

Landscape, site and post-disturbance forest stand characteristics modulate the colonisation of non-native invasive woody species

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ABSTRACT

Forests are exposed to human-induced and natural disturbances generating opportunities for new species to establish, including non-native woody species. Understanding how disturbance characteristics interact with the site context and invasive species traits to drive invasion processes is crucial for designing sustainable forest management. Here, we use the case study of the deciduous broadleaved forest belt of Canton Ticino (Switzerland) to identify the main factors determining the presence of non-native invasive woody species in recently disturbed forests. We identified and selected 851 forest gaps caused by natural, silvicultural or other anthropogenic disturbances between 2008 and 2015. For each gap, the presence of non-native invasive woody species as well as the characteristics of the corresponding landscape, site, and the gap itself were determined. For the six most frequent non-native invasive woody species, we identified the parameters that influenced their presence by means of modelling approach. The resulting variable coefficients were then used to create maps of colonisation risk. Among the six target species (i.e., *Ailanthus altissima*, *Buddleja davidii*, *Robinia pseudoacacia*, *Paulownia tomentosa*, *Prunus laurocerasus*, and *Trachycarpus fortunei*), the factors influencing their presence were either shared (e.g., distance to the next colonisation hotspot), partially shared (e.g., distance to buildings, altitude, aspect), or completely species-dependent (e.g., topography, slope, distance to powerlines). Like in other mountainous areas, non-native invasive woody species concentrate at low altitudes and near densely populated areas where hotspots of seed-bearing individuals can be found. Moreover, different life-history groups (i.e., wind-dispersed pioneer species vs. animals-dispersed evergreens) shared specific invasion patterns characteristics. In addition to general management strategies, we argue that more species-specific strategies should be adopted to prevent the colonisation by non-native invasive woody species. In this context, the consideration of seed-bearing individual hotspots should be given highest priority, followed by the type and the characteristics of the disturbance.

1. Introduction

Global change and increasing trade activities became in the last decades the most effective drivers of human-assisted migration and naturalization of non-native species (i.e., neobiota; Mack et al., 2000). Although only a small fraction of non-native introduced species naturalise and spread in an uncontrolled manner (Hulme et al., 2009), the related ecological and socio-economic impacts in the few cases in which this does occur may nevertheless be significant (e.g., Rumlerová et al., 2016; Fernandez et al., 2023).

In this context, forests are increasingly exposed to biological

invasions by recently introduced non-native terrestrial plants (Liebhold et al., 2017) and - sometimes relatedly - biotic threats such as new pathogens (e.g., Ghelardini et al., 2017) and insect pests (e.g., Brocknerhoff and Liebhold, 2017). In this respect, non-native invasive woody species (hereafter referred to as IWS) have gained increasing attention since they have the potential to represent a significant portion of stand biomass and thus may cause severe changes in forest ecosystem processes and functioning (Richardson and Rejmánek, 2011). Invasive evergreen shrubs and palms can for instance permanently darken the understory preventing the regeneration of forest trees (e.g., Fehr et al., 2024). Furthermore, IWS can significantly impact ecosystem services

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such as protection against natural hazards, wood production, recreation, climatic regulation, carbon fixation, and the provision of refuges for biodiversity (Adoyo et al., 2022; Fernandez et al., 2023).

On the other hand, forest disturbances remove resident vegetation, increase resource availability, and consequently provide opportunities for pioneer invasive species (Lozon and MacIsaac, 1997), depending on the properties of the disturbance (i.e., type, intensity, extent, frequency, and duration; Pauchard and Shea, 2006). Resulting light availability determines whether shade-tolerant or shade-intolerant species establish (Freeman et al., 2015; Subedi et al., 2024). There is a number of IWS displaying pioneer characteristics including heliophile and relatively short generation times that favour their process of colonising gaps created by natural and anthropogenic disturbances (Lozon and MacIsaac, 1997; Richardson and Rejmánek, 2011), where they become very difficult to manage and very hard to eradicate (Richardson & Rejmánek,

2011; Adoyo et al., 2022). This is an important finding given that in recent decades an increase in the frequency of natural and anthropogenic disturbances was observed in European forests (Senf and Seidl, 2021; Patacca et al., 2023). Accordingly, several studies have shown invasive species colonisation in gaps generated by treefalls (Freeman et al., 2015), fires (Maringer et al., 2012), windstorms (Daniels and Larson, 2020), and silvicultural management (Radtke et al., 2013; Isler et al., 2023).

After a disturbance, various factors play a role in influencing the establishment of IWS in the resulting gap. Primarily, the likelihood of a species to colonise is directly linked to propagule pressure (Waddell et al., 2020), which encompasses both the number of propagules and of introduction events (Lockwood et al., 2005). Factors such as the quantity of reproductive individuals, the species' dispersal strategies, and the presence of vectors and dispersal corridors are pivotal in this context

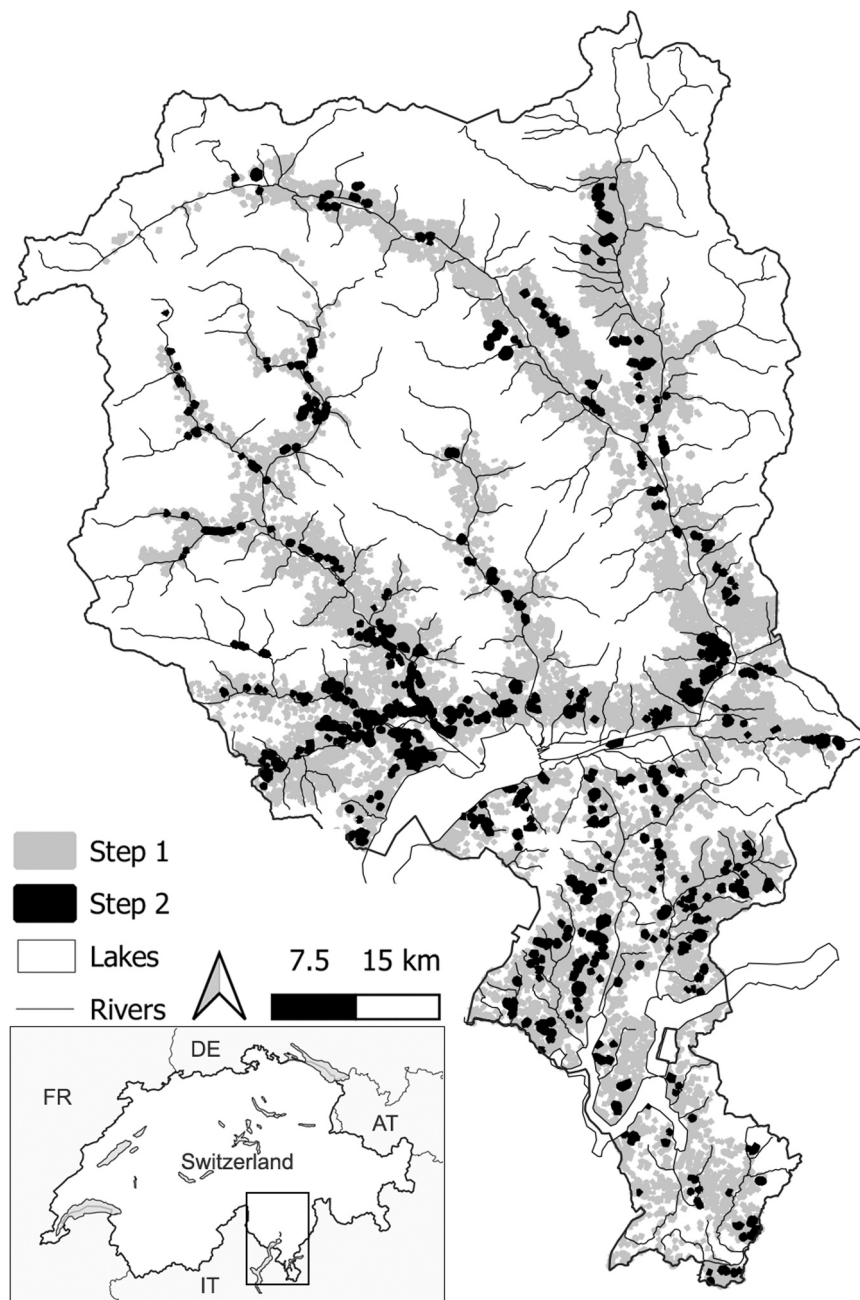


Fig. 1. Study area with gaps identified in Steps 1 and 2. Location of the study area (small bold rectangle in the subfigure) with respect to Switzerland and the surrounding countries.

(Lockwood et al., 2005; Radtke et al., 2013). Moreover, permanent disturbed landscape features such as roads and powerlines facilitate the penetration of IWS in particular into forests (Luken et al., 1992; Mortensen et al., 2009; Myśliwy, 2014). Additionally, the biotic and abiotic conditions of the microsite may vary in their suitability for IWS establishment (Freeman et al., 2015; Arellano-Cataldo and Smith-Ramírez, 2016).

Overall, understanding how disturbance properties interact with IWS traits, context and site conditions to modulate invasion processes is crucial for designing effective management and control measures (Kueffer et al., 2013).

In this paper, we use the case study of the broadleaved forest belt of Canton Ticino (southern Switzerland) to delve into the factors promoting the colonisation of invasive woody plants after a disturbance. Due to the advanced stage of this invasion process, planning silvicultural interventions has become a challenge, since the potential spread of these species must be considered.

The specific aims of this paper are to: (i) analyse and identify the most important factors modulating the presence of IWS in recently (i.e., 8–15 years) disturbed forests, (ii) provide a spatially explicit analysis of the likelihood of a post-disturbance colonisation by IWS in the study area, and (iii) propose possible strategies to manage disturbance properties and minimise the likelihood of colonisation by IWS. For this purpose, we selected 851 forest gaps caused by human-induced (silviculture, infrastructure maintenance, etc.) and natural (tree diebacks, coppice stool uprooting, forest fires, etc.) disturbances to assess the presence of the most common IWS and to detect possible recurrent patterns in the colonisation process.

2. Materials and methods

2.1. Study area

The study area encompasses the lower broadleaved forest belts of Canton Ticino (southern Switzerland), which may extend up to 1500 m a.s.l (Fig. 1). The climate is characterised by sunny and dry winters, along with wet spring and summer seasons. In summer, prolonged dry periods interrupted by heavy thunderstorms can occur. The mean annual temperature is approximately 12 °C and the annual precipitation is approximately 1900 mm (Climate Normals 1981–2010, Meteostation Locarno Monti, MeteoSwiss, 2021).

The vegetation is dominated by the forests of *Castanea sativa* Mill. mixed with *Tilia* Mill. spp., *Quercus* L. spp., *Prunus avium* L., *Acer* L. spp., *Fraxinus* L. spp., *Alnus glutinosa* (L.) Gaertn., *Ostrya carpinifolia* Scop., *Fagus sylvatica* L., etc. (Ceschi, 2014). Despite the essential protection function for settlements and infrastructures against natural hazards such as rockfall, shallow landslides, erosion, and debris flows, the management of these forests has undergone a significant reduction and, in some cases, has been nearly completely suspended throughout the post-World War II period. As a result, most of them at present act as ‘latent reserves’ *sensu* Portier et al. (2021) and are subject to a natural evolution toward mixed forest stands (Conedera et al., 2001), locally interrupted by natural disturbances such as tree uprooting (Vogt et al., 2006), tree diseases and dieback (Conedera et al., 2021), forest fires (Pezzatti et al., 2013), and heavy snow damage and windthrows (Scherrer et al., 2022). On the other hand, the most common anthropogenic forest disturbances are silvicultural treatments (coppicing, thinning, etc.), as well as road, powerline, and torrent channel bed maintenances. Depending on the site conditions and the disturbance status, broadleaved forests under concern may act as recipient ecosystems for invasion by IWS (Fridley et al., 2022).

2.2. Non-native target species

In the study area, ongoing invasions by IWS mainly consist of the colonisation of forest gaps by light demanding early successional

pioneer species such as *Ailanthus altissima* (Mill.) Swingle, *Buddleja davidii* Franch., *Robinia pseudoacacia* L., and *Paulownia tomentosa* (Thunb.) Steudel (e.g., Maringer et al., 2012; Conedera and Schoenenberger, 2014; Vítková et al., 2017), as well as the colonisation of intact mature broadleaved stands by shade-tolerant and late-successional evergreens such as, among others, *Prunus laurocerasus* L. and *Trachycarpus fortunei* (Hook.) H. Wendl. (Walther, 2002; Conedera and Schoenenberger, 2014; Conedera et al., 2018). Once established, shade-tolerant evergreens may also take advantage of individual disturbances that cause the opening of the main tree cover (Fridley et al., 2022), while they are limited or suppressed in the case of repeated disturbances such as recurrent forest fires in short intervals (Grund et al., 2005). These six selected species are among the priority species for the Cantonal Forest Service and among the most frequent non-native invasive woody species in forest according to the National Data and Information Centre of the Swiss Flora (infoflora.ch). Key information on the origin, ecology, and life traits of the target IWS is summarised in Supplementary Material 1.

2.3. Study design and data collection

The survey followed a two-step approach consisting of a pre-analysis of aerial images and a field study which assessed the presence of IWS in detected forest gaps. In the first step, we explored aerial images of the study area looking for forest gaps formed between 2008 and 2015 (see the forests detected with gaps in Step 1, Fig. 1, and Supplementary Material 2 for methodological details) and digitized the visible gap perimeters.

In a second step, we selected a subset of 851 forest gaps (Step 2, Fig. 1) homogeneously distributed throughout the study area and ensuring a balanced design with respect to the type of disturbance, i.e., natural (landslides, forest fires, uprooted coppice stools and trees, and dead trees) and human-induced (silvicultural treatments and maintenance of road slopes, powerline routes, and torrent channels). Anthropogenic disturbances were easy to recognise on aerial imagery (i.e., maintenance of road slopes, powerline routes, and torrent channels) or from the forest service archives (i.e., silvicultural interventions). Forest fire-induced disturbances were retrieved from the Swiss forest fire database (Pezzatti et al., 2019). The detailed assessment of the other natural disturbances (i.e., uprooted trees and coppice stools, landslides, dead standing trees etc.) and the verification of the correctness of the assigned type of disturbance has been verified in the field during the survey conducted between March and November in 2022 (Table 1). During the field work we further registered the presence (or absence) of deciduous and evergreen IWS inside the gap’s area and we defined 17 different forest typologies visually estimating the five most abundant tree species of the adult individuals standing in or surrounding the forest gap.

All the acquired data were stored in a dedicated PostgreSQL database with the GIS extensions of PostGIS (2018) allowing the storage of the geographic data and ensuring a structured and centralized handling of the collected information. Whenever needed, the database was directly accessed with the R software (v4.2.1; R Core Team, 2023) by the means of the RPostgreSQL R package (Conway et al., 2018).

The surveyed gaps were then characterised at the landscape, site, and gap level, respectively (Table 1). At landscape level, we used the digital Landscape Models (<https://www.swisstopo.admin.ch/en/geodata/landscape.html>) and used the sf R package (Pebesma & Bivand, 2018) to calculate the distances from the gap to the next human infrastructure such as buildings, roads, and powerlines, to natural elements such as rivers, and to potential hotspots of seed-bearing individuals of the target species. The presence (outside the gaps) of these latter was retrieved from the infoflora.ch database and the distance from gaps to the hotspot expressed as the average distance to the 20 nearest individuals of the concerned IWS. The distance from the next (potentially) seed-bearing individuals allows us to implicitly consider the species-specific seed

Table 1
Parameters considered for characterising the gaps.

	Parameter	Notes	Units
LANDSCAPE	Distance to hotspots	Average distance to the 20 nearest seed-bearing mature individuals (separately for each species) ^{a,b}	m
	Distance to rivers	Minimum distance to a river or stream (dry ones included) ^{a,c}	m
	Distance to buildings	Average distance to the 20 nearest buildings ^{a,c}	m
	Distance to powerlines	Minimum distance to a powerline ^{a,c}	m
	Distance to roads	Minimum distance to a carriageable road ^{a,c}	m
SITE	Forest typology	17 categories depending on the five most abundant tree species as visually estimated in the field	-
	Altitude	Average altitude ^d	m a.s.l.
	Slope	Average slope ^d	%
GAP	Aspect	Average aspect ^d according to cardinal points and transformed to southwestness using the equation from Beers et al. (1966); i.e. $\sin(\text{aspect} + 45) + 1$. Value range: 0–2. 0 = southwest facing (more xeric); 2 = northeast facing (more mesic)	-
	Topographic index	Average topographic position index (TPI) ^d . Negative values = concave, positive values = convex	-
	Disturbance type	Natural (i.e., uprooted tree, landslide, wildfire, death of trees), silvicultural treatment (i.e., coppicing, thinning), and other anthropogenic disturbances (i.e., maintenance of roads, powerlines, torrent channels, dumping sites).	-
	Area	Surface area ^e	m ²
	Perimeter	External perimeter ^e	m
	Width	Minimum width (i.e., minimum distance between two sides of the polygon) ^e	m
	Length	Maximum length (i.e., maximum distance between two sides of the polygon) ^e	m
	Direction	Gap direction, calculated by determining the direction of the maximal length compared to the steepest slope. Value range: 0–90. 0 = “vertical direction”: the maximum length of the polygon follows the direction of the steepest slope of the terrain; 90 = “horizontal direction”: the maximum length of the polygon is perpendicular to the direction of the steepest slope of the terrain	-
	Shape Complexity Index (SCI)	$SCI = \text{Perimeter} / (2 * \sqrt{(2 * \text{Area} * \pi)})$ from Koukoulas and Blackburn (2004). Value range: from 1 to ∞ . The closer the value is to 1, the more circular the gap is.	-

^a : calculated using the sf R package (Pebesma & Bivand, 2018).
^b : Invasive alien woody species’ data downloaded from infoflora.ch
^c : extracted from the digital Landscape Models (<https://www.swisstopo.admin.ch/en/geodata/landscape.html>).
^d : extracted from the digital elevation model (<https://www.swisstopo.admin.ch/en/geodata/height.html>) with a 25×25 m resolution via the terra R package (Hijmans, 2024).
^e : extracted by elaborating the polygon data using the PostGIS functions (PostGIS 2018).

dispersal patterns when modelling the influence of propagule pressure. Site characteristics such as altitude, aspect (transformed to southwestness), slope, and topographic index, were determined based on a digital elevation model with a 25×25 m resolution (<https://www.swisstopo.admin.ch/en/geodata/height.html>) and using the terra R package (Hijmans, 2024). Gap width (i.e., minimum distance between two

sides of the polygon), length (i.e., longest distance between two sides of the polygon), surface area, and perimeter were determined by elaborating the digitalized gap polygon data using the PostGIS functions (PostGIS, 2018). Finally, we defined for each gap the main direction and the shape complexity (see Table 1 for details).

2.4. Data analysis

The six target IWS (i.e., *A. altissima*, *B. davidii*, *R. pseudoacacia*, *P. tomentosa*, *P. laurocerasus*, and *T. fortunei*) were analysed separately. We first performed general descriptive statistics to explore the data and to evaluate possible associations (correlations) between explanatory variables. A pre-selection was then made to avoid issues related to high degrees of correlation (Pearson R > 0.6) among variables. When two variables were correlated, we retained the most appropriate one based on its ecological significance and the practical feasibility of its assessment in the field. To refine the variable selection from a practical and ecological point of view, the relationships between the binary response variable (presence or absence of the single considered species) and the landscape, site, and gap parameters (Table 1) were further inspected by means of a univariate comparative analysis.

The landscape, site, and gap parameters retained in the preselection were then used as explanatory variable to analyse their effect on the presence or absence of the six target IWS in a binomial logistic regression model. The only interactions considered were those occurring between the gap parameters (i.e. width, length, shape complexity index, and disturbance type) and the distance to the hotspots (see Table 1). Interactions were kept in the final models only if they significantly increased the overall model fit.

Since our study is based on a spatial-explicit sampling design, we tested our first models (i.e. the generalized linear regression models (binomial family, link function “logit”)) for spatial autocorrelation in the residual with the Moran test available in the spdep R-package (Bivand, 2022). To account for the spatial dependence that occurred in all the model, we used the spmodel R-package (Dumelle et al., 2023) which offers a variety of functions to fit, summarise, evaluate and predict spatial statistical models used in the subsequent analysis. For each target species, we then refitted three binomial logistic regression models varying in their covariance structure only (i.e., the first had no spatial covariance, the second had a spherical spatial covariance, and the third had a spherical spatial covariance that incorporates geometry anisotropy) using the spglm function. The models were evaluated using the AIC function and the one with the lower value selected as the best model. They were then further checked for correctness of model assumptions by the means of diagnostic metrics provided in the spmodel R-package.

Finally, invasion risk maps were computed by defining a 25×25 m geographical grid covering the Canton Ticino, corresponding to 1’773’603 points covering the entire cantonal forest area under 1500 m a.s.l. The predictions at each of these points were calculated using the augment function and using the best model for each considered species separately. The risk map was calculated and visualised only for the median value of the gap parameters and the average value between the three disturbance types. The resulting predictions were visualised using the free open-source geographic information system QGIS (QGIS Development Team, 2023). Due to the available space for the manuscript, we present in the results section the maps referring to three species only (*A. altissima*, *B. davidii*, and *T. fortunei*), whereas the remaining three are presented in the Supplementary Material 3 Fig. 3.4.

All analyses were performed in R v4.2.1 (R Core Team, 2023).

Table 2
Results of the spatial generalized linear binomial model for the six target neophyte species (i.e. *Ailanthus altissima*, *Buddleja davidii*, *Robinia pseudoacacia*, *Paulownia tomentosa*, *Prunus laurocerasus*, and *Trachycarpus fortunei*).

Species	<i>A. altissima</i>	<i>B. davidii</i>	<i>P. tomentosa</i>	<i>P. laurocerasus</i>	<i>R. pseudoacacia</i>	<i>T. fortunei</i>
Model coefficients						
Distance to hotspots	-0.001038 (0.000287)***	-0.001072 (0.000204)***	-0.000482 (0.000137)***	-0.000451 (0.000125)***	-0.001122 (0.000255)***	-0.000708 (0.000281)***
Distance to buildings			-0.001406 (0.000754)	-0.00415 (0.001122)***		-0.008406 (0.001692)***
Distance to powerlines	-0.000295 (1e-04)**				-0.003047 (0.000745)***	
Distance to roads						
Slope	0.036045 (0.013842)**	0.031856 (0.010876)**			-0.616816 (0.193916)**	
Aspect	-0.586446 (0.209505)**			-0.520752 (0.211717)*	-0.0863 (0.038292)*	
Topographic index			-0.100842 (0.035609)**		-0.004704 (0.001146)***	
Altitude	-0.006237 (0.001132)***				0.588563 (0.318988)	
Disturbance type: Other anthropic	1.633196 (0.328912)***	1.086324 (0.249888)***				
Disturbance type: Silviculture	0.805681 (0.341945)*					
Width	0.050613 (0.008779)***	0.017161 (0.005354)*	0.010344 (0.004586)*			
Length		0.001548 (0.000653)*	0.00162 (0.000752)*	0.002413 (0.000904)**	0.002858 (0.000846)***	0.00198 (0.001010)
Model fit						
Optimized value of the fitting function	2310.797	2589.015	2325.689	2147.294	2262.266	1984.725
AIC	2320.797	2599.015	2335.689	2157.294	2272.266	1994.725
AICc	2320.868	2599.086	2335.76	2157.365	2272.337	1994.796
logLik	-1155.398	-1294.508	-1162.845	-1073.647	-1131.133	-992.363
deviance	463.896	740.42	504.673	365.662	467.79	244.335
pseudo.r.squared	0.336	0.132	0.128	0.217	0.285	0.337

Note: the significant variables only are shown in the table. See [Supplementary Material 3](#) for the complete model summary and [Table 1](#) for further details on the variables. Values show the model estimates with its standard error in brackets. Other shared model fit data: sample size = 851, number of fixed effects: 15, number of estimated covariance parameters = 5.

* = p-value < 0.05; *' = p-value < 0.1.

** = p-value < 0.01;

*** = p-value < 0.001;

3. Results

3.1. Landscape and site-dependent distribution patterns

A total of 22 non-native invasive woody species (IWS) were found in the 851 visited gaps, among which the six target IWS were confirmed to be the most frequent ([Supplementary Material 3](#) Fig. SM 3.1). The target species that was detected most frequently was *B. davidii* (present in 40% of the visited gaps), followed by *A. altissima* (34%), *R. pseudoacacia* (27%), *P. tomentosa* (17%), *P. laurocerasus* (14%), and *T. fortunei* (9%).

The best models for all species included a spherical spatial covariance that incorporates geometric anisotropy suggesting that the model benefits from accounting for the spatial dependence. The modeled likelihood of the considered invasive woody species to colonise a gap show both common drivers shared among several species and species-specific factors ([Table 2](#)). The most evident shared pattern is the decrease in the probability of presence as a function of the distance to hotspots. This landscape variable is retained in all models with coefficient values ranging from -0.0005 for *P. laurocerasus* to -0.0011 for *R. pseudoacacia* ([Supplementary Material 3](#) Table SM3.1 and Fig. SM3.3). Since odds ($p/(1-p)$) are calculated like $\exp(\text{estimated coefficient})$, this means that if all other variables are kept constant, each additional 100 m distance to hotspots leads to a 5% decrease in the odds of presence for *P. laurocerasus*, 10% for *A. altissima*, and 11% for *R. pseudoacacia*, respectively. The distance to the hotspots is the most common variable in the models, while the distance to buildings is significant for both evergreen species (and for *P. tomentosa* although almost not significantly [Table 2](#)) only and with a higher estimate compared to the latter. In the latter cases, when holding all the other predictors constant, the probability of presence of *T. fortunei*, *P. laurocerasus*, and *P. tomentosa* individuals decreases by 84%, 41%, and 14% for every additional 100 m of distance to buildings, respectively ([Fig. 2](#), [Supplementary Material 3](#) Table SM3.1 and Fig. SM 3.3).

Similarly, the presence of target IWS decreases progressively with increasing altitude. Although altitude is retained only in the models of *A. altissima* and *R. pseudoacacia*, ([Table 2](#)), the presence of the other four species is generally also clearly correlated with altitude, with *B. davidii* displaying the weakest dependency ([Supplementary Material 3](#) Figs. SM3.2 and SM3.3).

The presence of *P. laurocerasus*, *A. altissima*, and *R. pseudoacacia* increased in south/south-west exposed sites (negative sign of Aspect in [Table 2](#), [Fig. 2](#), [Supplementary Material 3](#) Fig. SM3.3). Independently, the odds of the presence of *P. tomentosa* and *R. pseudoacacia* in a forest gap increases by 10% and 8%, respectively, when decreasing the topographic index by one unit (from convex to concave). Finally, species-specific effects can be observed. For example, there is a 3% decrease in the odds of the presence of *A. altissima* for each additional 100 m of distance to powerlines, a 30% decrease of the *R. pseudoacacia* presence per 100 m of distance to roads, and 3–4% decrease for each additional 1-unit increase of slope for *A. altissima* and *B. davidii*, respectively ([Fig. 2](#), [Table 2](#), [Supplementary Material 3](#) Table SM3.1 and Fig. SM3.3).

3.2. Disturbance-dependent effects

The disturbance type and the shape of the gap (i.e., width, length, and shape complexity) have different effects on the probability of presence depending on the target IWS ([Table 2](#) and [Supplementary Material 3](#) Table SM 3.1).

The disturbance type (i.e., natural, silvicultural, other anthropogenic disturbances) modulates the probability of the presence of *A. altissima*, *B. davidii*, and *R. pseudoacacia* which are significantly more present in anthropogenic disturbances compared to natural ones but has no significant influence on *P. tomentosa* and the evergreen species ([Table 2](#), and [Supplementary Material 3](#) Fig. SM3.3). For example, the odds of finding *A. altissima* are 5.1 (95% CI [2.7, 9.7]) times higher in anthropic disturbances than in natural disturbances when all other variables are

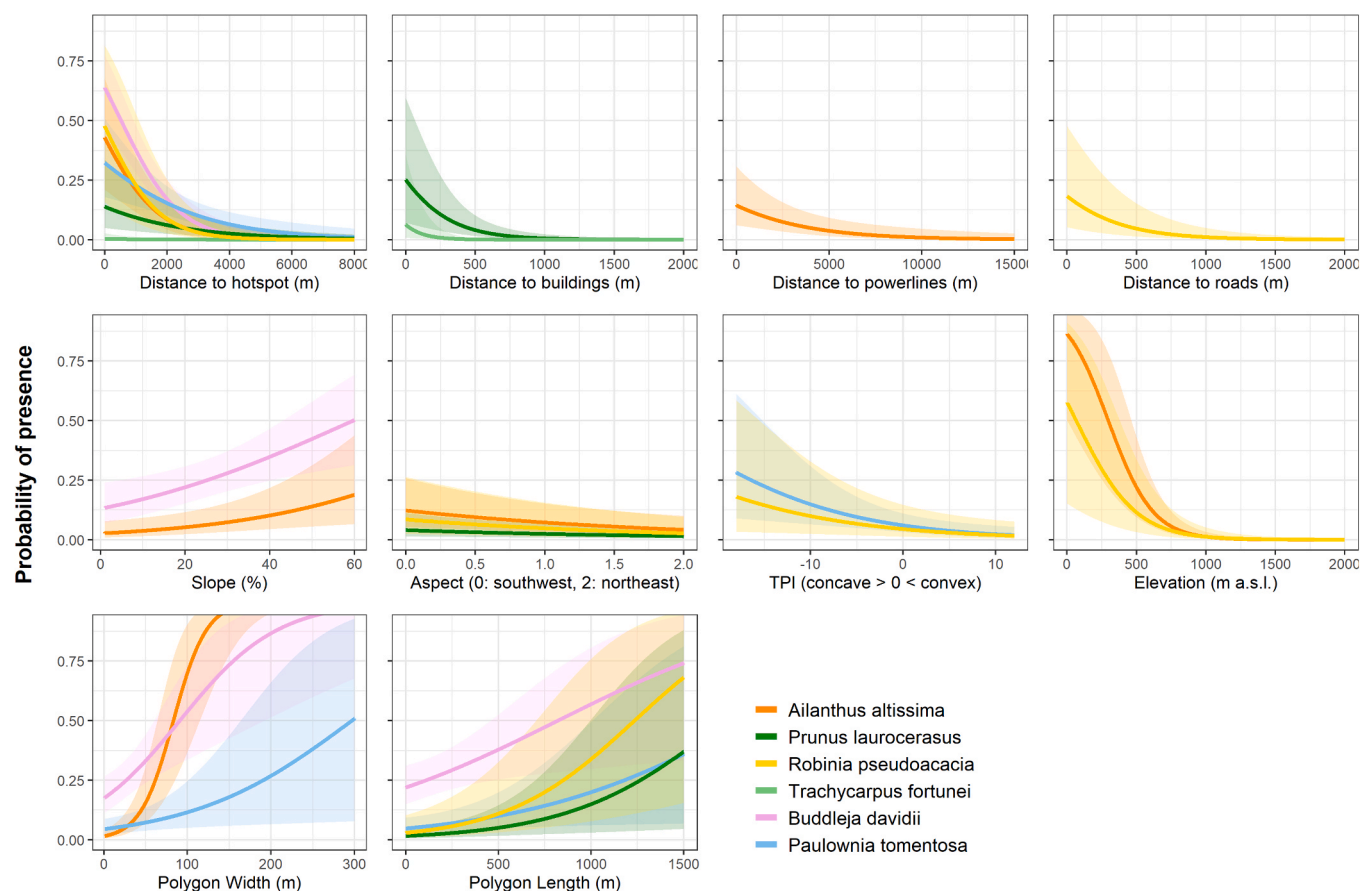


Fig. 2. Simple effects of model parameters on the probability of presence of the target invasive woody species. Only the significant parameters of the best models are shown and keeping all other variables constant at their average for the group silviculture (for the categorical variable “disturbance type”). The transparent area shows the 95% confidence interval.

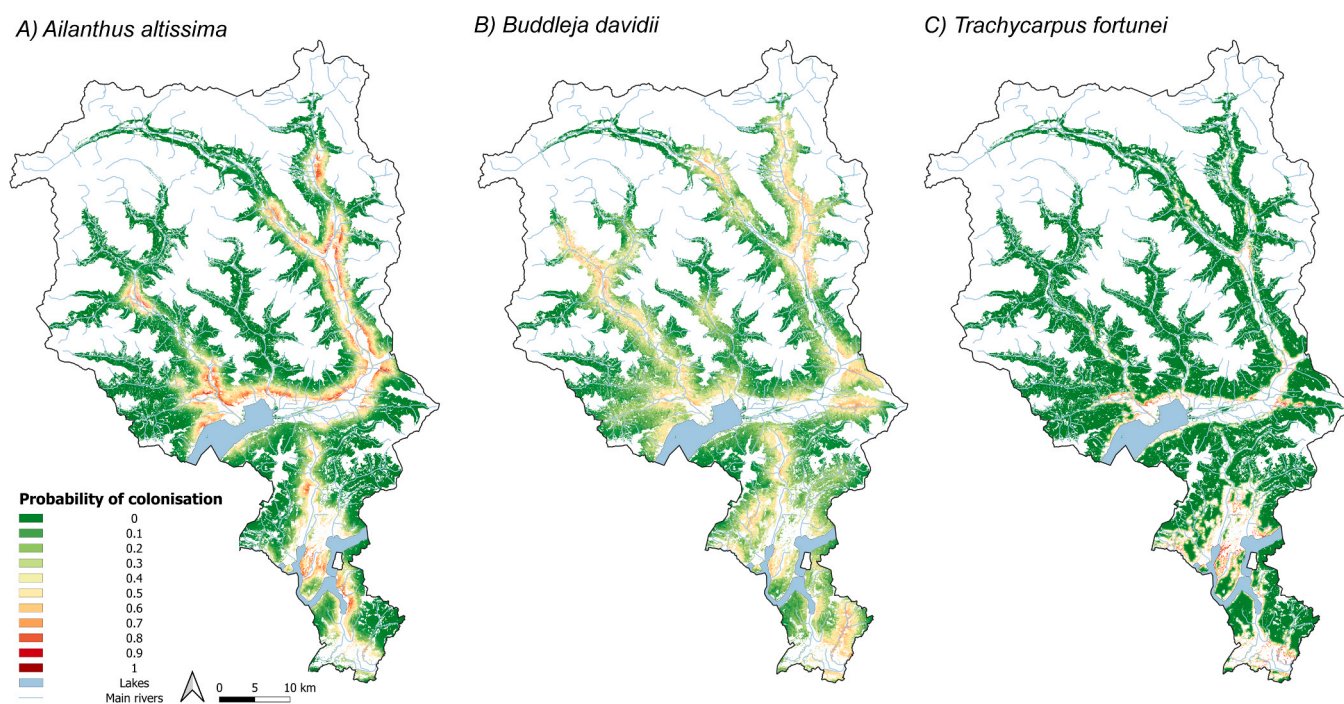


Fig. 3. Maps of Canton Ticino showing the probability of colonisation by A) *Ailanthus altissima*, B) *Buddleja davidii*, and C) *Trachycarpus fortunei*.

kept constant. A similar effect, although to a lesser extent (2.2 (95% CI [1.1, 4.4])), is found when switching from a natural disturbance to a silvicultural treatment (Table 2).

Against all expectations, the gap surface area has no effect on the probability of finding IWS. In fact, although gaps originated by silvicultural activities had the biggest surface (7803 m² [sd = 15497 m²]) and natural the smallest (3494 m² [sd = 14117 m²]), it is in other anthropic disturbances (area = 4486 m² [sd = 5713 m²]) where the probability of finding them is higher. Instead, other gap shape characteristics have a significant effect. For example, the narrow is the gap, the less likely it is to find a IWS, with the only exception of *R. pseudoacacia* (Fig. 2; Table 2, and Supplementary Material 3, Fig. SM 3.3). Similarly, the longer is the gap, the more likely it is that target species other than *A. altissima* are present (Fig. 2; Table 2).

3.3. Mapping the invasion risks

Based on the landscape and site parameters, the probability of colonisation of each target species predicted by the best model (Table 2) was visualized on a map, indicating the risk of colonisation by this species, should a disturbance at this location occur (Fig. 3 and for the other species Supplementary Material 3 Fig. SM 3.4).

Using these maps and averaging the predicted values across the entire study area, we determined that the probabilities of colonisation in case of a new disturbance for the six target species are 19% (sd 16%) for *B. davidii*, 14% (sd 22%) for *A. altissima*, 4% (sd 10%) for *T. fortunei*, 10% (sd 20%) for *R. pseudoacacia*, 7% (sd 9%) for *P. tomentosa*, and 6% (sd 11%) for *P. laurocerasus*. These probabilities increase significantly when considering only the forest area below 600 m asl where they may be twice (for *B. davidii* and *P. tomentosa*), three times (for *A. altissima* and *P. laurocerasus*), or even four times (for *T. fortunei* and *R. pseudoacacia*) as high.

4. Discussion

In this study, we have identified the landscape, site, and gap characteristics that influence the post-disturbance colonisation probability of the six prevalent invasive woody species (IWS) in the deciduous forest belt of Canton Ticino (southern Switzerland). Our findings indicate that these determining factors can be clearly ranked in terms of importance, with the propagule pressure at the landscape level being the most relevant.

All six target species share a common general pattern, namely that the presence of IWS is concentrated at lower altitudes, which is typical for mountain landscapes (e.g., Alexander et al., 2011). This is due on the one side to the strong environmental gradient and temperature, which rapidly drops, limiting the establishment of thermophilous plant species at higher altitudes (Becker et al., 2005; Steyn et al., 2017). On the other hand, the uneven distribution of settlements and infrastructure influences the probability of presence of target IWS by inducing a high spatial bias in the distribution of the propagule pressure (Becker et al., 2005; Alexander et al., 2011, 2016).

The same pattern was recently observed in Slovenia for both *Ailanthus altissima* and *Phytolacca americana*, which was attributed to the increased frequency of disturbances and, specifically, propagule pressure (de Groot et al., 2024), which is crucial for successful invasion processes to take place (Lockwood et al., 2005). With respect to propagule pressure, we found that the distance to the hotspots is the only variable present in the best models of all species. This suggests that in mountain habitats, at an early stage of invasion propagule pressure may have a greater influence on the distribution pattern than environmental factors, (Becker et al., 2005; Pauchard et al., 2009; Alexander et al., 2011, 2016; de Groot et al., 2024). However, we also observed that the probability of the presence of ornamental IWS such as *T. fortunei*, *P. laurocerasus*, and *P. tomentosa* depends on the proximity of the forest gap to settlements. We assume that this is related to the highly probable

presence of seed-bearing trees in the gardens in and around settlements (Conedera et al., 2018), which may not be registered as hotspots in neophyte databases such as www.infoflora.ch.

Similarly, *A. altissima* and *R. pseudoacacia* have two landscape features of their own which are the proximity to powerlines for the first, which takes advantage of greater light availability and the root sucker stimulation induced by the regular management consisting in cutting back the resprouts (Knüsel et al., 2019; Motti et al., 2021), and the proximity to roads for the second, which greatly profits from the side light induced by the maintenance of the slopes along the roads where it has long been used to consolidate the soil (Becker et al., 2005; Vítková et al., 2017). In agreement with other studies, our results evidence that these landscape features provide favourable conditions for the establishment of IWS thus also act as propagule corridors (Luken et al., 1992; Mortensen et al., 2009; McDougall et al., 2018; de Groot et al., 2024). Surprisingly the proximity to rivers for *B. davidii*, which is favoured by sandy and nutrient-poor soil conditions and frequent disturbances near torrent channels (Tallent-Halsell & Watt, 2009), is not retained in the best model, probably due to its widespread presence in any environment in the study area. After taking into consideration the dependence on the distance to hotspots and / or other landscape features, altitude (and the associated temperature gradient) does not appear to significantly influence the probability of the presence of *B. davidii*, *P. laurocerasus*, *T. fortunei*, or *P. tomentosa*. This is traceable for the slow growing, late sexual maturity, and bird-dispersed ornamental palm *T. fortunei* and *P. laurocerasus* and for the wind-dispersed *B. davidii*, which is largely frost resistant and already widespread along the altitude gradient but is less explainable for the wind-dispersed ornamental tree *P. tomentosa*. Given its still relatively limited propagation, it is possible that existing hotspots are still rather linked to the urban environmental and thus still concentrated at low altitudes. Becker et al. (2005) also observed invasive species with different responses to altitude, concluding the ones lacking a marked decline with altitude have a wide ecological amplitude in their native range and / or have been deliberately introduced at higher altitudes.

In general, species such as *A. altissima*, *B. davidii*, and *R. pseudoacacia* displaying the typical pioneer traits (e.g., germination on bare soil, light demanding and fast growing, early sexual maturity and massive production of light and seed-dispersed seeds) are more frequent on steeper slopes which usually correspond to drier and more disturbed environment (e.g. Pattison et al., 2019). Similarly, *A. altissima*, *R. pseudoacacia*, and *P. laurocerasus* profit of south-west site orientations usually linked to more xeric soil conditions. This may be surprising for the non-pioneer *P. laurocerasus*, which however tend to prefer dry soils more than moist ones and is not limited by prolonged drought periods (Berger and Walther, 2006).

Moreover, *A. altissima*, *B. davidii*, and *R. pseudoacacia* appear more frequently after silvicultural interventions and other anthropogenic disturbances than after natural disturbances (Radtke et al., 2013; Isler et al., 2023). This is because these species display a high resprouting capacity and thus greatly profit from the regular maintenance in other anthropic disturbances such as maintenance of roads, powerlines, torrent channels, dumping sites. On the other hand, the type of disturbance does not have any influence on the presence of the evergreens *P. laurocerasus* and *T. fortunei*, and of the pioneer *P. tomentosa*. Although this can easily be explained in the case of the two shade-tolerant evergreens, which tend to colonise intact deciduous broadleaved forests by regenerating in the shady understory prior to disturbances (Conedera et al., 2018), no obvious reason can be found for the pioneer *P. tomentosa* which is, however, sensitive to the gap width and length, like the other heliophilous species. During this study, however, we often observed *P. tomentosa* as a solitary tree growing in small rocky gaps (that is often a free niche) surrounded by a lot of litter or in concave sites (i.e., ample soil moisture and fertile soil), which is reflected in our model by the negative values of the topographic index.

Taken together, our results highlight that the relevance of the

proposed approach and of the obtained results go beyond the presented study case. In particular, studied deciduous pioneer species and evergreens seem to display different invasion syndromes (Kueffer et al., 2013; Novoa et al. 2020): post-disturbance early colonisation by the light demanding and wind-dispersed pioneer species (e.g., Knüsel et al., 2019), advanced colonisation in the understory of undisturbed and dark mature deciduous stands of the shade-tolerant evergreen species displaying a short-distance zoochore seed dispersion (e.g., Conedera et al., 2018) which then usually abundantly develop once exposed to light after stand disturbance. However, additional, and specific research is needed to confirm this.

4.1. Suggested management strategies

The maps of the invasion risk which were produced for each IWS can be used to adapt silvicultural interventions and to plan accompanying measures to reduce the likelihood of colonisation by unwanted IWS (de Groot et al., 2024). A possible, highly effective, pre-intervention management option consists in limiting the propagule pressure in the surroundings of the planned intervention (Ibáñez et al., 2009). However, reducing the number of seed-bearing individuals is in many cases a highly demanding task, which should be adapted to the life history of the species. For instance, for dioecious species such as *A. altissima* and *T. fortunei*, interventions could be limited to girdling the female individuals in the former case and to the removal of female inflorescences in the latter (Knüsel et al., 2019; Tonello et al., 2022). Simulating the effect of seed-bearing trees removal by re-run the models with different pre-intervention options could allow to optimise the cost-benefit balance of such measures (see Stringham and Lockwood, 2021). On the other end, simulating the raise in the colonisation probability of an area due a continuous spread of an invasive species following the lack of control measure may help highlighting the consequences of prolonged inaction.

When the likelihood of colonisation by heliophilous IWS is high, regulating the amount of light made available by the intervention (e.g., limiting the gap size, regulating the shape of the intervention area, leaving standing trees in the area) may be of paramount importance for preventing the post-treatment establishment of such species. Specifically, it is recognized that controlling gap size can serve as a practical measure to prevent the spread of IWS (Totland et al., 2005; Baret et al., 2008; Subedi et al., 2024). On the other hand, a possible management strategy targeting evergreens such as *P. laurocerasus* and *T. fortunei* is to keep the degree of shade maintained at the intervention site to limit the growth of the existing pre-regeneration. However, not all measures are equally effective and not all species respond the same to the planned measures. To ensure that any IWS individuals occurring despite careful planning are eradicated, it is therefore necessary to include into each management plan the post-intervention monitoring of the treated site. Finally, beyond our case study, these suggested management strategies can be considered for general management of invasive ornamental trees and included in existing global guidelines for the sustainable use of IWS (Brundu and Richardson, 2016; Brundu et al., 2020).

5. Conclusions

Due to the increasing incidence of invasive woody species, it is necessary to understand management strategies that reduce the likelihood of invasion in forests. With our approach we were able to highlight common patterns (e.g., the importance of propagule pressure) and species-specific factors (site, type, and gap shape) driving the colonisation of IWS in forest disturbances. The invasion risk maps created in this research allow to capture all these characteristics in a simple and effective manner and represent a practical tool for the practitioner. This may ease the planning of management strategies to minimise the likelihood of colonisation by unwanted IWS. Finally, increasing the knowledge on the ecology and life-traits of the target IWS is crucial for

decision-making process.

CRediT authorship contribution statement

Gianni Boris Pezzatti: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Marco Conedera:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Eric Gehring:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Melina Jeanette Aranda:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Authors' contributions

Marco Conedera and Gianni Boris Pezzatti developed the initial ideas and designed the methodology; Eric Gehring led and supervised the entire project and participated to the data collection and analysis; Melina Aranda analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122017.

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