



Patterns of *Prunus cerasifera* early invasion stages into a temperate primeval forest

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Abstract The cherry plum (*Prunus cerasifera* Ehrh.) is considered an invasive plant species in numerous areas of the temperate climate zones around the world. Although this exotic tree can naturalize in a wide spectrum of forest ecosystems, its invasion mechanisms remain totally unknown. This study is the first approach aiming to investigate potential drivers shaping the ecological success of *P. cerasifera* invasion, with an example of the temperate primeval forest as a model recipient ecosystem.

Using generalized linear models, we suggest that the distance to the propagule source may shape considerably this exotic species occurrence in primeval forest's understory, expressed by the presumably high role of birds and small mammals in short-, and large ungulates in long-distance seed dispersion. The probability of this invader occurrence decreased with decreasing functional and phylogenetic diversity of understory vegetation. This suggests the importance of habitat filtering generated in small tree-fall gaps in shaping the *P. cerasifera* success. Thus, interactions between natural disturbances, characteristics of recipient vegetation, as well as traits of various animal dispersers, may be identified as key drivers promoting the occurrence of *P. cerasifera* in the primeval forest ecosystem. However, further studies on the patterns of *P. cerasifera* invasion are needed to identify drivers promoting invasion, as well as the effects of this exotic plant on biodiversity and the functioning of ecosystems.

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Introduction

Understanding the mechanisms of biological invasions, with a special focus on their early stages, allows the formulation of effective strategies of alien species management, aiming the prevention of

recipient ecosystems from further spread of invaders, thus minimizing the range of detrimental effects on biodiversity, trophic interactions, biogeochemical cycles, and overall ecosystem functioning (Blackburn et al. 2011; Aerts et al. 2017). Because economic and environmental costs of invasive species eradication, monitoring, and controlling of invasion progress increase rapidly, assessment of invasions risks in their early stages can be considered one of the most cost-efficient methods of alien species management (Basnou et al. 2015). Thus, the knowledge of the alien species invasion patterns is essential for the assessment of ecosystems' invasibility and development of conservation priorities, of which accurate formulation is especially important for the maintenance of ecosystems identified as having the highest naturalness levels (Novoa et al. 2020; Sapsford et al. 2020).

Although primary forests are assumed to be of low invasibility and high invasion resistance (Cadenasso and Pickett 2001; Martin et al. 2009), they can often express even similar levels of alien plant invasions as secondary forests (Lapin et al. 2019). Due to the low contribution in the total forest cover of Europe (about 0.7%; Sabatini et al. 2018), and biases linked with the land-use history reconstruction, invasion mechanisms in primary forests are highly underexplored (von Holle et al. 2003; Levine et al. 2004; Wagner et al. 2017; Lapin et al. 2019; Nuñez et al. 2022). Moreover, the vast majority of previous studies have focused on high-intensity invasions, where exotic plants are well integrated with other ecosystem components (Elgersma and Ehrenfeld 2011), while less attention was paid to primeval forests (i.e. primary forests with the continuity of ecological processes not substantially transformed since deglaciation (Jaroszewicz et al. 2019) or forest ecosystems with early invasion stages (Lapin et al. 2019). A model ecosystem in Europe with an outstandingly high naturalness level is the Białowieża Forest (Faliński 1986; Sabatini et al. 2018). Despite the status of the most preserved forest ecosystem on the European lowland (Jaroszewicz et al. 2019) and relatively high invasion resistance, some exotic plants can successfully naturalize and spread in the Białowieża Forest (Faliński 1968, 1986; Mędrzycki and Pabjanek 2001; Łapok et al. 2018). One example of plant species belonging to this group is cherry plum *Prunus cerasifera* Ehrh. (= *P. divaricata* Ledeb., *P. myrobalana* (L.) Desf.).

Native geographical distribution of *P. cerasifera* comprises SE Europe, SW, and Central Asia (Kurtto 2009+, Popescu and Caudullo 2016, Weber 2017, POWO 2022), where it occurs in a wide elevation spectrum, up to 2200 m a.s.l. Cherry plum forms thickets developing at the forest edges, or grows in shrublands, and is an important component of shrub layers of numerous forest types. However, due to long-term and widespread cultivation as a fruit and decorative tree, the borders of its native range are obscured due to multiple escapes from cultivation and naturalisation events in newly colonised areas. For instance, POWO (2022) considers Ukraine and Romania to be within the native distribution of this species, whereas recent papers from these areas treat *P. cerasifera* as alien (Romania – Sîrbu and Oprea (2011), continental Ukraine – Burda and Koniakin (2019), Crimea – Yena (2012). In NW Europe *P. cerasifera* has been cultivated since 1592, where in general it is considered as invasive neophyte. In Italy and the Czech Republic, in turn, *P. cerasifera* has been cultivated before the year ~1500, where it is regarded as an invasive archaeophyte (Galasso et al. 2018; Pyšek et al. 2022). In Poland the species is considered as invasive neophyte, however precise time of its introduction is unknown (Tokarska-Guzik et al. 2012). Apart from some uncertainties in the assessment of *P. cerasifera* native range, it is considered as alien in numerous areas of the temperate climate zones around the world (Rejmánek and Richardson 2013), i.e.: NW Africa, W, and E North America, SW South America, New Zealand (Weber 2017; POWO 2022), and Europe (Popescu and Caudullo 2016; Dobrzycka-Krahel and Medina-Villar 2020). Similarly as regarded to the native range, *P. cerasifera* in the introduced range in Europe can naturalize in a wide spectrum of habitats, including rural and urban sites, post-agricultural wastelands, meadows, xerothermic grasslands and shrublands, Scots pine monocultures, secondary forests or even primary forests (Adamowski et al. 2002; Adamowski and Wołkowycki 2014). In North America, for instance, the species invades chaparral, roadsides, stream banks and canyons (Rohrer 2014). Despite relatively good recognisability by society and the status of alien, naturalized, or invasive species, *P. cerasifera* invasion mechanisms remain unknown (Dobrzycka-Krahel and Medina-Villar 2020).

This study is the first approach aiming to assess the *P. cerasifera* invasion mechanisms, with an example

of the Białowieża Forest as a model recipient ecosystem representing the early stages of an invasion by this exotic plant. In this study we ask: (i) whether the ecological success of *P. cerasifera* in this primeval forest may depend on the distance to the propagule sources and (ii) whether the ecological success of this invasive plant may be influenced by understory vegetation characteristics of a recipient forest ecosystem

Methods

Study site

Białowieża Forest is the transboundary forest ecosystem, located in NE Poland and W Belarus. Its high naturalness degree is reflected by substantially high species richness and biodiversity, the presence of

large old trees, high amounts of deadwood in various decomposition stages, high structural and spatial forest complexity and microhabitats heterogeneity, natural forest dynamics shaped by uncontrolled disturbances, and the continuity of ecological processes have not been substantially transformed over the last 12 000 years (Faliński 1986; Jaroszewicz et al. 2019). We conducted our study in the Strict Reserve of the Białowieża National Park (Fig. 1), which is the best-preserved part of this forest ecosystem, excluded from direct human impacts since 1921, thus playing the role of a unique living laboratory for ecological and evolutionary sciences (Jaroszewicz et al. 2019).

Our study was conducted in the oak-lime-hornbeam forest (*Tilio-Carpinetum*) of subcontinental character – a forest community predominating in the Polish part of the Białowieża Forest. The tree stand of *Tilio-Carpinetum* is composed of up to a three-layer

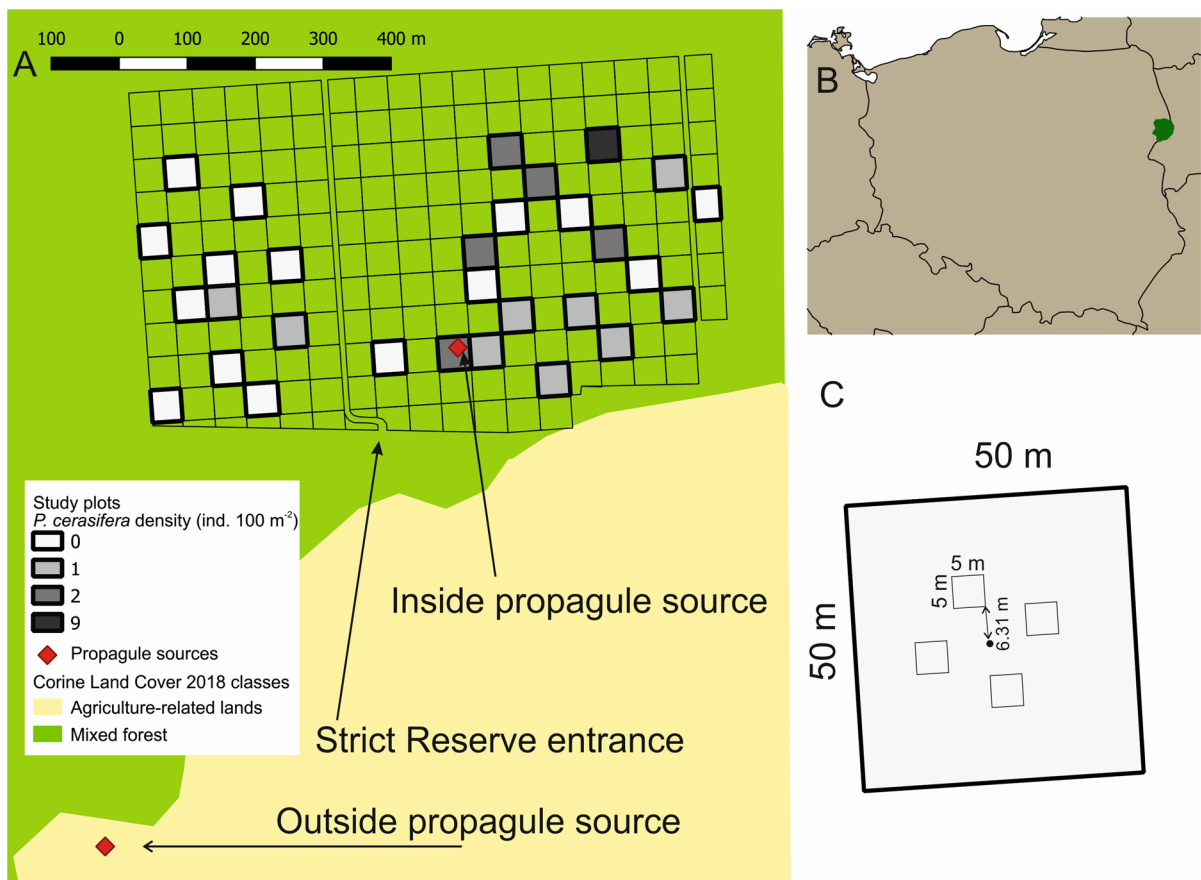


Fig. 1 Map of study plots (50×50 m) within a study site located at the entrance to the BNP Strict Reserve, with marked propagule sources (A), locality of BNP at the map of Poland (B), and scheme of vegetation subplots within a study plot (C)

tree canopy with a predominance of *Carpinus betulus*, *Tilia cordata*, *Quercus robur*, *Acer platanoides*, and *Picea abies*. *Tilio-Carpinetum* develops on various soils, including eutrophic brown soils, clay-illuvial soils, and stagnogleyic clay-illuvial soils. (Faliński 1986).

The earliest records of the cherry plum in the Białowieża Forest date back to the 1960s, when the cultivation of *P. cerasifera* in the Belarussian part of the Białowieża Forest was reported. In the next decades, through the usage of forest roads as migration corridors, the species started to spread into the Białowieża Forest, Naturalizing in ruderal sites or post-agricultural wastelands, and finally forest edges (Smirnov 1965; Łuczaj 1994; Adamowski et al. 1998, 2002). A recent survey of non-native flora conducted on areas located directly to the southern part of the Strict Reserve of the Białowieża National Park revealed a quick increase in the abundance of the spontaneous populations of *P. cerasifera* on abandoned farmlands, identifying them as one of the main propagule sources of this species in the Białowieża Forest (Adamowski 2016, unpubl.).

Data collection

Within the study site (located in the southern site of the Strict Reserve; $\sim 0.47 \text{ km}^2$), we used a random number generator to select 30 spatial units ($50 \times 50 \text{ m}$) for detail study, marked in the field using plastic tapes with alphanumeric codes. Within the center of each spatial unit, we regularly established four $5 \times 5 \text{ m}$ subplots, located each at 6.31 m from the unit center in four cardinal directions. Within each subplot, in July 2022 we recorded vascular plant species and their percentage cover in a non-transformed, nine-degree Braun-Blanquet scale (r – less than 0.01%, + – 0.1–1%, 1–1.1–3%, 2 m – 3.1–5%, 2a – 6–15%, 2b – 16–25%, 3–36–50%, 4–51–75%, and 5 – more than 75% cover). To estimate plant species cover at the plot level ($n=30$; 100 m^2 each), we averaged cover of plant species within all four $5 \times 5 \text{ m}$ subplots in each spatial unit. We also counted all *P. cerasifera* juveniles, assuming that all of them were older than one year as in each specimen we found annual height increment marks. Because we could not destructively sample seedlings and because browsing obscures the height-age relationship for individual seedling, we did not estimate seedling age. For each plot (using the

center of each spatial unit), we calculated distances from two propagule sources (Fig. 1): one inside the Strict Reserve (single fruiting tree with approximate age of ~ 15 years), and one outside (group of several fruiting trees with approximate age of ~ 40 years, nearest to study plots and connected with them via ungulates path). We used the former as a proxy for short-range distance spread, and the latter as a proxy for long-range distance dispersal of *P. cerasifera*.

Data preparation

We analyzed data using R software (R Core Team 2021). We obtained a phylogenetic tree for all species present in the study plots from the megatree included in the *V.phylo maker* package. We obtained values of species functional traits from LEDA, BIEN, BioFlor, and Pladias (Table 1). We choose functional traits describing the recipient community's ability to inhibit or facilitate the presence of invasive plant species (Wang et al. 2019, 2021; Anibaba et al. 2023; Czortek 2023). We included cardinal traits representing main components of plant economic spectrum (Westoby 1998; Díaz et al. 2016): two traits representing the leaf economic spectrum: specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$) and leaf dry matter content (LDMC, g g^{-1}), and two traits representing plant size: plant height (H, m) and seed mass (SM, mg). These traits represent trade-offs in resources acquisition, as well as adaptations to competition and environmental stress. Traits describing reproduction biology: flowering beginning and duration (months), as well as pollination vectors (insects, wind, or self-pollination), expressed by binary variables, provide information about plants reproductive strategies, abilities to spread, as well as provide information on adaptations to disturbances. Lastly, we included lifeform, as a categorical trait expressing the strategy of persistence across winter and plant longevity, adopted as additional indicator of habitat stability, and Ellenbers Ecological Indicator Values (EIVs), expressing species ecological requirements. EIVs are expert-based indicators of species ecological requirements (Ellenberg and Leuschner 2010), assessed by vegetation ecologists and widely used to reconstruct species ecological niche when there are no instrumental measurements (e.g. Evangelista et al. 2016; Czortek et al. 2018; Ridding et al. 2020). Despite drawbacks resulting from their discontinuous and expert-based character (Schaffers

Table 1 Traits used in the study, their ranges, variation coefficient (CV), and completeness

Numeric traits	Min	Max	Mean	CV [%]	Completeness [%]
Flowering beginning [months]	2	8	5.1	24.3	98.1
Flowering duration [months]	1	6	3.0	34.7	98.1
Specific leaf area (SLA) [cm ² g ⁻¹]	43.4	844.0	316.0	42.4	95.4
Lead dry mass content (LDMC) [mg g ⁻¹]	23.8	385.2	216.4	32.2	87.0
Seed mass (SM) [mg]	0.003	3146.9	55.0	604.3	92.6
Maximum height (H) [m]	0.1	50.0	4.2	243.2	99.1
Light EIV	1	9	5.0	33.2	98.1
Temperature EIV	2	7	5.2	16.1	62.9
Moisture EIV	3	10	5.9	23.0	85.2
Soil reaction EIV	2	8	6.1	23.4	70.4
Soil fertility EIV	2	9	5.8	30.2	87.0
Categorical traits	Number of classes	Classes and their frequency			Completeness [%]
Life form	8	Chamaephytes (3.7%), Geophytes (15.7%), Hemicryptophytes (56.5%), Lianas (1.9%), Phanerophytes (14.8%), Therophytes (7.4%)			100.0
Pollination mode–insect	2	Yes (74.2%), no (25.8%)			93.5
Pollination mode–selfing	2	Yes (60.4%), no (39.6%)			93.5
Pollination mode–wind	2	Yes (28.7%), no (71.3%)			93.5

and Sýkora 2000), these values were compared with instrumental measurements revealing their usefulness in indication of species requirements (e.g. Dzwonko 2001; Szymura et al. 2014).

Due to a lack of trait data completeness for some species (Table 1), we imputed missing values using the random forest-based imputation protocol (Penone et al. 2014) implemented in the *missForest* package. Prior to imputation we inspected structure of missing values to ensure that there are no patterns in traits completeness related to taxonomic structures. Trait completeness ranged from 70.4% (soil reaction EIV) to 100.0% (life form), and average completeness was high (92.3%), indicating that potential imputation error will have low influence on community-level variables. The imputation is based on the known trait values and phylogenetic eigenvectors (Diniz-Filho et al. 1998) obtained using the *PVR* package, and used in many trait-based studies (e.g. Pyšek et al. 2015; Paź-Dyderska et al. 2023). The first 15 phylogenetic eigenvectors covered 65.7% of the variation in phylogenetic distances among species. The

normalized root mean squared error (a measure of the random forest-based imputation validity) of imputed traits for continuous variables was 0.71, representing good fitness of imputation.

We decided to describe wide mechanisms shaping the composition of understory vegetation, the phylogenetic relatedness structure of species through phylogenetic diversity (Nicod and Gillet 2021), and community assembly processes through functional diversity (Czortek et al. 2021). As phylogenetic diversity allows a deep insight into species relatedness based on their phylogenesis and evolutionary trajectories, functional diversity allows assessments of the importance of main ecological mechanisms in shaping species composition (Czortek et al. 2021; Nicod and Gillet 2021). While low values of functional diversity metrics can be a reflection of a high role of environmental filters or interspecific competition, high values may illustrate the prominent role of niche partitioning in vegetation development (Carroll et al. 2011). We calculated functional richness (FRic), following Villéger et al. (2008),

and functional dispersion (FDis) following Laliberté and Legendre (2010). Functional richness provides information on the quantity of plants realized niches, indicating the occupancy of the niche space by plants differing in life strategies (Villéger et al. 2008). Functional dispersion measures the mean distances of the species functional traits combinations to the centroid (center point) of the trait hypervolume (Hedberg et al. 2014). Despite limitations of the usage of functional richness in evaluation of invasion dynamics (Kuebbing et al. 2018), we decided to use both FRic and FDis of recipient vegetation as metrics of *P. cerasifera* success in the Strict Reserve. Both high occupancy of the niche space (high FRic) and high range of functional dissimilarities among species (high FDis) may suggest that the vast majority of environmental resources could be effectively utilised by functionally divergent plants, thus making the number of empty niches available to colonization by invasive plants low (e.g. Dyderski and Jagodzinski 2018; Anibaba et al. 2023; Czortek 2023; Czortek et al. 2023). Due to the dependence of functional diversity indices on species richness, we calculated their standardized effect sizes (SEs), i.e. deviations of metric from the null model (Czortek et al. 2021). As null models, we used randomly assembled communities for 999 randomized community data matrices, based on the independent swap algorithm that maintains species occurrence frequency and sample species richness. We calculated SEs following the code presented by Czortek et al. (2021). This way, very high or very low values of SEs indicate that the observed value is higher or lower than expected by a chance, according to the null model for particular species richness. We calculated two phylogenetic diversity indices: Faiths phylogenetic diversity (PD; i.e. the sum of phylogenetic tree branch lengths, representing all species present in the community) and mean pairwise phylogenetic distance (MPD) between species within the community. We also standardized them using SEs, to exclude the effect of species richness. That way, negative values of PD and MPD indicate strong phylogenetic clustering, i.e. higher frequency of species representing particular clades than under random circumstances. We calculated PD and MPD using the *PhyloMeasures* package.

Data analysis

We used non-metric multidimensional scaling (NMDS) for the assessment of the understory vegetation and its main compositional gradients. We used the *vegan* package to conduct NMDS. For NMDS we used default settings for transformation and Bray-Curtis dissimilarity matrix and midpoints of percentage cover of species estimated using the Braun-Blanquet scale. We assessed correlations of the main gradients of species composition revealed by NMDS by passive fit of vegetation characteristics (i.e. CWMs of EIVs and plant functional traits, taxonomic, functional and phylogenetic diversity components) into the ordination space using the *vegan::envfit()* function. We assessed the goodness of this fit by a permutation test ($n=999$).

We assessed the relationship between *P. cerasifera* occurrence probability and propagule sources (one located inside and one located outside the Strict Reserve of the Białowieża National Park) or vegetation characteristics using generalized linear models assuming the binomial distribution of a dependent variable. Although we counted *P. cerasifera* natural regeneration, its distribution was uneven (only six plots with more than a single specimen and only one with more than three), and not allowed for using approaches typical of count data, e.g. Poisson or negative binomial models. We evaluated models using Akaike's Information Criterion, corrected for small sample size (AICc). For models based on the distance to propagule sources, we provided the AICc of models and the AICc of a null (intercept-only) model. For model accounting for vegetation characteristics, we first developed a full model, with all hypothesized characteristics (i.e. species richness, Shannons Index, MPD, PD, FRic, FDis, CWMs of functional traits: SLA, LDMC, H and SM, as well as CWMs of EIVs: light, moisture, soil reaction and soil fertility). Then, we excluded collinear variables based on the variance inflation factors, and we reduced the full model to minimize AICc, using the *MuMIn::dredge()* function. In such an approach we assumed models differing in AICc by <2 as equivalent, accounting for the most complex models within the set of models differing by AICc from minimum AICc value by 2 units. We visualized the result of the final model using marginal responses, i.e. predicted values assuming all other predictors at a constant (mean) level, using

the `ggeffects::ggpredict()` function. This allowed us to account the effect sizes and biological importance of the patterns obtained instead of focus on the statistical significance of the results only.

Results

Spatial patterns of *P. cerasifera* occurrence

During the investigation, we recorded *P. cerasifera* juveniles presence in 15 (50%) of the study plots. Among them, in nine plots there were single specimens, in five plots we found two specimens and in one we found nine specimens (Fig. 1). We did not find any specimens taller than 1.5 m except a single plot with one 1.8 m non-fruiting tree and one 3.5 m fruiting tree. Analysis of relationships between distance to propagule sources and *P. cerasifera* occurrence probability revealed that models accounting for sources located inside (AICc=41.3) and outside the Strict Reserve (AICc=42.7) had higher AICc than the null model (AICc=43.7). The probability of *P. cerasifera* occurrence increased with increasing distance from the propagule source outside the Strict Reserve (from 0.20 to 650 m to 0.77 at 1300 m) while decreasing with increasing distance from the propagule source inside the Strict Reserve (from 0.86 in the study plot with propagule source to 0.19 at 480 m; Table 2; Fig. 2).

Relationships between *P. cerasifera* occurrence and understory characteristics

Analysis of understory vegetation species composition revealed two main gradients in the ordination space (Table 3; Fig. 3). The gradient along the NMDS1 axis ordered communities along light requirements, expressed by light EIV CWM. The gradient along the NMDS2 axis divided sites with high soil moisture, reaction, and fertility requirements, high SLA and height CWMs, as well as high phylogenetic diversity from sites with high functional and taxonomic diversity, as well as high seed mass CWM.

Direct analysis revealed that the final model of *P. cerasifera* presence comprised of species richness, Faiths PD, functional dispersion SES, and light EIV (AICc=41.3, full model AICc=50.5, null model

Table 2 Generalized linear models of *P. cerasifera* occurrence probability in study plots, based on the distance to propagule sources and null (intercept-only model)

Variable	Estimate	SE	z	Pr (> z)
(Intercept)	1.9245	1.0642	1.808	0.071
Distance to propagule source inside ($R^2=0.164$)	-0.0070	0.0035	-1.975	0.048
(Intercept)	-4.0210	2.3829	-1.687	0.092
Distance to propagule source outside ($R^2=0.114$)	0.0041	0.0024	1.711	0.087

AICc=43.7; Table 4; Fig. 4). The probability of *P. cerasifera* presence increased with increasing species richness: from 0.01 to 16 species to 0.98 at 60 species within the study plot, and with increasing light EIV: from 0.25 to 3.0 to 0.72 at 5.0. The probability of *P. cerasifera* occurrence decreased with increasing functional dispersion SES: from 0.67 at 2.0 to 0.25 at 2.5, and with increasing Faiths PD: from 0.88 at 2.5 to 0.19 at 2.0.

Discussion

Spatial patterns of *P. cerasifera* occurrence

Our study revealed two contrasting patterns of *P. cerasifera* occurrence in the Strict Reserve, potentially shaped by the distance from two hypothesised propagule sources (i.e. one located inside and one located outside BNP). However, based on our observations we cannot accurately infer the significance of particular propagule sources for shaping the colonization abilities of this invasive tree. One plausible interpretation of our findings may be that the opposite impacts of two propagule sources on *P. cerasifera* success in the Strict Reserve are the effects of spatial arrangement of propagule sources (i.e. south-east of each other), thus making the importance of particular propagule source low. On the other hand, the observed patterns may suggest that different animal vectors could be responsible for short- and long-distance spread of *P. cerasifera* in the Strict Reserve. However, direct accounting for this aspect requires either molecular studies of *P. cerasifera* individuals

Fig. 2 Relationships between *P. cerasifera* occurrence probability and distances to propagule sources, assessed using generalized linear models (Table 2). For localities of propagule sources see Fig. 1)

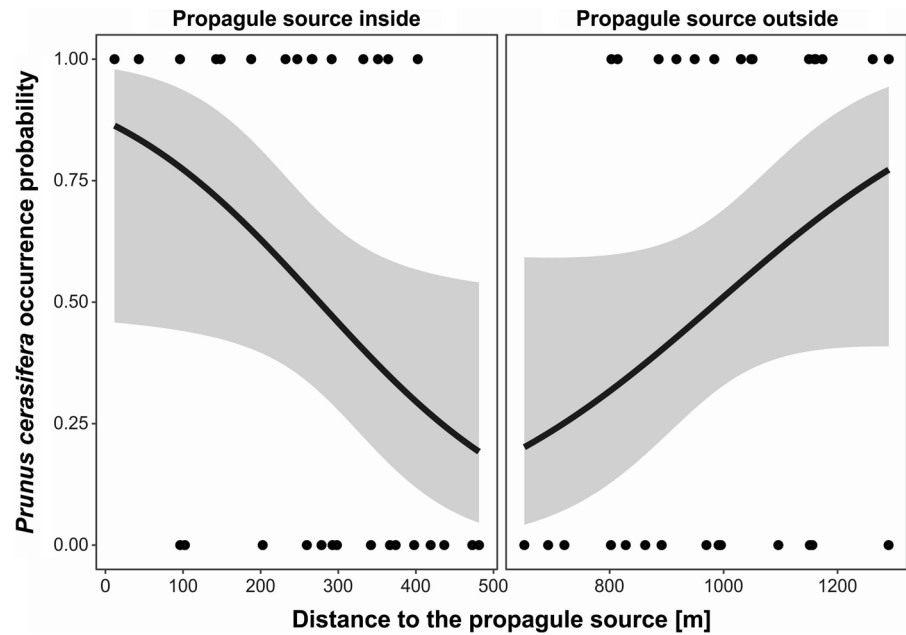


Table 3 The result of the passive fit of vegetation characteristics to non-metric multidimensional scaling evaluated using a permutation test

Variable	NMDS1	NMDS2	r ²	p
Species richness	0.3807	-0.9247	0.438	0.001
Shannon's index	0.2337	-0.9723	0.105	0.236
Faith's phylogenetic diversity	-0.3368	0.9416	0.048	0.501
Mean pairwise distance	-0.5726	0.8198	0.134	0.142
Light EIV	0.9704	0.2417	0.086	0.290
Moisture EIV	-0.5616	0.8274	0.024	0.719
Soil reaction EIV	0.5459	0.8378	0.226	0.031
Soil fertility EIV	0.2334	0.9724	0.142	0.154
SLA CWM	-0.5327	0.8463	0.124	0.177
Seed mass CWM	0.1209	-0.9927	0.246	0.043
Height CWM	-0.1838	0.9830	0.008	0.887
SES FDis	-0.5112	-0.8595	0.473	0.001
SES FRic	-0.1566	-0.9877	0.432	0.001

(e.g. Pairon et al. 2006, Dering et al. 2018) or tracking of animal dispersers and patterns of seed predation (e.g. Myczko et al. 2014, Vergara-Tabares et al. 2015) to identify main vectors of seed dispersal. Although this makes our inference highly limited, the observed patterns can be used as inspiration for further research on *P. cerasifera* dispersion mechanisms in forest ecosystems.

The probability of *P. cerasifera* occurrence decreased significantly with increasing the distance from the propagule source inside the Strict Reserve, reaching about 30% at the distance of ~400 m from the source. This may hint at potentially important role of birds in shaping the short-distance dispersion of *P. cerasifera* seeds. The trends revealed by some earlier studies investigating the dispersion of species phylogenetically similar to *P. cerasifera* (e.g. *Prunus* genus or Rosaceae family) may support this idea. *P. serotina*, for instance, can disperse from a single propagule source up to 600 m, confirmed by microsatellite markers (Pairon et al. 2006), while Starfinger et al. (2003) reported unpublished data on *P. serotina* spread up to 900 m. Distance from the propagule source was found as an important driver of *P. serotina* natural regeneration (Jagodziski et al. 2019). Especially, with increasing distance to the nearest seed source, perching bird density, dropping density, and seedling density decrease (Deckers et al. 2008). However, most of the seeds fall beneath the parental tree canopy (Pairon et al. 2006). There are no direct studies on *P. cerasifera* ornithochory, except reported low frequency of its seeds (0.05%) in *P. serotina*-dominated seed banks under electricity pylons (Dylewski et al. 2017). Other vectors that may be of potentially similar importance for the short-distance dispersion of *P. cerasifera* seeds as

Fig. 3 Result of non-metric multidimensional scaling (NMDS, stress=0.1382) ordination using study plots (dots, n=30), colored by presence/absence of *P. cerasifera*. Diamonds and lines indicate centroids and distance from centroids for plots with and without *P. cerasifera*. Black labels indicate passively fit of vegetation characteristics explaining dissimilarities in species composition amongst plots (for the goodness of fit see Table 3)

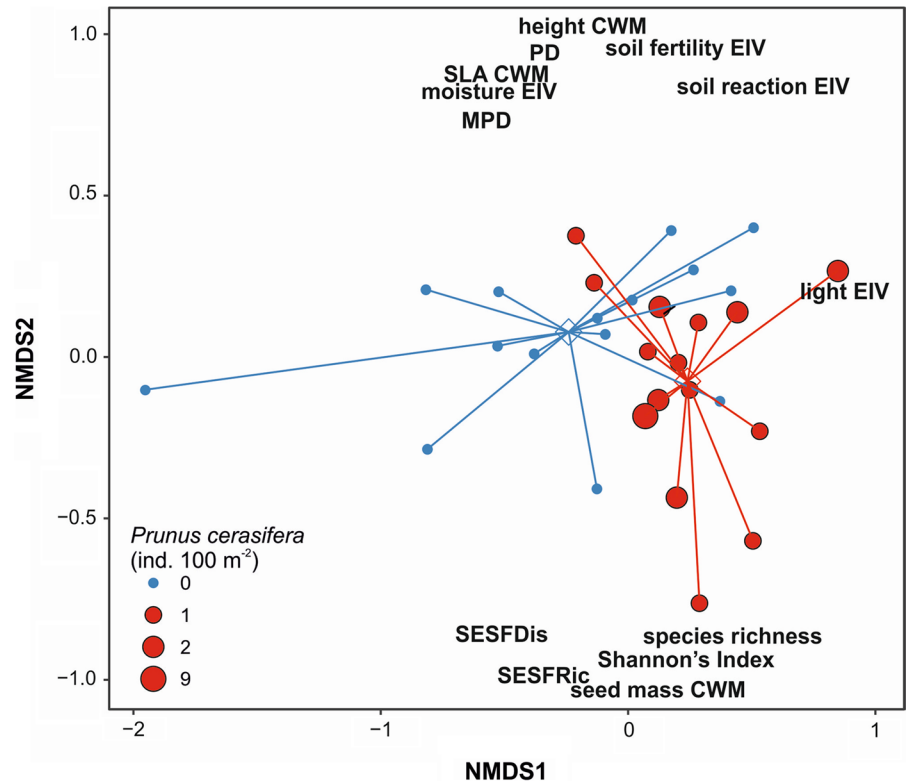


Table 4 A generalized linear model of *P. cerasifera* presence probability ($R^2=0.512$)

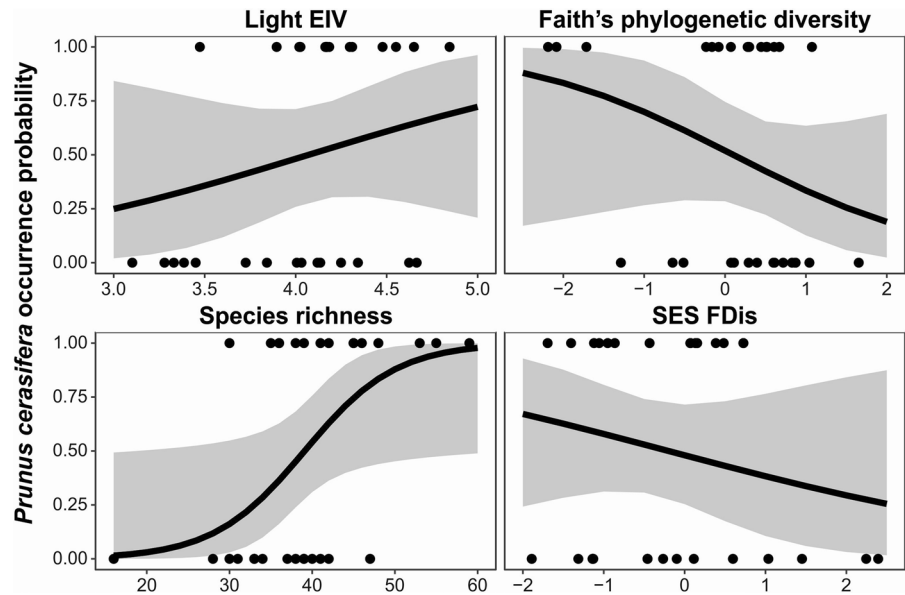
Variable	Estimate	SE	z	Pr(> z)
(Intercept)	-11.2412	5.8832	-1.911	0.056
Species richness	0.1814	0.0901	2.014	0.044
Faith's phylogenetic diversity	-0.7659	0.6246	-1.226	0.220
Light EIV	1.0301	1.2004	0.858	0.391
SES FDis	-0.3977	0.5077	-0.783	0.433

birds may be small mammals, e.g. yellow-necked mouse (*Apodemus flavicollis*) or bank vole (*Clethrionomys glareolus*) (Selva et al. 2012). Regarding the propagule source outside the Strict Reserve, we revealed that the probability of *P. cerasifera* occurrence was higher further away from the propagule source. The probability of about 75% for *P. cerasifera* to be present at a distance~1.2 km may suggest presumably higher ecological importance of endozoochory by large ungulates. European roe deer (*Cervus capreolus*), red deer (*Cervus elaphus*), European

bison (*Bison bonasus*) and wild boar (*Sus scrofa*) can potentially eat cherry plum fruits (see review in Delibes et al. 2019), and therefore may also transport the seeds over a long distance, as the daily movement distance of *B. bonasus* is on average 5.1 km, *S. scrofa* 6.8 km, while the daily range of *C. elaphus*, is 1.1, and *S. scrofa* is 1.3 km² (Rouys 2003; Kamler et al. 2007; Podgórski et al. 2013).

The success of invasive *P. cerasifera* in a primeval forest may be influenced by the forest type growing in the surrounding of each of the propagule sources investigated. Surrounding the propagule source outside the Strict Reserve is dominated by ash-alder riparian forest. Episodic flooding, water stagnation-driven anoxia, and the high role of interspecific competition in shaping the understory vegetation may be the main filters limiting the *P. cerasifera* occurrence in this forest type, thus highlighting the potential role of long-distance seed dispersers in shaping this invaders success. Moreover, the importance of both short- and long-distance seed dispersion may be modified by habitat properties and understory vegetation characteristics of oak-lime-hornbeam forest.

Fig. 4 Marginal responses of *P. cerasifera* presence probability, estimated using a generalized linear model (Table 4)



Relationships between *P. cerasifera* occurrence and understory characteristics

Based on the indirect ordination approach we revealed that the probability of *P. cerasifera* presence was higher in plots characterized by both higher and lower taxonomic, functional, and phylogenetic diversity of understory. Similar patterns were revealed regarding the the community weighted means of plant functional traits and ecological requirements of understory species: *P. cerasifera* occurred more frequently when coexisted, for instance, with plants of both higher and lower canopy height and specific leaf area, as well as with light- and shade-tolerant species, or of different soil moisture and fertility requirements. On the one hand, this indicates the potentially high abilities of *P. cerasifera* to colonize a high variety of microhabitats developing in the primeval forest, occupied by native understory species differing strongly in ecological requirements, strategies of resources acquisition and utilization, as well as evolutionary history and phylogenetic relatedness structure. Such ability is typical of other invasive *Prunus* species, e.g. *P. serotina* (Starfinger et al. 2003; Dyderski and Jagodzinski 2018). On the other hand, the occurrence of *P. cerasifera* in a wide spectrum of forest understory characteristics may be a visualization of its early invasion stages, suggesting that this exotic plant still did not colonize all available habitats. Moreover,

all observed *P. cerasifera* individuals were older than one year, pointing out that they survived the critical stage of their growth, as the tree seedlings mortality is the highest in the first year after germination (Closset-Kopp et al. 2007; Dyderski and Jagodzinski 2019). However, the ecological mechanisms shaping *P. cerasifera* seedlings survival remain unknown, so further studies are needed to address this issue.

We found that the probability of *P. cerasifera* occurrence increased if the total species richness and contribution of plant species of higher light demands were higher. This can correspond with the biotic acceptance theory, suggesting high resource availability is suitable for both alien and native species (Stohlgren et al. 2006). Knight et al. (2008) and Dyderski and Jagodzinski (2018) revealed a positive relationship between understory species richness and invasive *P. serotina* natural regeneration density or biomass. The positive relationship of *P. cerasifera* occurrence probability with species richness and light EIV may hint at the significant role of small-area disturbances, caused by collapsing of single trees damaged by windthrows or killed by insect outbreaks, which could increase the success of *P. cerasifera*. A similar pattern has been described for *P. serotina*, taking advantage of disturbances in the forest canopy (Jagodzinski et al. 2019). Following the gap dynamic model developed by Bobiec et al. (2000), the opening of the tree canopy increases the success of trees

natural regeneration (Dyderski and Jagodziski 2018; De Lombaerde et al. 2020) and allows the occurrence of light-demanding plants. This group includes, *inter alia*, ruderal species or plants typical of semi-natural grasslands, which in the subsequent stages of the forest succession are replaced by late-successional, shade-tolerant species (Faliński 1986; Orczewska et al. 2019). Seeds of these early-successional plants occur in high numbers in soil seed banks of the mixed deciduous oak-lime-hornbeam forest of the Strict Reserve (Jankowska-Baszczyk et al. 1998). The creation of gaps may trigger their germination and growth rates under improved light conditions, thus increasing temporarily the total species richness and taxonomic diversity of the understory (Orczewska et al. 2019). In addition, the probability of *P. cerasifera* occurrence increased alongside decreasing functional dispersion SES, expressing the positive role of habitat filters and lowered competition in shaping this invaders colonization abilities, generated by pioneer microhabitat conditions developing in gaps. Moreover, the probability of *P. cerasifera* occurrence was lower if Faiths phylogenetic diversity of co-existing vegetation was higher, indicating that *P. cerasifera* could co-occur more frequently with plant species similar in regards to their evolutionary history. On the one hand, the low heterogeneity of phylogenetic relatedness structure may be an expression of the development of evolutionary adaptations to occur in pioneer gap conditions, illustrated in high similarities of niches realized by these species (low values of functional dispersion SES).

High phylogenetic clustering may also visualize similar trajectories of the evolution of seed dispersal strategies (Jaroszewicz et al. 2023), with endozoochory identified as having one of the highest importance for understory species dispersal both in managed (Eycott et al. 2007) and primeval forest ecosystems (Heinken et al. 2002; Jaroszewicz et al. 2013). Kuijper et al. (2009) revealed that the visitation frequency of all five wild ungulates (i.e. *B. bonasus*, *C. capreolus*, *C. elaphus*, *A. alces* and *S. scrofa*) considered in their experiment was almost twice higher in forest gaps than in a closed forest. Improved light availability may increase food quality, driven by the higher photosynthesis abilities of graminoids and forbs growing in forest gaps, reaching there higher richness and biomass (Modry et al. 2004). Moreover, Jaroszewicz et al. (2013) in their

study on endozoochory in the Białowieża Forest demonstrated that the same ungulate species as investigated by Kuijper et al. (2009) were of the unique and high importance of seed dispersal of numerous species representing a wide habitat spectrum. Thus, forest gaps may be identified not only as substantial places for grazing and browsing, but as important sites where the probability for *P. cerasifera* seed dispersion may be high. Apart from feeding activities, ungulates spend there much time walking (i.e. almost 43% in the case of *C. elaphus* or above 50% regarding *B. bonasus*) or rooting (i.e. about 89% of the time spent by *S. scrofa*) (Kuijper et al. 2009). Therefore, the development of trampling- or rooting-created microhabitats with disturbed and lowered vegetation cover (expressed by high habitat filtering and low competition), may increase substantially the success of species of higher light demands, as well as of similar functions and phylogenesis. These plants may germinate from seed banks (Sondej and Kwiatkowska-Faliska 2017) or colonize these microhabitats through endozoochory (Jaroszewicz et al. 2013; Delibes et al. 2019) as may occur in case of *P. cerasifera* spread.

Conclusions

Our study suggests that both short- and long-distance spread of *P. cerasifera* to a large extent can increase potentially the success of this invasive plant species in the primeval forest ecosystem. Interactions between natural disturbances, characteristics of recipient vegetation, as well as dispersal abilities may be identified as other presumably important driver promoting the occurrence of *P. cerasifera* in the Białowieża Forest. A high tendency of *P. cerasifera* to occur in a wide spectrum of forest understory characteristics may hint at a high adaptive potential to invade and spread onto new habitats in the primeval forest. Our study is the first insight to illustrate the invasion mechanisms of *P. cerasifera* under conditions of the primeval forest ecosystem, however indicating that most of the mechanisms of this plant species invasion are not known. Therefore, further studies on the patterns of *P. cerasifera* invasion in different types of recipient ecosystems are needed to identify drivers promoting invasion, as well as the effects of this exotic plant on biodiversity and the functioning of ecosystems. This knowledge would be crucial in developing

early-warning systems, which may not only minimize the risk of further invasion, but reduce the range of effects on indigenous ecosystems functioning, and potential costs of *P. cerasifera* invasion management both in managed and protected forests. Monitoring of potential *P. cerasifera* spread should focus on recently-disturbed sites near propagule sources. Our insights suggest that promoting high canopy closure can be helpful in preventing spread of the studied species.

Author contributions PC, MKD, WA and AZ conceived the ideas and designed methodology. PC, MKD, KKK and OK collected the data; PC and MKD analysed the data. The first draft of the manuscript was written by PC and all remaining authors. All authors read and approved the final manuscript.

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Data availability Raw data used for the conductance of this study are stored in the figshare under the following link: <https://figshare.com/s/8567ceacbde96e091195>. The DOI number (<https://doi.org/10.6084/m9.figshare.22146680>) related for these data will be active after the potential acceptance of our article for publication in the Biological Invasions.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Consent to participate The authors agreed to be included as co-authors of the manuscript.

Consent for publication The authors declare agreement for publication of the manuscript in the Biological Invasions journal.

Ethics approval The study did involve human or animal participants as a study subjects.

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