ENVIRONMENTAL SCIENCES

APPLICATION NATURA 2000 DATA FOR THE INVASIVE PLANTS SPREAD PREDICTION*

J. Pěknicová, D. Petrus, K. Berchová-Bímová

Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Prague, Czech Republic

The distribution of invasive plants depends on several environmental factors, e.g. on the distance from the vector of spreading, invaded community composition, land-use, etc. The species distribution models, a research tool for invasive plants spread prediction, involve the combination of environmental factors, occurrence data, and statistical approach. For the construction of the presented distribution model, the occurrence data on invasive plants (*Solidago* sp., *Fallopia* sp., *Robinia pseudoaccacia*, and *Heracleum mantegazzianum*) and Natura 2000 habitat types from the Protected Landscape Area Kokořínsko have been intersected in ArcGIS and statistically analyzed. The data analysis was focused on (1) verification of the accuracy of the Natura 2000 habitat map layer, and the accordance with the habitats occupied by invasive species and (2) identification of a suitable scale of intersection between the habitat and species distribution. Data suitability was evaluated for the construction of the model on local scale. Based on the data, the invaded habitat types were described and the optimal scale grid was evaluated. The results show the suitability of Natura 2000 habitat types for modelling, however more input data (e.g. on soil types, elevation) are needed.

invasive species; habitat type; modelling scale; species distribution models (SDMs)



doi: 10.1515/sab-2015-0031 Received for publication on July 31, 2014 Accepted for publication on September 5, 2015

INTRODUCTION

Biological invasions have been in the scientists' focus for more than three decades. Generalization and theoretical integrations, based on large data sets and a high number of experimental studies, have been postulated (K u e ff e r et al., 2013). Despite the enormous knowledge, the ability to predict the spreading of non-native species is still elusive (Pyšek et al., 2012b). The spread of invasive plants depends on several ecological factors, primarily on the environmental requirements, nutrient saturation, invaded community composition, distance from the vector of spreading, effect of human activities and land-use. On a local scale, the non-native species spread is shaped by the spatio-temporal interaction with invaded habitat types and host communities (Pyšek, Richardson, 2006). Using the species distribution data, it is possible to identify the potentially invaded habitat types in the study area, and to facilitate prediction trials on the spread of invasive species (C h y trý et al., 2008; D u l l i n g e r et al., 2009; L o s o s o v á et al., 2012; P y š e k et al., 2012a). This knowledge, in combination with employing the geographic information system (GIS) and statistical tools, serves for constructing the species spread models. Beside the urgency of obtaining at least some predictive power in invasive species spread models (K u e f f e r et al. 2013), the evaluation of different types of models is an addition to the continuous and progressive development of species predictive modelling, as pointed out by A u s t in (2007).

Predicting the potential spread of species is generally based on various mathematical models and statistical processing of their responses to different gradients or factors (Brych, 2009). These models

^{*} Supported by the Internal Grant Agency of the Czech University of Life Sciences Prague (IGA 2014), Project No. 422201312423170, and by DKR -Wetland Group, Project No. 4222013223243.

are generally based on various hypotheses how the environmental factors control the distribution of species and communities. Besides its prime importance as a research tool in autecology, predictive geographical modelling has recently gained importance as a tool for assessing the impact of accelerated land use and other environmental changes on the distribution of organisms, and is mostly used in environmental protection, ecology and evolutionary development studies (Guisan, Zimmermann, 2000; Zimmermann et al. 2010). The models combine species occurrence data with spatially environmental layers. This method simulates the ecological requirements of species. The geographical spread of species is then predicted by mapping the areas where these environmental requirements are met (Elith et al., 2006).

Based on the type of data, the species distribution models (SDMs) can be divided into two groups: the first group utilizes presence records, while the second employs regression methods (Elith et al., 2006). From the group of SDMs based on regression approaches, the most widely used are generalized linear models (GLM) and generalized additive models (GAM). These have a strong statistical base and the ability to realistically model the ecological relationships (Austin, 2002). For the modelling, the potential distribution of species together with GIS has been used for long-term predictions (Moisen et al., 2006). GAMs use non-parametric, data-defined smoothers to fit non-linear functions, whereas GLMs fit parametric terms - usually some combination of linear, quadratic and/or cubic terms. Data for GLMs can be selected from a variety of distributions including normal, binomial, Poisson or negative binomial (Guisan et al., 2002). The Multivariate Adaptive Regression Splines (MARS) models are very similar to the GAM models, but instead of data smoothing the former uses segmentation (Peterson et al., 2011). However, for creating predictive GIS maps, the application of MARS is easier and faster than that of GAM (Elith et al., 2006). Generalized boosted regression models (GBM or BRT) are a relatively new and modern method. It repeatedly creates and combines simple methods, e.g. classification trees related to one explanatory variable (Brych, 2009). Artificial Neural Networks (ANN) is a nonlinear technique which works with the absence and presence of data (Pearson et al., 2002; Elith et al., 2006). GARP (Genetic Algorithm for Rule-set Prediction) models and maximum entropy modelling (MAXENT) are suitable for datasets with only few observations (Elith et al., 2006; Pearson et al., 2007). As published by Elith et al. (2006) and Brych (2009), the most accurate models, BRT and GLM/GAM, were evaluated using AUC (Area under Curve) statistics.

One of the important things for model design is to consider the scale and to determine the predictive

time. Data on large (continental) scales are collected often from several countries and are averaged for the rest of the continent or transferred to another country outside the continent (Pit et al., 2011; Chytrý et al., 2012). For large areas, only general data are available and it is difficult to cover the whole territory with the intensity which would be sufficient for input data collection. Hence, such an approach reduces the accuracy of prediction. Chytrý et al. (2012) constructed maps of future plant invasions under different European land-use changes for the years 2020, 2050, and 2080. Prediction for such a long time period is highly inaccurate due to unexpected changes and unpredictable anthropogenic influence. Niche-based species distribution models (meaning models on a local scale) have become an important tool for assessing the potential range of species under current as well as under predicted future environmental conditions. Such an approach is fundamentally more accurate than models on regional or larger scales (Dullinger et al., 2009; Pyšek et al., 2012b). Brych (2009) tested models with a 1×1 km grid size. He could not demonstrate the influence of habitat type because of the scale size being too large (medium), and recommended a scale of 100×100 m for better model accuracy. N e h r b a s s et al. (2007) simulated the spread of Heracleum mantegazzianum in different habitats for a 5×5 m grid size and short-term data. For such a local scale model, it is possible to compare suitable habitats for invasive plants spread and to evaluate the effect of land-use changes. Despite the accuracy, such detailed models demand detailed input data and have only limited scale-temporal impacts.

Natura 2000 is the EU-wide network of nature protection areas which aims to maintain European biodiversity under the 1992 Habitat Directive. The layer of habitat mapping provides information on the existence and state of natural biotopes on the whole territory of the Czech Republic. Biotopes should be classified uniformly across Europe, and specifically in the Czech Republic this is done based on the Habitat Catalogue of the Czech Republic and the Habitat Assessment Handbook (HAH), utilizing primarily the formation-vegetation (physiognomic) approach and secondarily the floristic approach. Each basic map is provided with the number of the district on a 1:10 000 scale (Nature Conservation Agency of the Czech Republic, http://www.nature.cz/natura2000design-en/hp.php).

The main objectives of the study are: (a) verification of accuracy of the map layer Natura 2000 habitats type in connection with selected invasive species distribution and its following use for prediction SDMs, (b) evaluation and selection of suitable scales for prediction models in accordance with the occupied habitat types, (c) construction of suitable SDMs for selected species distribution data together with GIS tools.

MATERIAL AND METHODS

Data collection

Distribution (presence/absence) data on *Fallopia* species, *Solidago* species, *Heracleum mantegazzianum*, and *Robinia pseudoacacia* have been collected in the study area. The mapped area was located in the Protected Landscape Area (PLA) Kokořínsko, Central Bohemia; the area covered by mapping was about 80 km². Field research was carried out from June to September 2013. Locations of invasive plants were saved by a GPS device and recorded in a paper map. Areas of continuous populations larger than 1 m² were saved by their edge coordinates. For each occurrence, the habitat type was recorded.

Data processing

GPS records of invasive plants occurrence were uploaded as a shapefile layer in the ArcGIS program and then intersected with the shapefile habitat layer of Natura 2000 (provided by the Nature Conservation Agency of the Czech Republic, http://www.nature.cz/ natura2000-design-en/hp.php). The final layer contains the attribute table with information about Natura 2000 habitat types and information about the presence data of invasive plants, which was statistically evaluated for different classification scale habitats. Data analysis focused on (1) verification of the accuracy of maps and correct intersection of species with mapped habitat type and (2) finding habitat type preferences, meaning environmental requirements. This allowed the evaluation of the data suitability for the model construction on a local scale. Afterwards, the vector layer was transformed to a raster layer and square grids were constructed with various grid sizes: about 20×20 m (scale I), 30×30 m (scale II), and 50×50 m (scale III). This layer of preferred habitats was used for predictive models. The accuracy of the intersection of layers was analyzed on different scales by identifying the type of habitat from the Habitat Catalogue of the Czech Republic (Chytrý et al., 2001). Scale I corresponds to the subunit of a habitat (e.g. L2.2A code); scale II corresponds to the classification unit of a habitat (e.g. L2 code), and scale III corresponds to the formation III group (e.g. L code).

Data analysis

The dataset containing the presence/absence data of invasive plant species and habitat types was statistically evaluated by R software (Version 2.15.1). Agreement of the intersection of the occurrence of the invasive plant and the habitat type layer with reality was evaluated as 1; disagreement was evaluated as 0. After that, data agreement was statistically evaluated

Table 1. Comparison accuracy of intersect for scale I - 20 \times 20 m (P < 0.001 for 106 disagreement and 389 agreement, probability of success 0.7858586)

	Disagreement with real habitat	Agreement with real habitat
Solidago species	43	145
Robinia pseudoacacia	57	209
Fallopia species	6	35

using a binomial test. A second data analysis evaluated the most invaded habitats according to the frequency of occurrences using one-way analysis of variance (ANOVA), where the habitat type and species were taken as predictors and the number of localities per species and habitats was taken as a response variable. The species *Heracleum mantegazzianum* was not used in this analysis due to its low abundance in the study area.

Models

Seven distribution modelling algorithms (GLM, GAM, GBM, ANN, SRE, and CTA), implemented in R statistical software (biomod2 package) were used for the spread prediction. The stand-alone model MAXENT was used for modelling, too. For evaluating the model prediction, the True Skill Statistic (TSS), Relative Operating Characteristic (ROC), Cohen's kappa statistic (KAPPA), Success Ratio (SR), Probability of Detection (POD) methods were used (Inside-R: A community site for R, http://www.inside-r.org/node/166097). They were rescaled to all have a perfect score at 1. For ROC, POD, SR evaluation, the range of the index form is 0 to 1; 0.5 indicates no skill. For TSS and KAPPA, the range is -1 to 1; where 0 indicates no skill. The pilot sets of models were run for Fallopia sp., Solidago sp., and Heracleum mantegazzianum. Robinia pseudoacaccia was not included to the pilot modelling run due to incomplete distribution mapping.

RESULTS

The results are based on the information stemming from 495 occurrences from the south-eastern part of the PLA Kokořínsko (80 km²). The agreement between the intersection of the species occurrence data layer and the Natura 2000 habitat type *in situ* was evaluated.

Results in Table 1 compare the occurrence records for the most detailed scale of biotopes. 389 records were evaluated as being the same as in real habitats, 106 records were a bit different from real habitats. Such a scale is very detailed and the probability of success was 78%. Results in Table 2 were a little generalized compared to scale I. 439 occurrences were

Table 2. Comparison accuracy of intersect for scale II -30×30 m (P < 0.001 for 56 disagreement and 439 agreement, probability of success 0.8868687)

	Disagreement with real habitat	Agreement with real habitat
Solidago species	23	165
Robinia pseudoacacia	30	236
Fallopia species	3	38

Table 3. Comparison accuracy of intersect for scale III – 50×50 m (P < 0.001 for 41 disagreement and 454 agreement, probability of success 0.9171717)

	Disagreement with real habitat	Agreement with real habitat
Solidago species	16	172
Robinia pseudoacacia	22	244
Fallopia species	3	38

evaluated as being the same as in the real habitat and 56 occurrences were different. The probability of success (i.e. of obtaining a good intersection) was 88%. Results in Table 3 were similar to the results in Table 2. 454 occurrences were the same in the actual habitats and in the intersection layer, 41 occurrences differed. The probability of success was 91%. With the increasing generalization of habitats, the probability of intersection increased. However, the habitats in Table 3 are generalized and not too accurate. For further research, as the most suitable scale appeared the scale II (30 × 30 m), which describes the habitats at the level of basic units, e.g. alluvial forests (L2).

The most invaded habitats for each invasive plant were also evaluated. The results of one-way ANOVA

(F = 1.901, df = 8, P = 0.0622) show that the most invaded habitat of *Solidago* species are grasslands, intensively managed fields, and mosaic segments (segments containing two or more different habitats). *R. pseudoaccacia* is most common in the habitat of acidophilous oak woods, forests with non-native trees, and at the edges of intensively farmed fields. *Fallopia* species is most common in the following habitats: mosaic segments, urbanized areas, and floodplain forests. *Heracleum mantegazzianum* was detected only at 5 localities and its most invaded habitat type were forests with non-native vegetation. The results are shown in Fig. 1.

The pilot set of models for *Fallopia* sp., *Solidago* sp., and *Heracleum mantegazzianum* was run and ac-

Species	No. of localities	Model type	Evaluation characteristic			
			TSS	ROC	KAPPA	POD
Fallopia sp.	107	GAM	0.982	0.992	0.069	1.000
		GBM	0.824	0.936	0.000	0.955
		СТА	0.763	0.893	0.000	0.955
		GLM	0.563	0.801	0.004	0.818
		ANN	0.517	0.772	0.005	0.727
		SRE	0.555	0.778	0.002	0.909
	980	GAM	0.982	0.992	0.069	1.000
<i>Solidago</i> sp.		GBM	0.824	0.936	0.000	0.955
		СТА	0.763	0.893	0.000	0.955
		GLM	0.563	0.801	0.004	0.818
		ANN	0.517	0.772	0.005	0.727
		SRE	0.555	0.778	0.002	0.909
Heracleum mantegazzianum	5	GAM	1.000	1.000	1.000	1.000
		GBM	1.000	1.000	0.000	1.000
		СТА	0.921	0.968	0.000	1.000
		GLM	0.979	0.990	0.005	1.000
		ANN	0.000	0.498	0.001	0.000
		SRE	0.000	0.498	0.000	0.000

Table 4. Conclusion of evaluating characteristics for a run of the pilot set of models for the distribution of three invasive species in the PLA Kokořínsko. Evaluation characteristics as per Biomod modelling¹ are shown for each model and each species

TSS = True Skill Statistic, ROC = Relative Operating Characteristic, KAPPA = Cohen's kappa Statistics, POD = Probability of Detection ¹Inside-R: A community site for R (http://www.inside-r.org/node/166097)

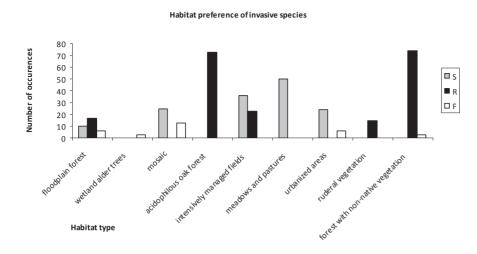


Fig. 1. The most invaded habitats in PLA Kokořínsko by *Solidago* species (S), *Robinia pseudoacacia* (R), *Fallopia* species (F) (P = 0.0622, F = 1,901 df = 8)

cording to the above-mentioned (see the Material and methods section) evaluating methods, the most suitable models for predicting each of the invasive species were selected. For the genera *Fallopia* sp. and *Solidago* sp. the best models were GAM, GBM, and CTA (Table 4). Other models either strongly underestimated (ANN) or highly overestimated (SRE) the predicted spread. *Heracleum mantegazzianum* spread was best predicted by the GLM and ANN models. The MAXENT model achieved very good results for the genera *Fallopia* sp. and *Solidago* sp., although its results for the species *Heracleum mantegazzianum* were not so good.

Fig. 2 shows the predictions using six different model techniques on the same distribution (presence/ absence) data for *Fallopia* sp. The most realistic prediction, according visualization and statistic research,

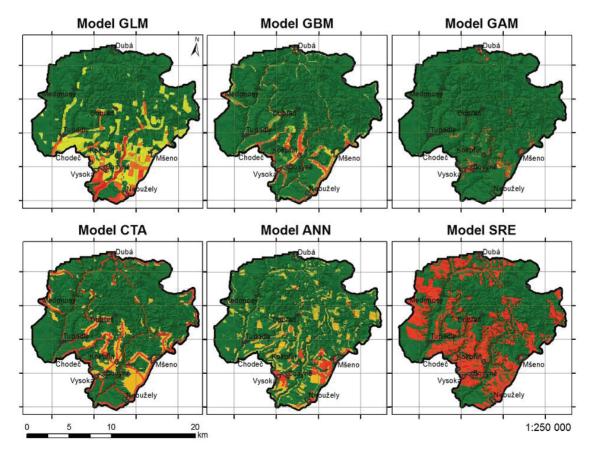


Fig. 2. Map of prediction spread (*Fallopia* species). Red colour marks high likelihood of being invaded by alien species, green colour low likelihood of being invaded by alien species.

were GBM, GAM, and CTA. The evaluation characteristics of GLM, ANN, and SRE were lower than those of the other compared models. Moreover, model SRE marked almost the whole area threatened by invasion.

DISCUSSION

One of the present study objectives was the evaluation of different habitat scales for Natura 2000 habitats and their suitability for the creation of the invasive species spread predictive model. Scale I (20×20 m) was very detailed and some habitats were different from reality. Scale III (50×50 m) introduced too much generalization. Therefore, scale II (30×30 m) was evaluated as the most suitable for a prediction model. The loss of information due to generalization is relatively low (Table 2) and intersection rates of occurrence records and actual habitats are very good.

Of the seven tested algorithms, it was concluded that GAM, GBM, and CTA were the most suitable for the prediction of invasive plants spread. Other models (GLM, ANN, and SRE) yielded inaccurate results (Table 4). This can be due to the (insufficient) quality and number of input datasets. Heracleum mantegazzianum was detected only at 5 localities, which might have influenced the accuracy of prediction. According to Brych (2009), GLM, GAM, and GBM yield stable and good results. The most accurate algorithm was evaluated to be GBM, which corresponds to the results of Elith et al. (2006). Leathwick et al. (2006) and Moisen et al. (2006) concluded that GAM had significantly better results than the other compared models. N e h r b a s s et al. (2007) created a simulation model consisting of population dynamics, neighbourhood dispersal, long-distance dispersal, and dynamic landscape structure, and combined these characteristics with the empirical field. The model included some aspects of reality in a very crude manner, but even this simple design can be applied to the invasion of the other species (e.g. Rhododendron ponticum). Such a model for a local scale can describe the relationships of habitats and invasive species. Firstly, the Natura 2000 habitat types were not found as a significant predictor in models based on such a dataset. The reason for this could lie in the high abundance of the 'mosaic' habitat type which combines more than one habitat type in the dataset. After a thorough analysis and removing the unnecessary habitat type 'unnatural and unmapped segment', the Natura 2000 habitat was shown to be an important variable for SDMs.

C h y t r ý et al. (2008) concluded that no and/or only few non-native plant species occur in extreme and nutrient-poor habitats, such as bogs, moors, and alpine grasslands. In contrast, most non-native species have been found in regular disturbed habitats with fluctuating nutrient availability (e.g. B í m o v á et al., 2004). Those habitats can be influenced by human activities (croplands, ruderal vegetation, hiking trails, etc). Other habitats preferred by non-native plant species are coastal and river areas. Despite this generalizing summary of the occurrence of invasive species, it is necessary to determine the ecological requirements for each species separately. According to Walck et al. (1999), the Solidago species can be found on the edges of forests, along rivers, and in disturbed habitats such as abandoned pastures, edges of roads, abandoned fields, lawns, and urban areas. To the PLA Kokořínsko this species has spread from urbanized areas, where it was mostly grown in gardens. From anthropogenic gardens it escaped to pastures and meadows (Fig. 1). Most localities were sunny and often composed of Calamagrostis epigejos populations. Solidago was the most predominant invasive plant in the mapped area (980 localities). Robinia pseudoacacia is tolerant to air pollution and drought and grows in sandy, saline, and poorly drained substrates (Musil, 2005). The populations have spread from the places where they were dropped off around road trips and cultivated fields. Seedlings were found close to other Robinia trees. In the study area, the species was discovered at 266 localities and mostly in acidophilous oak forests. All three Fallopia species have spread mostly by vegetative form (Bailey et al., 2007). They have a very good regenerative capacity of rhizomes and stem parts and can be transported by land and water (Bímová et al., 2003; Pyšek et al., 2003). They require moisture and nitrogen input (Pyšek et al., 2012a). In the mapped area, they were discovered at 107 localities and usually occupied habitats close to urban areas, mostly road sides and hiking trails.

CONCLUSION

It may be concluded that scale II $(30 \times 30 \text{ m}; \text{ cor-}$ responding to the classification unit of habitat) is the most suitable for the prediction model. The habitat type data of Natura 2000 mapping were evaluated as being suitable and accurate for particular habitat types, but not for the mixed habitat type - mosaic. Replications of field mappings will be necessary for the absolute verification of the results in other study areas. The observed occurrences of invasive plants in habitats are very similar to those in other studies (C h y t r ý et al., 2008; Pyšek et al., 2012). The source of spreading is usually an urbanized area where these species are grown as ornamental plants in the gardens. The species were found also in atypical habitats, e.g. Fallopia × bohemica in coniferous forests and Solidago sp. in Calamagrostis epigeios populations.

Suitable prediction models are selected according to data distribution, number of observations, etc. The best solution is tested and compared to several types of models and different predictors. A preliminary analysis suggests that GBM and GAM are suitable for *Solidago* species, whereas GLM is suitable for *Heracleum mantegazzianum* in our case study, i.e. for species with a low abundance in the study area. Using different model types in combination with different species distribution data, we found that the quality of input data, both environmental and on the species distribution, were crucial for model accuracy.

REFERENCES

- Austin MP (2002): Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling, 157, 101–118. doi: 10.1016/ S0304-3800(02)00205-3.
- Austin M (2007): Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling, 200, 1–19. doi: 10.1016/j. ecolmodel.2006.07.005.
- Bailey JP, Bimová K, Mandák B 2007): The potential role of polyploidy and hybridization in the further evolution of the highly invasive Fallopia taxa in Europe. Ecological Research, 22, 920–928. doi: 10.1007/s11284-007-0419-3
- Bímová K, Mandák B, Pyšek P (2003): Experimental study of vegetative regeneration in four invasive *Reynoutria* taxa. Plant Ecology, 166, 1–11.
- Bímová K, Mandák B, Kašparová I. (2004): How does *Reynoutria* invasion fit the various theories of invasibility? Journal of Vegetation Science, 15, 495–504.
- Brych P (2009): Potential spatial distribution models of invasive plants in the Czech Republic: comparison of methods and their implementations, data availability and effect of species ecology on prediction results. Master's Thesis, University of South Bohemia in České Budějovice. (in Czech)
- Dullinger S, Kleinbauer I, Peterseil J, Smolik M, Essl F (2009): Niche based distribution modelling of an invasive alien plant: effects of population status, propagule pressure and invasion history. Biological Invasions, 11, 2401–2414. doi: 10.1007/s10530-009-9424-5.
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton J McC, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006): Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129–151.
- Guisan A, Zimmermann EN (2000): Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186. doi: 10.1111/j.2006.0906-7590.04596.x.
- Guisan A, Edwards TC Jr, Hastie T (2002): Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling, 157, 89-100. doi: 10.1016/S0304-3800(02)00204-1.

- Chytrý M, Kučera T, Kočí M (eds) (2001): Habitat Catalogue of the Czech Republic. Nature Conservation Agency of the Czech Republic, Prague.
- Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008): Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology, 45, 448–458. doi: 10.1111/j.1365-2664.2007.01398.x.
- Chytrý M, Wild J, Pyšek P, Jarošík V, Dendoncker N, Reginster I, Pino J, Maskell LC, Vilà M, Pergl J, Kühn I, Spangenberg JH, Settele J (2012): Projecting trends in plant invasions in Europe under different scenarios of future land-use change. Global Ecology and Biogeography, 21, 75–78. doi: 10.1111/j.1466-8238.2010.00573.x.
- Kueffer C, Pyšek P, Richardson M (2013): Integrative invasion science: model systems, multi-site studies, focused metaanalysis and invasion syndromes. New Phytologist, 200, 615–633. doi: 10.1111/nph.12415.
- Leathwick JR, Elith J, Hastie T (2006): Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling, 199, 188–196. doi: 10.1016/j.ecolmodel.2006.05.022.
- Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Láníková D, Otýpková Z, Řehořek V (2012): Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. Biological Conservation, 145, 179–184. doi:10.1016/j.biocon.2011.11.003.
- Moisen GG, Freeman EA, Blackard JA, Frescino TS, Zimmermann NE, Edwards Jr. TC (2006): Predicting tree species presence and basal area in Utah: a comparison of stochastic gradient boosting, generalized additive models, and treebased methods. Ecological Modelling, 199, 176–187. doi: 10.1016/j.ecolmodel.2006.05.021.
- Musil I (2005): Deciduous forests 2. Czech University of Life Sciences Prague, Prague. (in Czech)
- Nehrbass N, Winkler E, Müllerová J, Pergl J, Pyšek P, Perglová I (2007): A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. Biological Invasions, 9, 383–395. doi: 10.1007/s10530-006-9040-6
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011): Ecological niches and geographic distributions. Princeton University Press, New Jersey.
- Pearson RG, Dawson TP, Berry PM, Harrison PA (2002): SPE-CIES: A spatial evaluation of climate impact on the envelope of species. Ecological Modelling, 154, 289–300. doi: 10.1016/S0304-3800(02)00056-X.
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007): Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography, 34, 102–117.

- Pit JPW, Kriticos DJ, Dodd MB (2011): Temporal limits to simulating the future spread pattern of invasive species: *Buddleja davidii* in Europe and New Zealand. Ecological Modelling, 222, 1880–1887. doi: 10.1016/j.ecolmodel.2011.03.023.
- Pyšek P, Brock JH, Bímová K, Mandák B, Jarošík V, Koukolíková I, Pergl J, Štěpánek J. (2003): Vegetative regeneration in invasive *Reynoutria* (Polygonaceae) taxa: the determinant of invasibility at the genotype level. American Journal of Botany, 90, 1487–1495. doi: 10.3732/ ajb.90.10.1487.
- Pyšek P, Richardson DM (2006): The biogeography of naturalization in alien plants. Journal of Biogeography, 33, 2040–2050. doi: 10.1016/j.ecolmodel.2011.03.023.
- Pyšek P, Chytrý M, Pergl J, Sádlo J, Wild J (2012a): Plant invasions in the Czech Republic: current state, introduction

dynamics, invasive species and invaded habitats. Preslia, 84, 575-629.

- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012b): A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology, 18, 1725–1737.
- Walck JL, Baskin JM, Baskin CC (1999): Relative competitive abilities and growth characteristics of a narrowly endemic and geographically widespread *Solidago* species (Asteraceae). American Journal of Botany, 86, 820–828. doi: 10.2307/2656703.
- Zimmermann NE, Edwards TC, Graham CG, Pearman PB, Svenning J-C (2010): New trends in species distribution modelling. Ecography, 33, 985–989. doi: 10.1111/j.1600-0587.2010.06953.x.

Corresponding Author:

Ing. Jana Pě k n i c o v á , Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Applied Ecology, Kamýcká 129, 165 21 Prague 6-Suchdol, Czech Republic, phone: +420 224 383 862, e-mail: peknicovaj@fzp.czu.cz