

PRESENCE OF ALIEN *PRUNUS SEROTINA* AND *IMPATIENS PARVIFLORA* IN LOWLAND FOREST FRAGMENTS IN NE SLOVENIA

PRISUTNOST STRANIH VRSTA *PRUNUS SEROTINA* I *IMPATIENS PARVIFLORA* U FRAGMENTIMA NIZINSKIH ŠUMA U SI SLOVENIJI

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SUMMARY

Temperate alluvial, riparian and lowland forests are the European forests with the greatest presence of invasive alien plants. Consequently, identifying the environmental conditions for and other drivers behind the establishment of invasive species in natural forest communities is crucial for understanding the invasibility of these habitats. We focused on fragments (patches) of Illyrian oak-hornbeam forest in NE Slovenia, which are the least studied in this regard.

Because alien phanerophytes and therophytes are significantly over-represented compared to native plants in lowland forests, we selected two representative invasives: the phanerophyte *Prunus serotina* and the therophyte *Impatiens parviflora*. By using logistic regression models on vegetation surveys, environmental data based on Ellenberg's indicator values, and patch metrics, we identified patch characteristics explaining the presence of each species. Moreover, we included human impact in the models.

We reveal significant characteristics differentiating *P. serotina* from *I. parviflora*. We also show that the perimeter-area ratio and soil nutrients of the forest patches correlate significantly with the presence of *P. serotina*, while human disturbance correlates significantly with the presence of *I. parviflora*. Our results and a similar approach for other invasive plant species can be applied to assess habitat invasibility on potential and species' current geographic distribution, as well as to develop management plans.

KEY WORDS: biological invasions, forest fragmentation, landscape metrics, habitat characteristics, human presence, neophytes

INTRODUCTION

UVOD

Stable natural habitats allowing establishment of long-lived forest communities are generally expected to be relatively resistant to alien plant invasion (Von Holle et al., 2003). However, forest types occurring on temperate river flo-

odplains are the habitats with the highest frequency of alien species present (Essl et al., 2011; Wagner et al., 2017). This is also the case for Slovenian forests, where the highest presence of invasive alien plants was recorded for floodplain forests (Zelnik, 2012). On the Drava river and Mura river plains, three dominant forest types are present: alluvial forests with *Alnus glutinosa* (L.) Gaertn. and *Fraxinus excel-*

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sior L. (*Alnion glutinosae* Malcuit 1929, *Alnion incanae* Pawlowski in Pawlowski, Sokolowski & Wallisch 1928, *Salicion albae* Soó 1930); riparian mixed forests of *Quercus robur* L., *Ulmus laevis* Pall. and *Ulmus minor* Mill., *F. excelsior* or *F. angustifolia* Vahl (*Ulmenion minoris* Oberd. 1953); and on higher elevations Illyrian oak-hornbeam forests (*Erythronio-Carpinion* Horvat 1938/ Marinček et Wallnöfer et al. 1993), which are otherwise predominantly forests of colline belt (Davies et al., 2004). In all these forests, invasive alien species are present (Marinšek and Kutnar, 2017); however, the Illyrian oak-hornbeam forests are the least studied in this regard. This is why we focus on this forest type in our study.

Because of the long presence of humans in these plains, conversion of Illyrian oak-hornbeam forests into productive agricultural land has resulted in a very reduced, patchy distribution of forest remnants (Čarni et al., 1998). The remaining forest patches vary in size and are under continuous anthropogenic pressures.

What is more, previous studies in similar forest types have shown that among life forms, alien phanerophytes and therophytes are significantly over-represented compared to native plant species in lowland forests (Wagner et al., 2017). Therefore, we selected two very common alien invasive plants in studied forest patches (and Slovenian lowland forests in general): the phanerophyte *Prunus serotina* Ehr. and the therophyte *Impatiens parviflora* DC., aiming to assess the drivers behind their occurrence. The second goal of this study was to introduce a model based on forest patch characteristics to explain the presence of both species in a forest patch. We focused on environmental data and particularly on human pressure. Therefore, we included patch metrics in the assessment of occurrence drivers. We hypothesized that by combining environmental characteristics, patch metrics, and the influence of human pressure, we could assess which patch characteristics influence vulnerability to invasion and contribute to the successful spread of *P. serotina* and *I. parviflora* into the studied lowland forest remnants.

METHODS

METODE

Study area – Područje istraživanja

The study was conducted in Illyrian oak-hornbeam (*Erythronio-Carpinion*) forest patches of various configurations on the alluvial plains of the Mura and Drava rivers in the Danube basin (according to EUNIS habitat classification; Davies et al., 2004), with an average altitude between 220 and 250 m a. s. l. The study area is situated in the sub-Pannonian biogeographic region, with a temperate continental climate. Mean annual precipitation and mean annual

temperature are approximately 900 mm and 10.9°C, respectively (ARSO, 2021). The dominant trees are *Quercus robur*, *Q. petraea* Liebl., *Carpinus betulus* L., *Prunus padus* L. and *F. excelsior*.

The geological bedrock of the study area are silicate gravel deposits. The prevailing soil is a dystric ranker containing around 10% of water. As the rankers dry quickly drought is common phenomenon during hot summers with little precipitation. Soil reaction is acidic, soils are poorly saturated with bases and have low cation exchange capacity (Vovk, 1996; Vidic et al., 2015).

Both riverbeds are regulated, and in the past, extensive oak-hornbeam forests were converted into intensively managed arable land. Only small patches of forest have been preserved, mostly in areas less favourable for agricultural use. The main crops on both plains are corn and various cereals for livestock. On Apaško polje, oilseed rape and oilseed pumpkins are also planted frequently (Ščap, 2018). Land ownership structure is traditionally fragmented; therefore, modest small farm cultivation is predominant. Beside, the settlements are scattered, with the mostly rural inhabitants living in family houses with courtyards behind (Ščap, 2018). On the other hand, settlements on the Dravsko polje are relatively large, dense and located at roadsides (Rebernik, 2011). The majority of inhabitants is concentrated in two major urban centres: Maribor and Ptuj.

Studied species – Istraživane vrste

Prunus serotina is deciduous woody perennial native to North America. The species has been globally naturalized, including South America, South Africa, Oceania, Asia and Europe. In several European countries, *P. serotina* is widely naturalized and invasive (CABI, 2020a). Even more, the species is recognized as one of the most invasive trees in Europe (Klotz, 2009). Its negative impact on native ecosystems is shown by reductions in forestry production and in the biodiversity of native trees (CABI, 2020a). *Prunus serotina* is fast growing and tolerant of shaded habitats. In central Europe, *P. serotina* trees mostly exhibit shrubby growth, rarely reaching 20 m in height, while in its native range it can grow up to 38 m. Its juicy fruits are eaten by various birds and mammals, who disperse the seeds over long distances and thus contribute to the expansion of its range (CABI, 2020a).

Impatiens parviflora is an annual herb native to central Asia. Its invasive range extends in the northern hemisphere to North America, including Canada (CABI, 2020b) and Oregon in the USA (USDA, 2013) and to most of Europe, from the southern to the most northern countries (CABI, 2020b). Florianová and Münzbergová (2017) reported that *I. parviflora* in the Czech Republic has had a negative impact on native understorey plant richness by reducing the abun-

dance of spring ephemeral geophytes; however, a general impression persists that it has exerted only a minor impact, if any, on native species diversity (Hejda, 2012). *Impatiens parviflora* is a very successful invasive plant with the ability to extend its range extremely rapidly. It is able to form dense stands even in undisturbed forests with a closed canopy (CABI, 2020b). The seeds are dispersed by birds or other animals and by water; however, they can also be dispersed by humans during the transport of contaminated soil and timber (CABI, 2020b).

Data collection – *Prikupljanje podataka*

We surveyed the occurrence of native and alien plant species in Illyrian oak-hornbeam forest patches: 25 on Apaško polje and 23 on Dravsko polje. Detailed flora inventarisation was performed by recording vascular plants during the exploration of each entire forest patch. To ensure the maximum coverage of species in a patch we recorded species in the entire patch perimeter (edge), along existing walking paths inside the forest patch, and finally by crossing each forest patch diagonally for additional accuracy. For patches with larger area, we increased the inventarization effort comparably. We recorded the presence of all vascular plants found in each patch and classified them as native or alien according to Martinčič et al. (2007) and Jogan et al. (2012). Based on the native species composition of each patch, environmental characteristics including nutrients, moisture, light and temperature were estimated from mean Ellenberg's species indicator values (Table 1; Ellenberg et al., 1992).

Patch landscape metrics were determined using ArcGIS (Table 1; ESRI, 2014). We measured the perimeter and area on satellite images. Additionally, we extracted land use shares in a 200 m buffer around each forest patch from Corine Land Cover 2018 (CLC) data layer (EEA, 2018) and categorised these as follows: urban areas, roads, arable land, forest area and meadows. To obtain patch complexity, we calculated the patch indices P/A ratio and SHPI. P/A ratio is determined as the perimeter (p) – area (a) ratio ($P/A \text{ ratio} = p/a$, $P/A \text{ ratio} > 0$) and SHPI (Patton 1975) as $SHPI = p/(2(\sqrt{\pi a}))$, $SHPI > 1$).

Variables indicating human pressure were determined at the time of flora sampling in terms of the presence of any sort of waste (household waste, bulky waste), garden waste or walking paths in the forest patch (Table 1). These variables have been chosen because alien plant propagules can be introduced into the studied forest patches with waste, especially garden waste (Šipek and Šajna, 2020 and references therein). Additional human presence was indicated by the presence of walking paths in a patch, since paths can serve as corridors for the spread of alien plants propagules attached to clothing (anthropochory). Other human related disturbances such as tree felling were not carried out in the time of recording.

Data analysis and modelling – *Analiza i modeliranje podataka*

Patch metrics for each patch and land cover shares in the 200 m buffer surrounding each patch as well as environmental characteristics obtained as mean Ellenberg's species indicator values for native flora belonged to continuous variables (Table 1). They were compared between forest patches where the species of interest was present or absent using the *stat_compare_means* function and method t-test in package "ggpubr".

Table 1. Landscape metrics for a patch, environmental characteristics and human pressure variables included in the full logistic models as predictors of *Prunus serotina* and *Impatiens parviflora* presence in studied lowland forest patches in Slovenia.

Tablica 1. Krajobrazna metrika fragmenata, okolišne karakteristike i varijable antropogenog pritiska uključeni su u cjelovite logističke modele kao prediktori prisutnosti *Prunus serotina* i *Impatiens parviflora* u istraživanim nizinskim šumskim fragmentima u Sloveniji.

	Variable (type) Varijabla (vrsta)	
Landscape metrics for a patch <i>Krajobrazna metrika fragmenata</i>	Urban area share in 200 m buffer (continuous) Udio gradskog područja unutar 200 m zaštitne zone (kontinuirano)	
	Roads share in 200 m buffer (continuous) <i>Udio cesta unutar 200 m zaštitne zone (kontinuirano)</i>	
	Arable land share in 200 m buffer (continuous) <i>Udio obradivog zemljišta unutar 200 m zaštitne zone (kontinuirano)</i>	
	Forest area share in 200 m buffer (continuous) <i>Udio šumskog područja unutar 200 m zaštitne zone (kontinuirano)</i>	
	Meadows share in 200 m buffer (continuous) <i>Udio livada unutar 200 m zaštitne zone (kontinuirano)</i>	
	P/A ratio (continuous) <i>Omjer P / A (kontinuirano)</i>	
	SHPI (continuous) <i>SHPI (kontinuirano)</i>	
	Environmental characteristics <i>Okolišne karakteristike</i>	Nutrients (continuous) <i>Hranjive tvari (kontinuirano)</i>
		Moisture (continuous) <i>Vlaga (kontinuirano)</i>
		Light (continuous) <i>Svjetlo (kontinuirano)</i>
Human pressure <i>Antropogeni pritisak</i>	Temperature (continuous) <i>Temperatura (kontinuirano)</i>	
	Waste (dummy) <i>Otpad (binarno)</i>	
	Garden waste (dummy) Vrtni otpad (binarno)	
	Walking paths (dummy) <i>Pješačke staze (binarno)</i>	

Additionally, patch metrics, environmental estimates together with human pressure variables were tested with binomial multivariate logistic regression models to describe the presence of *P. serotina* and *I. parviflora* related to patch characteristics, using the *glm* function with binomial family distribution. In the full models, all variables shown in Table 1 were included. Continuous variables were z-standardized before the models were implemented to allow comparison of variable effects. Regression coefficients were transformed using the exponential function to yield the odds ratio associated with a one-unit increase in the case of continuous variables or comparison with the baseline level in the case of factors.

The best model (final model) was selected according to the lowest AIC value with the *dredge* function in the “MuMIn” package (Barton, 2009). The absence of multicollinearity among the explanatory variables included in the final model was determined by calculating the variance inflation factor ($VIF < 2$; Fox and Monette, 1992) in the “car” package (Fox and Weisber, 2019). Goodness of model fit was evaluated with Chi-square test (X^2) statistics at a significance level $P < 0.05$. X^2 was calculated as the deviance of the null model subtracted from the deviance of the model

fit (Δ deviance) and degrees of freedom of the null model subtracted from degrees of freedom of model fit. Statistical analyses were conducted in the statistical software environment RStudio for R (Version 1.3.1093 for Windows; R Core Team, 2019).

RESULTS REZULTATI

Prunus serotina and *Impatiens parviflora* were detected in 25% and 48% of studied forest patches, respectively. Comparison between forest patches with *P. serotina* present or absent revealed significant differences in P/A ratios and estimated nutrients and light conditions (Fig. 1). On the other hand, we did not find differences between forest patches where *I. parviflora* was present and those where it was absent (Fig. 1). Nevertheless, with further analyses using logistic regression we detected some interesting trends discussed below.

Variables that significantly affected the probability of each species being present in the forest patch were species specific. Comparing alternative multivariate models predicting the presence of each species (Appendix 1 and Appendix 2)

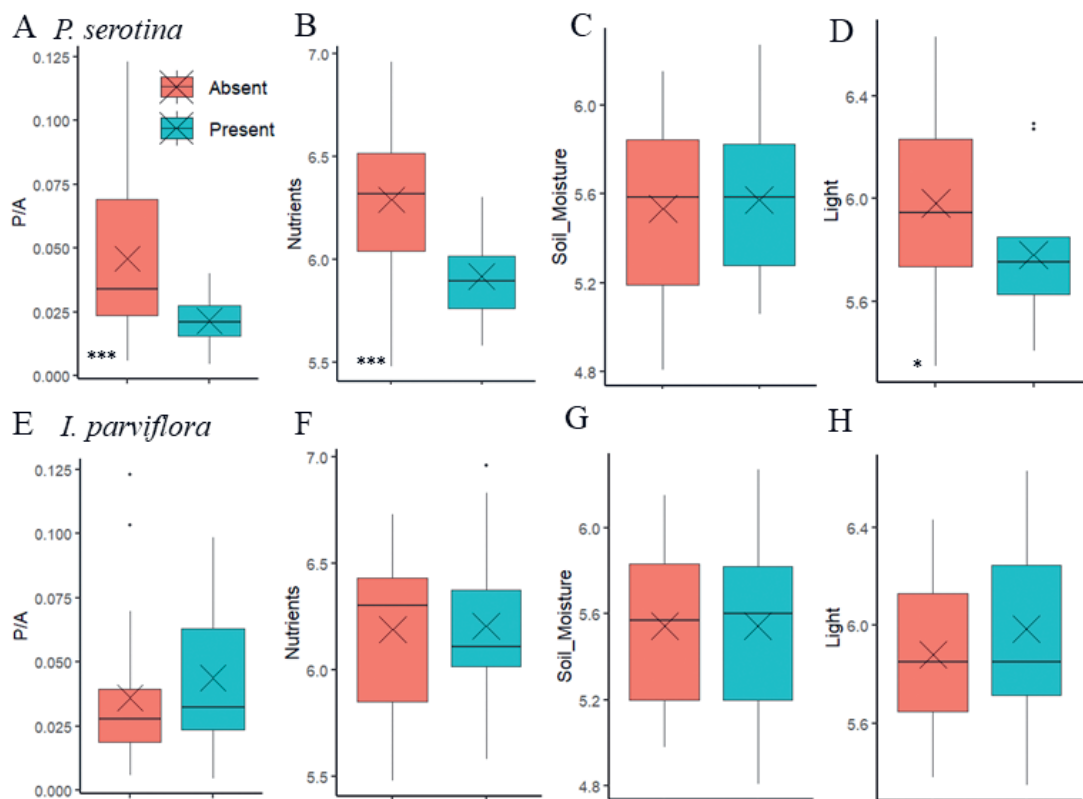


Figure 1. Comparison of **A, E** perimeter to area ratio and environmental conditions based on mean Ellenberg's bioindicator values – **B, F** nutrients, **C, G** soil moisture and **D, H** light, in forest patches according to the presence and absence of *Prunus serotina* and *Impatiens parviflora*, respectively. Asterisks indicate significant result of t-test: $P < 0.001$ ***, < 0.01 **, ≤ 0.05 *.

Slika 1. Usporedbe omjera P/A (A, E) i okolišnih uvjeta fragmenata temeljenih na srednjim Ellenbergovim vrijednostima: B, F hranjive tvari; C, G vlaga; i D, H svjetlo prema prisutnosti *Prunus serotina* i *Impatiens parviflora*. Znak * označava da je rezultat t-testa signifikantan: $P < 0.001$ ***, < 0.01 **, ≤ 0.05 *. uvjeti okoliša

Table 2. Results of final logistic regression models according to the lowest AIC value for *Prunus serotina* and *Impatiens parviflora* presence in a forest patch. Probability ratios are shown, values in parentheses representing 95% confidence interval. Significant estimates at $P < 0.05$ are in bold. $P < 0.001$ ***; < 0.01 **; < 0.05 *; < 0.1 +.

Tablica 2. Rezultati konačnih modela logističke regresije prema najnižoj AIC vrijednosti za prisutnost *Prunus serotina* i *Impatiens parviflora* u šumskom fragmentu. Prikazani su omjeri vjerojatnosti, vrijednosti u zagradama predstavljaju interval pouzdanosti od 95%. Značajne procjene pri $P < 0.05$ podebljane su. $P < 0.001$ ***; < 0.01 **; < 0.05 *; < 0.1 +.

	<i>P. serotina</i>	<i>I. parviflora</i>
Intercept / Prekid	0.18 (0.03 – 0.75)*	0.84 (0.17 – ∞)
Roads / Ceste		26.70 (1.38 – ∞)
P/A ratio / P/A omjer	0.10 (0.01 – 0.58)*	1.80 (0.93 – 3.84) +
Nutrients / Hranjiva	0.19 (0.04 – 0.53)**	
Moisture / Vlaga		2.11 (0.96 – 5.49) +
Light / Svjetlost	0.32 (0.08 – 0.98) +	
Waste / Otpad		6.54 (1.46 – 38.43)*
Walking paths / Pješačke staze	0.15 (0.01 – 1.14) +	
Pseudo R ² / Lažni R ²	0.45	0.26
Chi-square test / Chi-square test	$X^2 = 24.51$ ***, df = 4	$X^2 = 17.50$ ** , df = 4
AIC / AIC	39.47	58.96

revealed the optimal model for each species (Table 2, Fig. 2). Only the P/A ratio was included in both final models; however, the effect of this shape index was opposite and statistically significant only for *P. serotina*.

Our results suggest that the probability of *P. serotina* occurring in forest patches decreased as the P/A ratio, estimated nutrients and light indicator values increased. The effects of the P/A ratio and nutrients were statistically significant. Surprisingly, the probability of *P. serotina* being present also decreased if walking paths existed in a forest; however, this effect was only marginally significant (Table 2).

The probability of *I. parviflora* occurring in a forest patch increased with the increasing presence of roads in the bu-

ffer zone surrounding the patch, increasing P/A ratio, higher estimated soil moisture indicator value and with the presence of waste in the forest patch. However, only waste presence had a significant effect. The probability of *I. parviflora* being present in a patch was 6.54 times greater if there was waste detected, compared to patches without waste (Table 2).

DISCUSSION RASPRAVA

The lowland forests in this study patches exhibited the general pattern observed for European woodlands (Wagner et al., 2017): *I. parviflora*, which is the most common alien

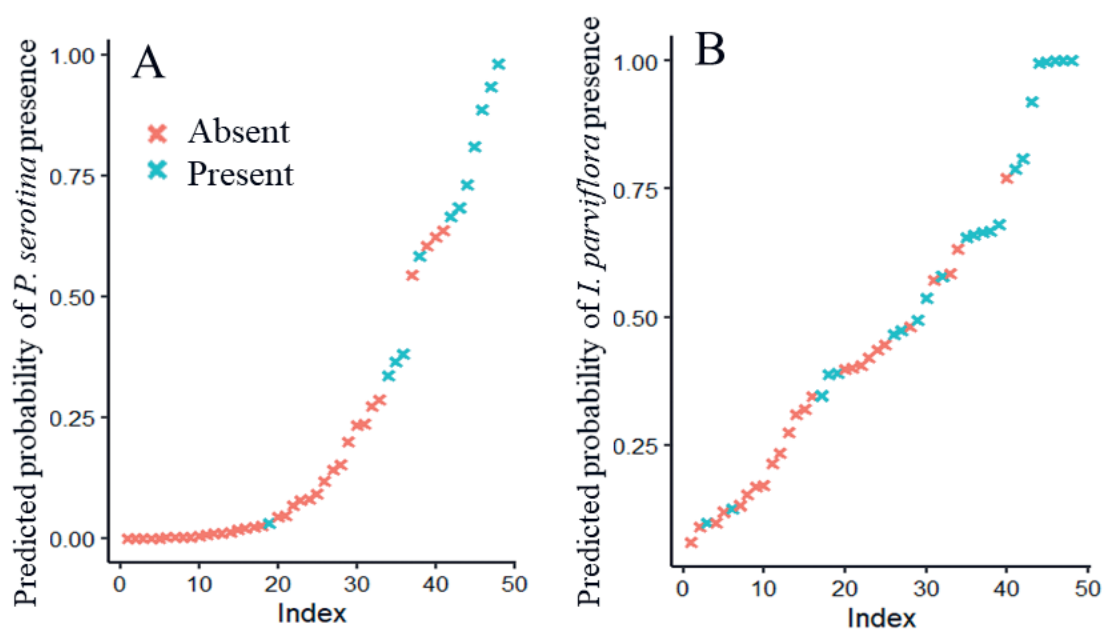


Figure 2. Predicted probability of the occurrence of **A** *P. serotina* and **B** *I. parviflora* in the given forest patches, according to the final model.
Slika 2. Predviđena vjerojatnost pojave **A** *P. serotina* i **B** *I. parviflora* u danim šumskim fragmentima, prema konačnom modelu.

species in European woodlands, was found almost twice as frequently as *P. serotina*. Current spatial occurrence of alien invasive plants is determined by species' eco-physiological requirements, by biotic interactions, particularly with native vegetation, and by local disturbance, which in our study, is mainly human-induced. The latter two, native vegetation and local disturbance, are key factors for the level of invasion: the actual number or proportion of alien species in a habitat (Chytry et al., 2008 and references therein). The findings of our study concerning the establishment of *P. serotina* and *I. parviflora* in these forest patches show that factors predicting their occurrence differed between the two species. We detected different significant determinants for habitats invaded by *P. serotina* or *I. parviflora*, even though we limited our research to forest patches.

Our models predicted that *P. serotina* was significantly more likely to grow in poor sites (low-light and low-nutrient conditions indicated by Ellenberg's value for native species) and in patches with regular shapes (low perimeter – area ratio). This pattern is consistent with the study of *P. serotina* seedling survival in temperate forests (Dyderski and Jagodziński, 2019; Jagodziński et al., 2019; Kawaletz et al., 2013). Seedling survival was positively affected by low-light, understorey cover and pH, but negatively affected by increasing canopy openness and soil moisture. On the other hand, greater light availability was positively associated with *P. serotina* biomass (Dyderski and Jagodziński, 2018a). These results suggest that *P. serotina* saplings are able to survive in an environment with low resource availability, where competition is low, while later on they need more resources to increase their growth (Vanhellemont et al., 2008). On our study site, the majority of the *P. serotina* plants were indeed saplings no higher than 1 meter, while trees were found mainly on forest edges. The edaphic niche of *P. serotina* tends to constitute sites with low levels of nutrients or at least levels similar to those of non-invaded sites in nitrogen values; however, phosphorus values might be higher (Chabrierie et al., 2008). Given the preference for dry soil and a closed canopy, we can expect further spread of *P. serotina* in our study area and in the vicinity because suitable habitats are available and have not yet been invaded by *P. serotina*. Among these, *Pinus sylvestris* L. dominated stands are frequent, and those are habitats where *P. serotina* is known to establish abundantly (Dyderski and Jagodziński, 2019a).

On the other hand, according to our models, *I. parviflora* was more likely to occur in habitats with native flora exhibiting high mean Ellenberg's soil moisture indicator value and high perimeter – area ratio, a metric indicating increased length of forest edge. This is in accordance with *I. parviflora* habitat preferences as it mainly grows in human disturbed forests and forest edges (CABI, 2020b). In the literature, the enormous success of *I. parviflora* in colonizing European woodlands is often explained by its broad habitat niche (Quinet et al., 2015), although its edaphic niche is still not well understood, since

the literature reports a preference for both nutrient-rich and nutrient-poor sites (Wagner et al., 2017). Our models showed that study site nutrients obtained from Ellenberg's indicator value for native flora were not a significant predictor. The opposite was true for soil moisture. The model corresponds well with the facts that annual *I. parviflora* germinates in the first year after seeding, that it is only slightly limited by low soil nitrogen, and that it does not form a persistent seed bank (Skálová et al., 2019). Florianová and Münzbergová (2018) argue that factors affecting *I. parviflora* success differ depending on the life stage. For example, a dense understorey and low soil moisture repress seedling emergence, while a dense understorey has little effect after seedling establishment.

Our results indicate the importance of several habitat characteristics for susceptibility to invasion. In our studied habitats, it could be that habitat characteristics are better determinants of the level of invasion than propagule pressure or climate, as was stressed by Chytry et al. (2008). Moreover, we recognized one additional, important patch characteristic: human pressure, which we can expect to increase worldwide (Wang et al., 2021). *Prunus serotina* was connected to less disturbed forest patches, while *I. parviflora* was also frequent in patches with greater disturbance and more disturbance-related changes, which affected not the patch alone but the adjacent surroundings as well. Just as the traits of successful invaders are specific and context-dependent, and cannot be united into one general trait (Sol et al., 2012), this seems to be true also of habitat characteristics defining susceptibility to invasion.

What we found very concerning is that our models for *I. parviflora* occurrence indicate that several human-related activities, like the presence of waste in the forest and the high frequency of roads in the surrounding landscape, do coincide with this species. The altered landscapes surrounding habitat fragments are rarely static, but instead undergo continuous changes in land use and succession (Laurance, 2002; Laurance et al., 2007). Therefore, we can probably expect the existing dynamics to change eventually, thus influencing the forest remnants in new or additional and more severe ways. As an example, according to a survey, 12% of garden owners in Slovenia do occasionally deposit green garden waste in nearby forests, unaware that they could thus be introducing invasive alien species into nature (Šipek and Šajna, 2020). We further hypothesize that *P. serotina* was less common in disturbed patches dissected by walking paths because frequent human presence might have a negative impact on birds, which disperse *P. serotina* seeds; however, further observations are needed, since the results of studying disturbance effects on *P. serotina* are contradictory. In a study by Dyderski and Jagodziński (2018b), disturbance was of little importance for the ecological success of *P. serotina*, while, in contrast, some earlier studies found a positive effect (Closset-Kopp et al., 2007; Chabrierie et al., 2008). It is worrying

that the survival potential of *P. serotina* in forests might be greater than the seedling survival potential of native trees ($3.9 \pm 1.2\%$ against 0.03% for *Acer platanoides* L. and *A. pseudoplatanus* L., 0.02% *Q. petraea* and none of *F. sylvatica* L.; Dyderski and Jagodziński, 2019a); this could contribute to future decline in native tree diversity.

According to our results, which indicate species-specific patterns, we would like to suggest that, when studying invasive species, conclusions not be based on habitat characteristics alone, particularly not on remote sensing alone. We need to distinguish between factors related to the invasiveness of the species, the susceptibility of the ecosystem, and the introduction effort mediated by humans. Additionally, stochastic events may also influence invasions (Dyderski and Jagodziński, 2019b). This is of prime importance for preventing further spread of alien species in general. However, at the same time, identifying these factors allows us to focus on a particular species to consider possible novel environmental pressures and how the species might respond to these.

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REFERENCES

LITERATURA

- ARSO, 2021: ARHIV - opazovani in merjeni meteorološki podatki po Sloveniji. <https://meteo.arso.gov.si/met/sl/app/webmet/#webmet==8Sdwx2bhR2cv0WZ0V2bvEGcw9ydlJWblR3L-wVnaz9SYtVmYh9iclFGbt9SaulGdugXbsx3cs9mdl5WahxX-YyNGapZXXZ8tHZv1WYp5mOnMHBvZXXZulWYnwCchJXYt-VGdlJnOn0UQQdSf>
- Barton, K., 2009: Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mu-min/>
- CABI, 2020a: *Prunus serotina* [Terwei A.]. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc
- CABI, 2020b: *Impatiens parviflora* [Tanner R.]. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc
- Čarni, A., M. Jarnjak, K. Oštir-Sedej, 1998: Past and present forest vegetation in NE Slovenia derived from old maps. *Appl Veg Sci*, 1: 253–258.
- Chabrierie, O., K. Verheyen, R. Saguez, G. Decocq, 2008: Distinguishing relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. *Divers Distrib*, 14: 204–212.
- Closset-Kopp, D., O. Chabrierie, B. Valentin, H. Delachapelle, G. Decocq, 2007: When Oskar meets Alice: does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? *Forest Ecol Manag*, 247: 120–130.
- Davies, C.E., D. Moss, M.O. Hill, 2004: EUNIS Habitat Classification Revised 2004. Paris: European Topic Centre on Nature Protection and Biodiversity.
- Dyderski, M.K., A.M. Jagodziński, 2018a: Drivers of invasive tree and shrub natural regeneration in temperate forests. *Biol Invasions*, 20: 2363–2379.
- Dyderski, M.K., A.M. Jagodziński, 2018b: Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. *Plant Ecol*, 219: 1369–1380.
- Dyderski, M.K., A.M. Jagodziński, 2019a: Seedling survival of *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. in temperate forests of Western Poland. *Forest Ecol Manag*, 450: 117–498.
- Dyderski, M.K., A.M. Jagodziński, 2019b: Functional traits of acquisitive invasive woody species differ from conservative invasive and native species. *NeoBiota*, 41: 91–113.
- Ellenberg, H., H.E. Weber, R. Dull, V. Wirth, W. Werner, D. Paulissen, 1992: *Zeigerwerte von Pflanzen in Mitteleuropa*. *Scripta Geobotanica*, 18: 1–248.
- ESRI, 2014: ArcGIS 10.2.2 for Desktop. Redlands, California (USA): Environmental Systems Research Institute.
- Essl, F., N. Milasowszky, T. Dirnböck, 2011: Plant Invasions in Temperate Forests: Resistance or Ephemeral Phenomenon? *Basic Appl Ecol*, 12: 1–9.
- European Environment Agency (EEA), 2018: Data and Maps: Copernicus Land Monitoring Service - Corine Land Cover. <https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-corine>
- Florianová, A., Z. Münzbergová, 2017: Invasive *Impatiens parviflora* has negative impact on native vegetation in oak-hornbeam forests. *Flora*, 226: 10–16.
- Florianová, A., Z. Münzbergová, 2018: Drivers of natural spread of invasive *Impatiens parviflora* differ between life-cycle stages. *Biol Invasions*, 20: 2121–2140.
- Fox, J., G. Monette, 1992: Generalized collinearity diagnostics. *J Am Stat Assoc*, 87: 178–183.
- Fox, J., S. Weisberg, 2019: An {R} Companion to Applied Regression, California, USA: Thousand Oaks SAGE Publications.
- Hejda, M., 2012: What is the impact of *Impatiens parviflora* on diversity and composition of herbal layer communities of temperate forests? *PLoS ONE*, 7: e39571.
- Jagodziński, A.M., M.K. Dyderski, P. Horodecki, K.S. Knight, K. Rawlik, J. Szmyt, 2019: Light and propagule pressure affect invasion intensity of *Prunus serotina* in a 14-tree species forest common garden experiment. *NeoBiota*, 46: 1–21.
- Jogan, N., M. Bačič, P. Strgulc P., S. Krajšek, 2012: Neobiota Slovenije: Invazivne tujerodne vrste v Sloveniji ter vpliv na ohranjanje biotske raznovrstnosti in trajnostno rabo virov. Univerza v Ljubljani (Biotehniška fakulteta). Končno poročilo. CRP »Konkurenčnost Slovenije 2006 – 2013« Ljubljana.
- Kawaletz, H., I. Mölder, S. Zerbe, P. Annighöfer, A. Terwei, C. Ammer, 2013: Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. *J Plant Ecol*, 6: 305–315.
- Klotz, S., 2009: *Prunus serotina* Ehrh., black cherry (Rosaceae, Magnoliophyta). In: Hulme, P.E., W. Nentwig, P. Pyšek, et al.

- (eds). Handbook of Alien Species in Europe. Dordrecht, the Netherlands: Springer, 355–355.
- Laurance, W.F., 2002: Hyperdynamism in fragmented habitats. *J Veg Sci* 13: 595–602.
 - Laurance, W.F., H.E.M. Nascimento, S.G. Laurance, A. Andrade, R.M. Ewers, K.E. Harms, R.C.C. Luizão, J.E. Ribeiro, 2007: Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. *PLoS ONE*, 2: e1017.
 - Marinšek, A., L. Kutnar, 2017: Occurrence of invasive alien plant species in the floodplain forests along the Mura River in Slovenia. *Period Biol* 119: 251–260.
 - Patton, D.R., 1975: A diversity index for quantifying habitat "edge". *Wildlife Soc B*, 3: 171–173.
 - Martinčič, A., T. Wraber, N. Jogan, A. Podobnik, B. Turk, B. Vreš, V. Ravnik, B. Frajman, S. Strgulc Krajšek, B. Trčak, T. Bačič, M.A. Fischer, K. Eler, B. Surina, 2007: Mala flora Slovenije. Ključ za določanje praprotnic in semenk. Četrta, dopolnjena in spremenjena izdaja. Tehniška založba Slovenije, Ljubljana.
 - Quinet, M., C. Descamps, Q. Coster, S. Lutts, A.-L. Jacquemart, 2015: Tolerance to Water Stress and Shade in the Invasive *Impatiens parviflora*. *Int J Plant Sci*, 176: 848–858.
 - R Core Team, 2019: R: A language and environment for statistical computing. R Foundation for Statistical Computing (Vienna, Austria). <https://www.R-project.org/>
 - Rebernik, D., 2011: Sustainable development of Spodnje Podravje region (in Slovenian: Spodnje Podravje pred izzivi trajnostnega razvoja). Dela - Oddelek za geografijo Filozofske fakultete v Ljubljani, 36: 127–128.
 - Ščap, D., 2018: Apaško polje throughout history (in Slovenian: Apaško polje po poti strpnosti skozi zgodovino). Apače, Slovenia: Municipality Apače.
 - Šipek, M., N. Šajna, 2020: Public opinions and perceptions of peri-urban plant invasion: the role of garden waste disposal in forest fragments. *Manag Biol Invasions*, 11: 733–746.
 - Skálová, H., L. Moravcová, J. Čuda, P. Pyšek, 2019: Seed-bank dynamics of native and invasive *Impatiens* species during a five-year field experiment under various environmental conditions. *NeoBiota*, 50: 75–95.
 - Sol, D., J. Maspons, M. Vall-llosera, I. Bartomeus, G.E. García-Peña, J. Piñol, R.P. Freckleton, 2012: Unraveling the life history of successful invaders. *Science*, 337: 580–583.
 - USDA, 2013: Weed Risk Assessment for *Impatiens parviflora* DC. (Balsaminaceae) – Smallflower touch-me-not, small balsam. https://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/wra/Impatiens_parviflora_WRA.pdf
 - Vanhellemont, M., K. Verheyen, L. De Keersmaecker, K. Vandekerckhove, M. Hermy, 2009: Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? *Biol Invasions*, 11: 1451–1462.
 - Vidic, N.J., T. Prus, H. Grčman et al., 2015: Tla Slovenije s pedološko karto v merilu 1 : 250.000 = Soils of Slovenia with soil map 1: 250.000 Evropska komisija, Skupno raziskovalno središče (JRC) Luxembourg: Urad za publikacije Evropske unije EUR, Scientific and Technical Research Series, 152 pp.
 - Von Holle, B., H.R. Delcourt, D. Simberloff, 2003: The importance of biological inertia in plant community resistance to invasion. *J Veg Sci*, 14: 425–432.
 - Vovk, A., 1996: Regional ecological units of northeastern Slovenia. *Geografski zbornik* 36: 69–134.
 - Wagner, V., M. Chytrý, B. Jiménez-Alfaro, J. Pergl, S. Hennekens, I. Biurrun, et al., 2017: Alien plant invasions in European woodlands. *Divers Distrib*, 23: 969–981.
 - Wang, Y., S. Fei, Z. Tang, Y. Sun, G. Chen, X. Wang, S. Wang, J. Fang, 2021: Alien woody plant invasions in natural forests across China. *J Plant Ecol*, 14(5): 749–756.
 - Zelnik, I., 2012: The presence of invasive alien plant species in different habitats: case study from Slovenia. *Acta Biol Slov*, 55: 25–38.

SAŽETAK

Aluvijalne, priobalne i nizinske šume umjerenih područja europske su šume s najvećom prisutnošću invazivnih stranih biljaka. Slijedom toga, utvrđivanje okolišnih uvjeta i drugih pokretača invazije tih vrsta u prirodnim šumskim zajednicama presudno je za razumijevanje izloženosti ovih staništa invazivnim vrstama. Fokusirali smo se na fragmente ilirske šume hrasta kitnjaka i običnog graba u SI Sloveniji, koje su u tom pogledu najmanje proučavane.

Budući da su alohtoni fanerofiti i terofiti znatno prezastupljeni u usporedbi s autohtonim vrstama u nizinskim šumama, odabrali smo dvije reprezentativne invazivne vrste: fanerofit *Prunus serotina* i terofit *Impatiens parviflora*. Korištenjem logističkih regresijskih modela na vegetacijskim podacima, okolišnim podacima na temelju Ellenbergovih indikatorskih vrijednosti i krajobrazne metrike na razini fragmenata (zakrpi), identificirali smo karakteristike fragmenata šumske vegetacije koji objašnjavaju prisutnost svake vrste. Štoviše, u modele smo uključili utjecaj čovjeka.

Otkrivene su značajne karakteristike koje međusobno razlikuju invazivnost vrsta *P. serotina* i *I. parviflora*. Također pokazalo se da omjer površine i hranjive tvari šumskih fragmenata značajno koreliraju s prisutnošću vrste *P. serotina*, dok antropogeni poremećaj staništa značajno korelira s prisutnošću vrste *I. parviflora*. Naši rezultati te sličan pristup za druge invazivne biljne vrste mogu se primijeniti za procjenu podložnostistaništa na potencijalnu i trenutnu rasprostranjenost tih vrsta, kao i za izradu planova upravljanja.

KLJUČNE RIJEČI: biološke invazije, fragmentacija šuma, metrika krajobraza, karakteristike staništa, ljudska prisutnost, neofiti

Appendix 1. Comparison of alternative multivariate logistic regression models for *Impatiens parviflora* presence in studied lowland forest patches within 2 AIC units. Model with the lowest AIC value is considered as optimal and shown in detail in Table 2. Sign + indicates that the variable is included in the model.

Prilog 1. Usporedba alternativnih multivarijantnih modela logističke regresije za prisutnost *Impatiens parviflora* u nizinskim šumskim fragmentima unutar 2 AIC jedinice. Model s najnižom vrijednosti AIC smatra se optimalnim i detaljno je prikazan u tablici 2. Znak + označava da je varijabla uključena u model.

Intercept	Urban	Roads	Arable	P/A ratio	Nutrients	Moisture	Light	Waste	Garden waste	df	AICc	Delta	Weight
Prekid	Urbano	Ceste	Obradivo	Omjer P/A	Hranjiva	Vlaga	Svjetlost	Otpad	Vrtni otpad	df	AICc	Delta	Težina
-13.4		+		+		+		+		5	60.4	0.00	0.143
-9.84		+				+		+		4	60.9	0.51	0.111
-0.81		+						+		3	60.9	0.52	0.11
-1.49		+		+				+		4	61.3	0.90	0.091
-22.84		+				+	+	+		5	61.6	1.19	0.079
-13.8		+		+		+		+	+	6	62.0	1.59	0.065
-0.77	+	+						+		4	62.0	1.66	0.062
-0.8								+		2	62.1	1.70	0.061
-7.2		+			+			+		4	62.2	1.84	0.057
-14.39		+	+		+			+		5	62.2	1.86	0.056
-21.63		+		+		+	+	+		6	62.2	1.86	0.056
-10.32		+				+		+	+	5	62.3	1.87	0.056
-0.801		+						+	+	4	62.4	2.00	0.053

Appendix 2. Comparison of alternative multivariate logistic regression models for *Prunus serotina* presence in studied lowland forest patches within 2 AIC units. Model with the lowest AIC value is considered as optimal and shown in detail in Table 2. Sign + indicates that the variable is included in the model.

Prilog 2. Usporedba alternativnih multivarijantnih modela logističke regresije za prisutnost *Prunus serotina* u nižinskim šumskim fragmentima unutar 2 AIC jedinice. Model s najnižom vrijednosti AIC smatra se optimalnim i detaljno je prikazan u tablici 2. Znak + označava da je varijabla uključena u model.

Intercept Prekid	Urban Urbano	Roads Ceste	Arable Obradivo	Forest Šuma	P/A ratio Omjer P/A	SHPI SHPI	Nutrients Hranjiva	Moisture Vlaga	Light Svjetlost	Temperature Temperatura	Garden waste Vrtni otpad	Walking paths Pješачke staze	df	AICc AICc	Delta Delta	Weight Težina
-51.18					+		+		+			+	5	40.90	0.00	0.07
-2.52	+		+		+	+		+				+	8	41.43	0.53	0.05
-53.34					+	+			+			+	6	41.58	0.68	0.05
-39.18					+		+		+				4	41.72	0.82	0.05
-55.97		+			+		+		+			+	6	41.84	0.95	0.04
-76.01	+				+	+		+		+		+	7	41.90	1.00	0.04
-22.74					+		+						3	42.07	1.17	0.04
-82.56	+		+		+	+		+		+		+	7	42.10	1.20	0.04
-50.38					+	+			+		+	+	6	42.22	1.32	0.04
-83.69	+		+		+	+		+		+	+	+	8	42.28	1.38	0.03
-60.94	+		+		+	+		+		+		+	9	42.32	1.42	0.03
-27.92					+	+						+	5	42.33	1.44	0.03
-22.93	+				+	+		+		+		+	7	42.34	1.44	0.03
-93.30	+	+	+		+	+				+		+	8	42.34	1.44	0.03
-52.70	+				+	+			+			+	7	42.35	1.45	0.03
-19.02					+	+		+					4	42.36	1.46	0.03
-24.63					+	+						+	4	42.42	1.52	0.03
-48.87	+				+	+			+			+	6	42.45	1.55	0.03
-63.45					+	+				+		+	6	42.49	1.59	0.03
-46.79					+	+		+		+			4	42.62	1.72	0.03
-29.38	+				+	+						+	6	42.66	1.77	0.03
-20.64					+	+		+				+	5	42.71	1.81	0.03
-45.87					+	+		+	+			+	6	42.74	1.84	0.03
-23.02					+	+		+				+	6	42.81	1.91	0.03
-91.87	+	+			+	+				+		+	8	42.81	1.91	0.03
-79.83					+	+		+		+	+	+	7	42.80	1.92	0.03
2.06	+	+	+		+	+		+			+	+	9	42.80	1.94	0.03
5.67	+	+	+	+	+	+		+			+	+	9	42.80	1.95	0.03
-48.87		+			+	+		+				+	7	42.90	1.99	0.03