. where the species occur infrequently may still be feasible and could be considered as a management option. In the case of *S. canadensis*, proscription of its sale could restrict its further spread. Assuming the successful restriction of the trade, eradication in the eastern and central parts of the region, where the species is still uncommon, will be achievable. Similarly, the control of invasive plant species populations in human settlements and their surrounding area seems to be reasonable method. In contrast, the management of *S. gigantea* should focus on areas with a high value for nature conservation that are close to already existing populations of this species. The model outputs seem to be transferable into other areas with similar climate, land-use history, economy, and invasion history, including the Carpathian mountains and the surrounding regions in Slovakia, Ukraine, Hungary, and Romania.

Model limitations, and methodological problems

Recently, numerous SDM have been based on presence-only data and employ so-called background points (pseudo-absences). Nonetheless, data not only on species presence but also their true (i.e., confirmed) absence are considered more relevant for modelling (Brotons et al., 2004; Barbet-Massin et al., 2012; Elith et al., 2020). Unfortunately, confirmed absence data are problematic because they need a high sampling effort (Barbet-Massin et al., 2012; MacKenzie & Royle, 2005) to be realistic. Our results show that in spite of the high-quality data employed here, exclusion of squares with a richness of neophytes (considered here as target species group) improves the model's performance. This suggests an issue of sampling bias, which can be mediated by appropriate procedures. Our approach seems to be promising, but it needs further study in order to better understand its operation. The typical assumption, such as higher sampling effort in densely populated areas and near roads, is not adequate for invasive species because they typically occur in urban areas and along communication routes (Niinemets & Peñuelas 2008; Szymura et al., 2016).

Another problem consists of causality in our model: the approach applied represents a correlative type of model that is unable to directly capture the underlying processes driving the observed patterns of distribution. Contrary to this, the mechanistic (or process-based) models, which are built using explicit descriptions of biological mechanisms, are free from this disadvantage (Yates et al., 2018). However, they need appropriate formulation including detailed data on species response to environment, preferably coming from experiments, which are typically unavailable. In practice, the models rely to a considerable degree on parametrization based on observational data, and as a result, the difference between correlative and mechanistic models is often fuzzy (Yates et al., 2018). To conclude, regarding the recent state of knowledge regarding processes driving *Solidago* invasion, the mechanistic models do not have a lot of advantages compared with correlative models, especially given the lack of data for parametrization. Such data will come from experiments, not from observational study.

4.6 Conclusions

* The PAB framework enhanced the iSDM by helping in the selection of explanatory variables, as well as the ecological interpretation of the models. Nonetheless, in practice it needs high-quality data that are typically unavailable to fulfil this approach, especially regarding biotic interactions. In case of plant invasion, adequate data on the biotic component could be delivered by phytosociological relevés.

* The models reveals that two alien species with similar ecology and biology can vary considerably in their invasion pattern due to direct human interference. Therefore, the conservation options, derived from iSDM, should be focused on a particular species, not groups of species, even if they have similar ecology and are closely related taxonomically.

* The presence/absence data, in addition to their pre-eminence compared with opportunistic, presence-only data for species distribution modelling purposes, are still prone to some bias. Results of this study suggest that the bias is correlated with mistakenly reported species absence. The realistic confirmation of species absence can be assumed to need a high sampling effort for confirmed absence. Exclusion of the potentially undersampled plots increased the model performance; however, additional data are needed (e.g., richness of target species group).

* The employment of maps showing the historical distribution of invasive species enhanced the modelling by revealing potential differences in patterns of species spread into a region.

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CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHOR CONTRIBUTIONS

Peliyagodage Chathura Dineth Perera: Conceptualization (Supporting); Formal analysis (Supporting); Funding acquisition (Equal); Investigation (Supporting); Methodology (Equal); Visualization (Supporting); Writing-original draft (Lead); Writing-review & editing (Lead). **Tomasz H. Szymura:** Conceptualization (Equal); Data curation (Lead); Formal analysis (Lead); Methodology (Equal); Software (Equal); Supervision (Equal); Visualization (Equal); Writing-original draft (Equal); Writing-review & editing (Equal). **Adam Zajac:** Data curation (Equal); Resources (Lead). **Dominika Chmolewska:** Software (Equal); Visualization

(Equal); Writing-review & editing (Equal). **Magdalena Szymura:** Conceptualization (Equal); Data curation (Equal); Formal analysis (Equal); Funding acquisition (Equal); Investigation (Equal); Supervision (Lead); Visualization (Equal); Writing-original draft (Equal); Writing-review & editing (Equal).

DATA AVAILABILITY STATEMENT

All data used are available publicly from the sources given in the manuscript and appendices.

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FIGURE LEGENDS

FIGURE 1 The study region location (green) on a background of land relief (a), and distribution of communication network and settlements on the background of altitude within the study region (b).

FIGURE 2. Distribution of invasive *Solidago* species (orange color) in studied region. The light gray color show distribution of squares with confirmed *Solidago* absence. Squares excluded from analysis, are not shown (left blank).

FIGURE 3. The values of area under curve (AUC) for simplified models of *S. canadensis* and *S. gigantea* distributions, with spatially blocked, 5-fold cross-validation.

FIGURE 4. Variables importance for each variable involved in the simplified models. The whiskers denote the standard deviation calculated basing on spatially blocked cross-validation.

FIGURE 5 The modeled responses of *Solidago* species for particular environmental variables. The shape of the response was modelled using the evaluation strips method (Elith et al., 2005), with spatially blocked, 5-fold cross-validation. The graphs are sorted according decreasing value of variables' importance, upper panel for *S. canadensis*, lower – for *S. gigantea*.

FIGURE 6 The projected probability of presence of the invasive *Solidago* species. The optimal cutoff value was 0.205 for *S. canadensis* and 0.539 for *S. gigantea*.

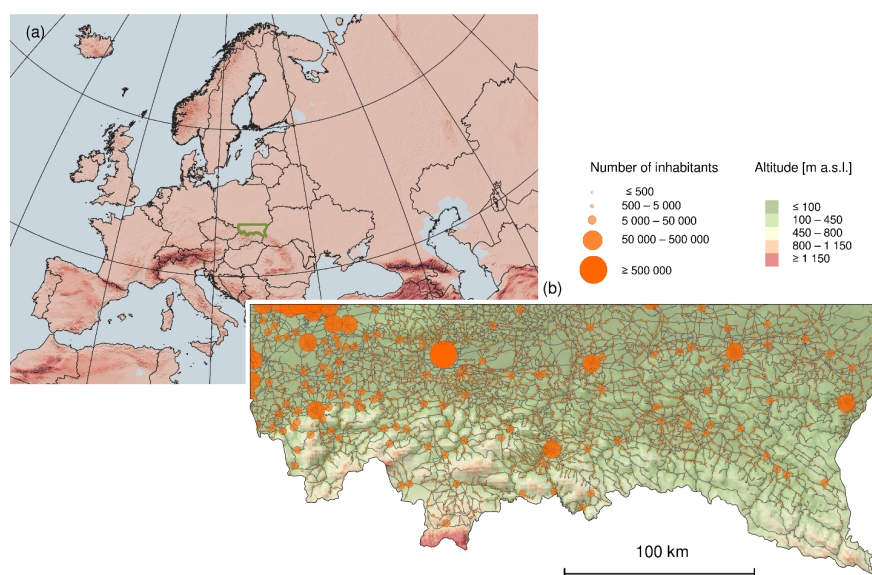
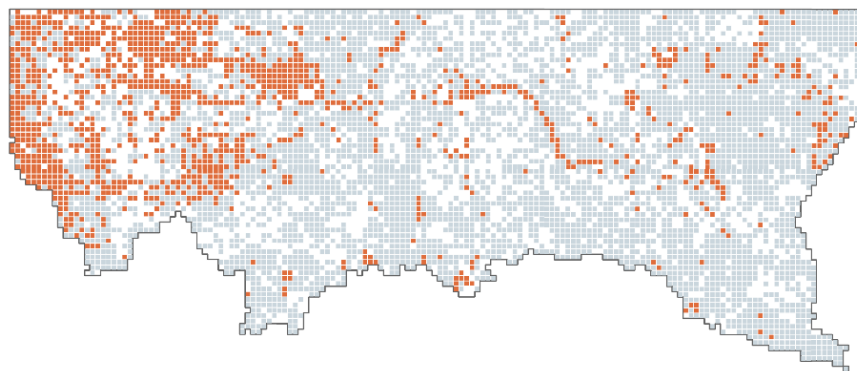
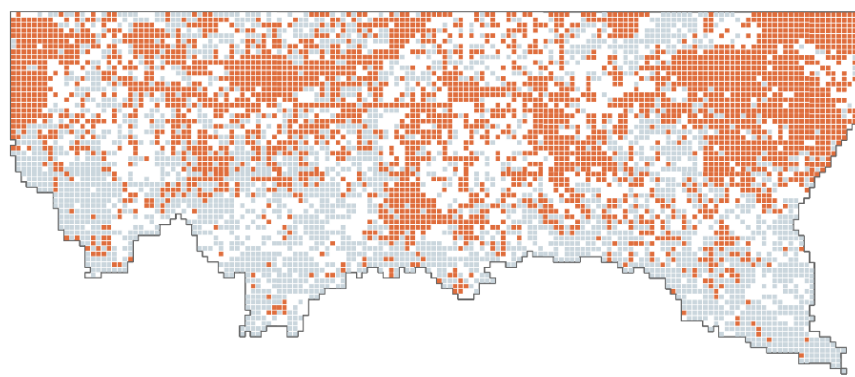


FIGURE 1 The study region location (green) on a background of land relief (a), and distribution of communication network and settlements on the background of altitude within the study region (b).

S. canadensis



S. gigantea



100 km

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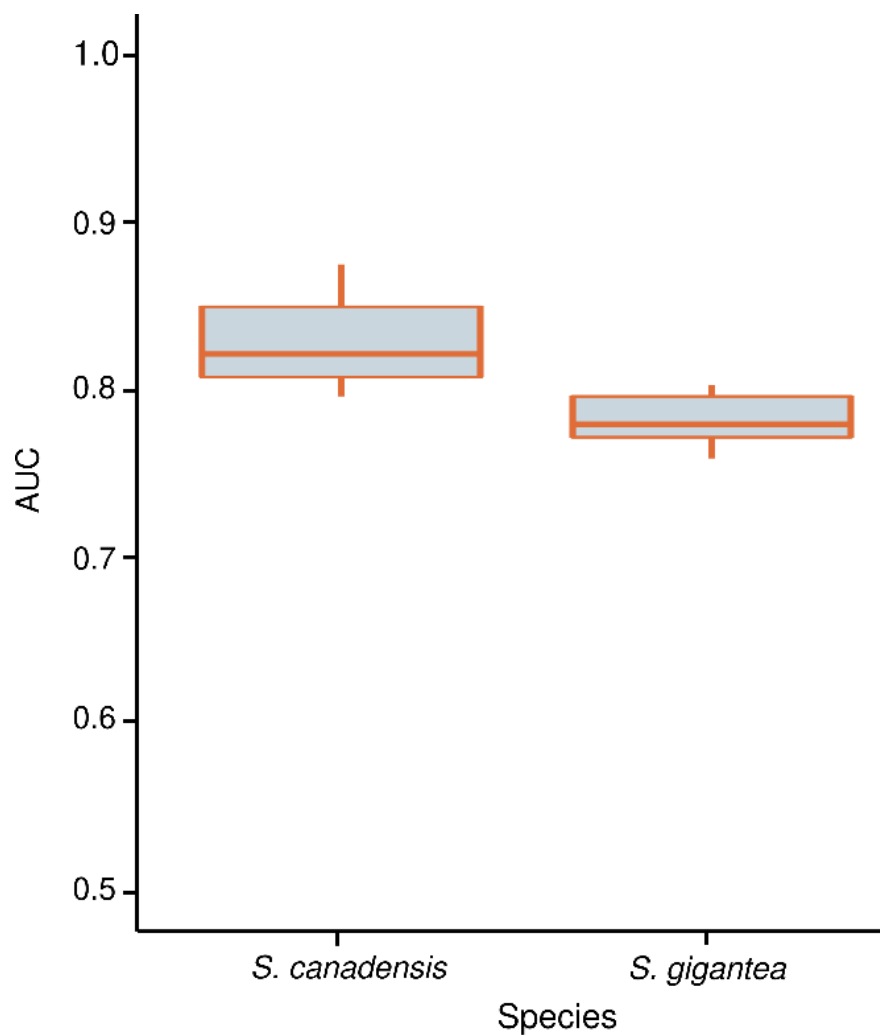


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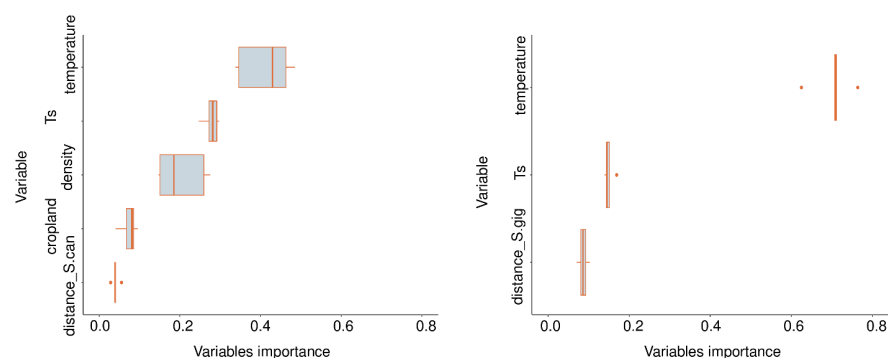


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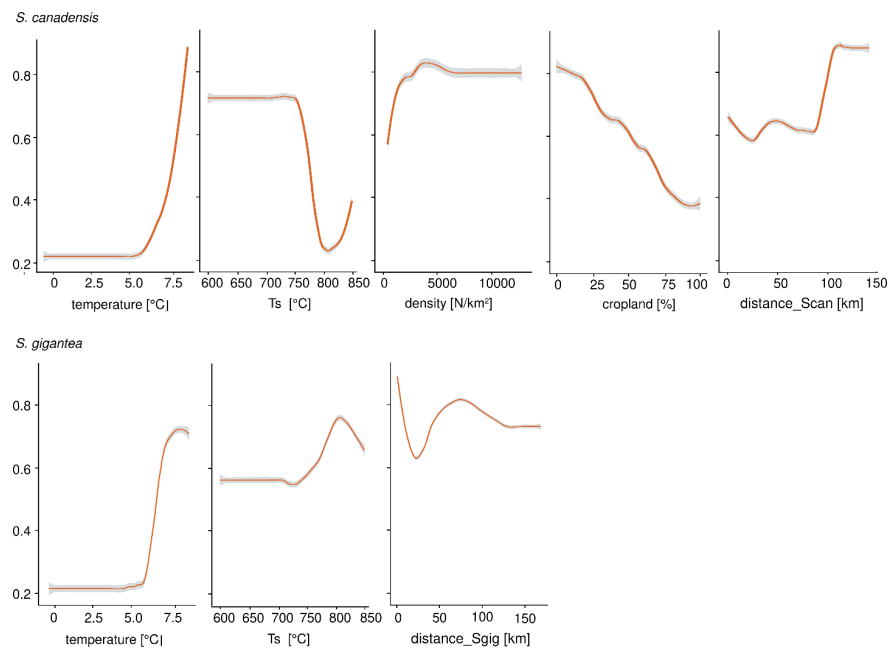


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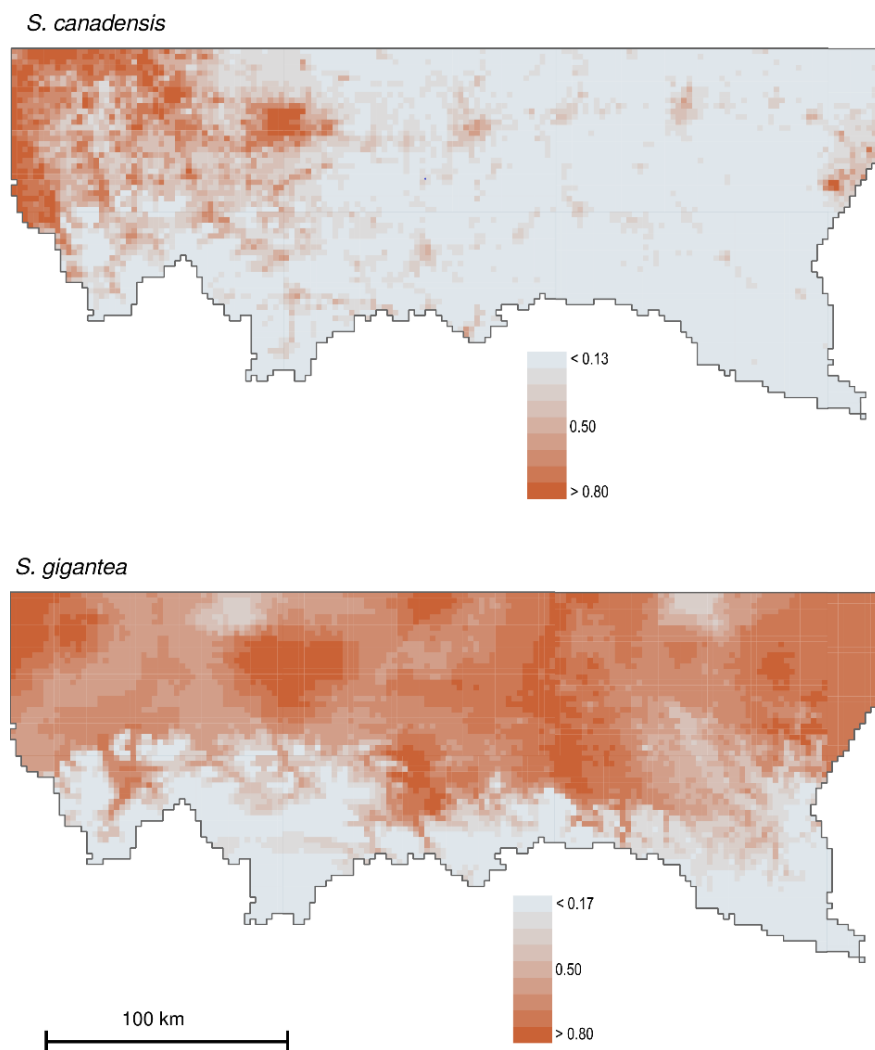
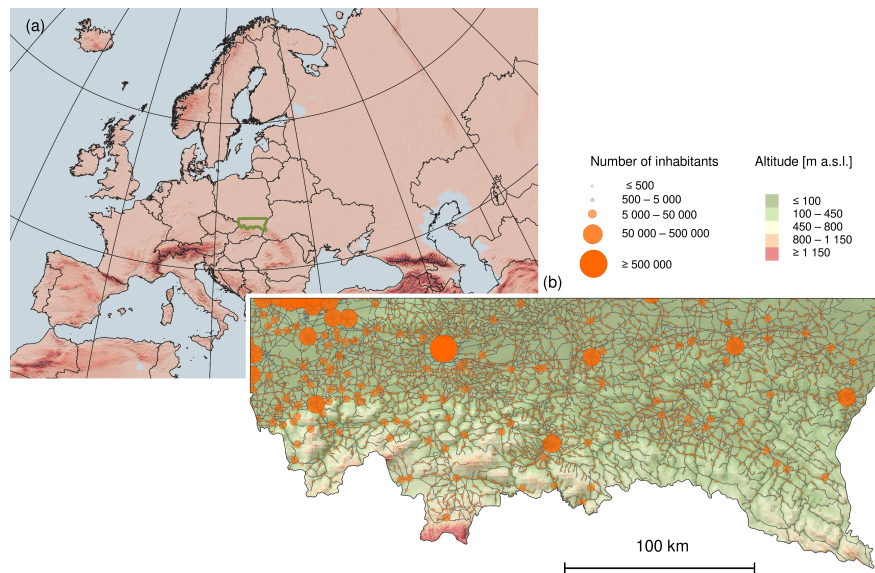
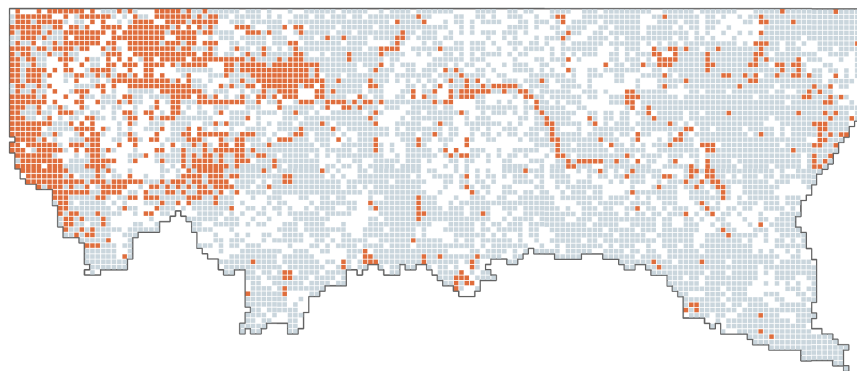


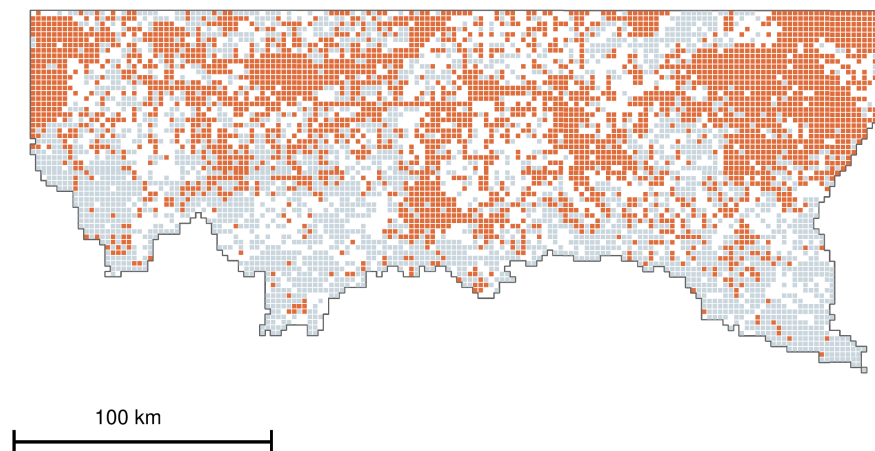
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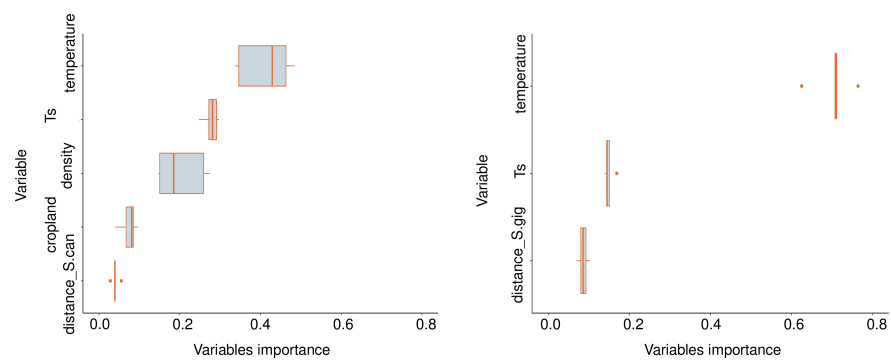
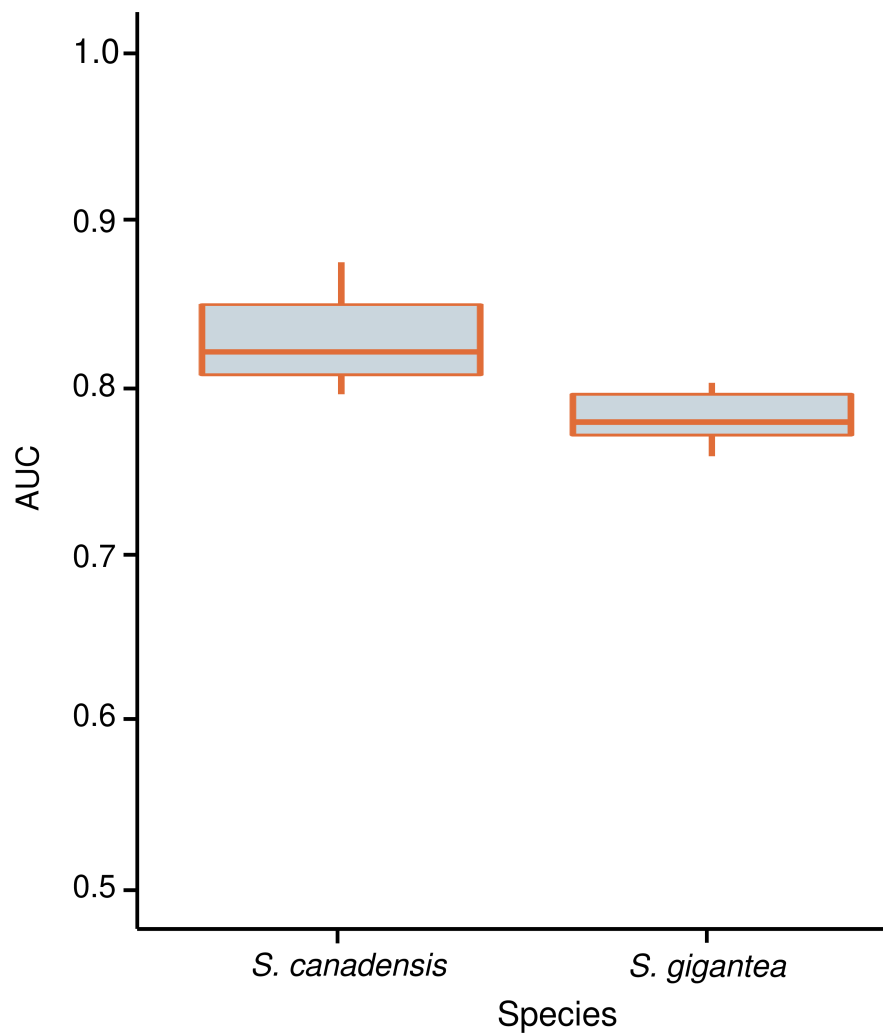


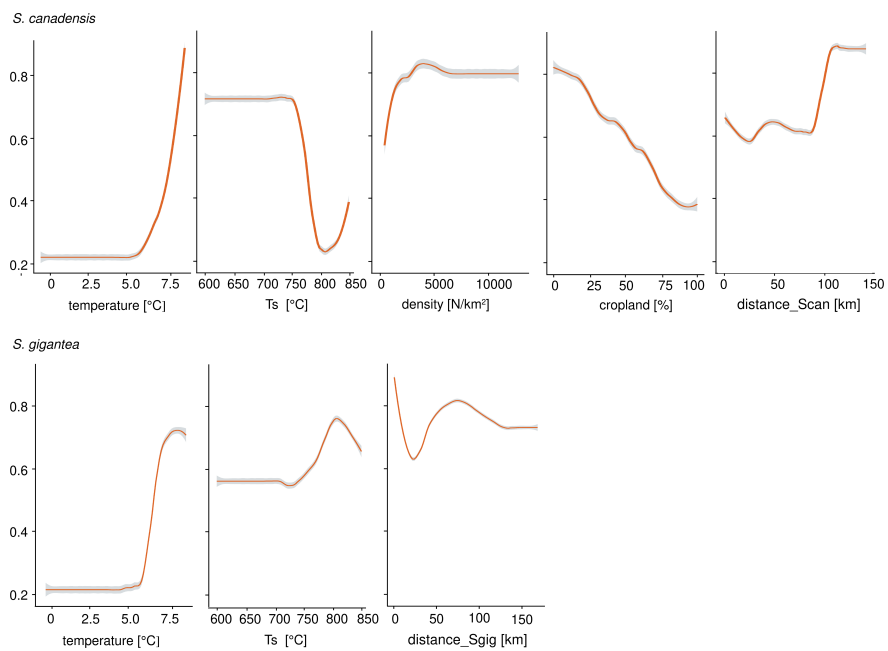
S. canadensis



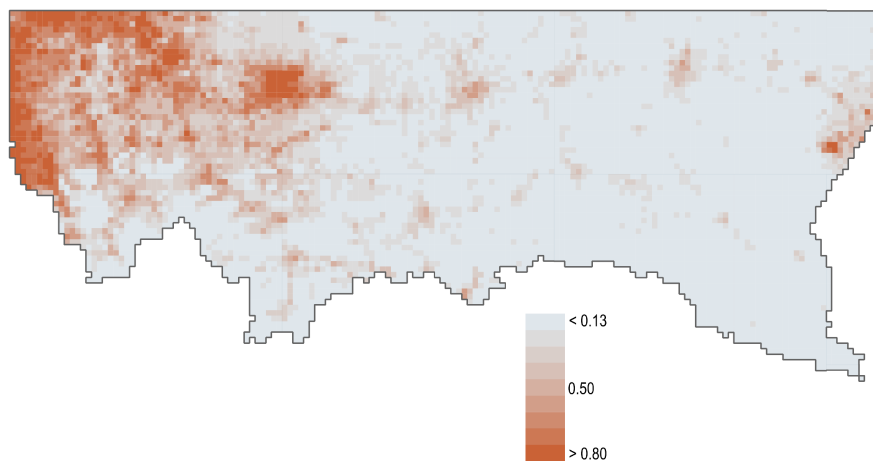
S. gigantea







S. canadensis



S. gigantea

