



Comparing forest expansion (1930s–present) by invasive and native trees in relation to climatic, socio-economic, and landscape variables

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ABSTRACT

Over the past century, large areas of agricultural land across Europe have been abandoned, often transitioning to forests. This study examines the relationships between climatic, socio-economic, and landscape variables and forest expansion by the invasive non-native black locust (*Robinia pseudoacacia* L.) and native tree species in the Italian municipalities. Forest expansion was assessed by comparing a digitised 1936 forest type map with more recent forest maps (1999–2017), reclassified into black locust, native forests, and non-forested land. We modelled the probability and extent of forest expansion, accounting for non-linear relationships and non-Gaussian distributions. Expansion by native trees and black locust shows both similarities and differences. For black locust, spatial patterns and landscape diversity are strongly linked to both the probability of establishment and subsequent expansion. In contrast, expansion by native trees is primarily linked to landscape diversity, temperature, and rainfall, while spatial patterns are more relevant after expansion begins. Farm size is also associated with these dynamics: native tree expansion decreases with farm size but increases beyond 20 ha, whereas black locust expansion consistently declines as farm size grows. Mean individual income does not appear to influence either process. This study shows that native and invasive trees respond differently to landscape structure, spatial context, and farm size, while economic variables such as income play a minor role. These contrasting patterns support the use of the municipal scale to interpret forest change and to inform spatial planning aimed at distinguishing areas of natural recovery from those susceptible to invasion.

1. Introduction

A non-native tree species is considered naturalised when it can survive and reproduce consistently despite abiotic and biotic barriers (Richardson et al., 2000). It becomes invasive when it establishes self-replacing populations that persists for at least a decade, either without or despite human intervention, and produce offspring that spread considerable distances from parent plants (Richardson and Rejmánek, 2011). This process is influenced by a combination of biological, ecological, climatic, and biogeographic factors (Pyšek and Richardson, 2006).

Socio-economic development and transportation networks (Vilà and

Pujadas, 2001), as well as trade openness (Hulme, 2009), have been identified through direct measures or proxies as playing an important role in explaining a region's susceptibility to invasion. In general, an economic perspective, combined with appropriate policies, can enhance the study of biological invasions beyond assessing their monetary and non-monetary costs (Dalmazzone and Giaccaria, 2014).

While directly linking an economic variable to a biological process like invasion is challenging, comparing its influence on similar processes involving native and non-native species may be more feasible. Agricultural land abandonment provides such an opportunity, as abandoned lands often transition into forests driven by both native and invasive trees. This phenomenon is particularly evident in many parts of Europe,

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especially in mountain regions, where agricultural land has been abandoned (MacDonald et al., 2000).

This study provides new insights by comparing, for the first time at the national scale, the contrasting dynamics of native and invasive tree expansion on abandoned agricultural land, using harmonised historical and recent forest maps and a two-part modelling framework that distinguishes between establishment and spread.

In Europe, the most wide-spread invasive tree species is black locust or Robinia (*Robinia pseudoacacia* L.) that, according to recent data, covers around 24,370 km² (Brus et al., 2019). Time of first introduction is variable among European countries and occurred mainly between the XVII and XIX century (Nicolescu et al., 2020). Its extensive use has been registered between the end of the XIX and the beginning of the XX century, but the invasion potential become evident in the middle of the last century (Maltoni et al., 2012; Vítková et al., 2017). Humans have played a key role in fostering its spread for social and economic reasons, as it serves a wide range of purposes, including ornamental uses, land reclamation, soil stabilization, timber, firewood, honey, and other edible products (Cierjacks et al., 2013; de Gomez and Wagner, 2001).

Conservationists often emphasize containment of invasive species to prevent biodiversity loss (García-Llorente et al., 2008). However, black locust stands are widespread on several ecological conditions, have a specific species composition and can have high structural diversity (Campagnaro et al., 2018). Like with other widespread invasive tree species, its long-term persistence, the impracticality of eradication, and the services it provides suggest a pragmatic acceptance as part of the local biodiversity, controlling it only in specific situations (Starfinger et al., 2003). *Robinia pseudoacacia* is not only one of the most widespread invasive tree species in Europe but also exemplifies traits common to other invasive trees, such as fast growth, disturbance tolerance, and human-mediated dispersal. As such, it serves as a useful model to explore broader ecological and spatial dynamics of invasive tree expansion in human-modified landscapes.

This study adopts such a perspective to characterise municipalities, administrative entity that hold responsibility for environmental management. These municipalities may benefit from exploring and regulating new management techniques, moving beyond traditional approaches that often focused narrowly on biodiversity loss and resulted in a case-by-case, unguided management and not coordinated and not science-based policies (Pötzelsberger et al., 2020). Furthermore, this research offers an interpretative and methodological framework to take informed decisions for other widespread invasive tree species, addressing their implications for landscape management and policy.

In parallel, also native tree species have expanded into abandoned agricultural lands. Although not explicitly stated, several studies have documented forest expansion processes that largely involve native species. For example, studies in the European Alps illustrate how the factors influencing forest expansion vary regionally. For example, in the Southern French Alps, high-altitude grasslands are less likely to be abandoned compared to those at lower altitudes (Hinojosa et al., 2016). Similarly, in Tyrol, grasslands with high management intensity expanded in municipalities characterized by larger populations, higher livestock density, smaller farms, more remote locations, and fewer municipal grasslands or natural parks (Hinojosa et al., 2019). Furthermore, Alpine municipalities have been classified into agrarian structure types based on shared environmental, agro-economic, and demographic conditions (Schirpke et al., 2022), with agricultural income identified as a key factor influencing landscape change and related ecosystem services (Tasser et al., 2024). As Garbarino et al. (2020) emphasise, predicting forest landscape dynamics in mountain areas with a long history of cultural use requires understanding how the magnitude and timing of land-use changes align spatially and temporally with conditions suitable for tree establishment and growth.

Similar socio-economic and landscape factors may also influence the expansion of non-native trees such as black locust. The initial process of forest expansion by black locust should be strongly influenced by

climatic variables, such as sub-Mediterranean to warm continental climates, where high heat-sums favour its growth (Cierjacks et al., 2013). Once established, its expansion is often facilitated by disturbances like railways, roads, land fragmentation, dispersed settlements, and increased landscape diversity (Vítková et al., 2017). The last three may result from land abandonment, creating opportunities for forest expansion by both native and black locust trees (Sitzia et al., 2012). In both cases, relationships are likely non-linear.

We hypothesise that forest expansion is driven by two processes. The first process involves a probabilistic threshold that determines whether the environmental conditions are suitable for black locust or native trees to begin to expand. The second process comes into effect once forest expansion begins and determines the extent of tree cover that develops as the trees spread and colonise the abandoned land. Focusing on regions where black locust and native trees have similar opportunities to establish, our study had the following specific objectives: (1) to quantify forest expansion by native trees and *Robinia pseudoacacia* across Italian municipalities using harmonised historical and recent forest maps; (2) to identify and compare the climatic, socio-economic, and landscape variables associated with the probability of forest expansion initiation; (3) to assess the influence of the same variables on the extent of forest expansion once it has begun; and (4) to evaluate whether these drivers differ between native and invasive tree expansion processes.

2. Materials and methods

2.1. Study area

The study area encompasses Italy, a country covering 301,340 km² and characterized by a wide range of climates. These include temperate climates with dry and hot summers or arid steppe climates in the south, transitioning to cold climates with no dry season and warm summers near the alpine timberline in the north. The country is administratively divided into almost 8,000 municipalities belonging to 20 regions, one of which includes two autonomous provinces. These municipalities, which serve as the units of analysis in this study, correspond to the Local Administrative Units (LAU) as defined by Eurostat. The boundaries and names of the municipalities we refer to in the study are those of the 2011 census (ISTAT, 2011a).

2.2. Data collection

A historical forest type map of Italy published in 1936 (Milizia Nazionale Forestale, 1936) which has been digitised (Ferretti et al., 2018), has been used. Most Italian regions had prepared more recent forest type maps, defined as forests distinguished by their tree canopy composition, including those dominated by black locust, published between 1999 and 2017. However, they were not consistently available across all regions. This, combined with factors such as codification issues, boundary changes, and the omission of islands, resulted in an initial dataset comprising 6,316 municipalities for the study, 73 % of the Italian territory. The analysis, detailed in the [Supplementary materials](#), reclassified the maps into native tree woodlands, black locust woodlands, and non-forest cover. Through a comparison between the historical and the recent forest type maps we measured two response variables: f_{rob} (forest expansion by invasive black locust) and f_{nat} (forest expansion by native tree species). To minimise the risk of detecting spurious or insignificant changes, both historical and recent forest maps were aggregated to 1 km × 1 km grids using a majority-rule zonal statistic. This procedure filters out isolated patches smaller than approximately 0.5 ha and ensures that only substantial, consistent changes in land cover were included in the forest expansion estimates. Then, we omitted municipalities with a mean black locust survivability value below 0.5, based on de Rigo et al. (2006), to exclude areas with climatically unsuitable conditions. This reduced the number of municipalities to 1,493.

Mathematically, f_{nat} represents the ratio of non-forested land cells within a municipality that transitioned to native tree woodland during the current mapping period (1999–2017) to the total number of cells in that municipality. In contrast, f_{rob} represents the proportion of each municipality's area currently covered by black locust woodlands.

In practice, f_{nat} quantifies the forest expansion by native tree species in municipalities over time. Conversely, f_{rob} captures the forest expansion by invasive black locust, primarily over previously non-forested areas.

For each municipality we collected the following values: temperature (bio1), rainfall (bio12), continentality (tconmean), farm size (numazr), railway density (lenferr), population density (popde), road density (lenroadr), landscape diversity (shdi), dispersed settlement (popdi), urbanization (urbr), mean income (redre) (Table 1).

These variables were not statistically intercorrelated, with pairwise correlation values ranging from -0.47 to 0.46 . This indicates that each variable captures distinct aspects of the climatic, socio-economic, and landscape conditions within the study area. The low correlations ensure that the analyses are not confounded by redundancy among predictors, allowing for a more robust interpretation of their individual contributions to the observed patterns.

Temperature was the mean annual temperature ($^{\circ}\text{C}$), rainfall the mean annual rainfall (mm) and continentality the mean difference (mm) between mean temperature for July and mean temperature for January. The values were retrieved from the World Clim database (Fick and Hijmans, 2017), with resolution 2.5 min and averaged within each municipality using zonal statistics. Given that most municipalities in the dataset exceed the spatial resolution of the climate data, this approach provides a representative estimate of mean climatic conditions.

Farm size was the mean farm size in hectares retrieved by dividing the total agricultural utilised area by the number of utilised farms from the 2010 national agricultural census (ISTAT, 2011b). Railway and road density was expressed as km per 100 ha as of 2007 (CISIS, 2007). Population density was expressed as number of residents per km^2 as for 2004 from ISTAT (2025), urbanisation as the urban area divided by the total area as for 2001, dispersed settlement as the proportion of population living in dispersed settlements or isolated homes as for 2001, mean income as taxable income in euros per inhabitant as for 2002. These values were retrieved from a database collected by Tenuta (2006) in which the sources used are cited. Landscape diversity was calculated through the Shannon-Wiener diversity index of CORINE Land Cover 2012 classes, level 3 (European Environment Agency, 2019), using surface area as the frequency metric of each class, without any modifications to the original map.

Although the socio-economic variables span different years (from 2001 to 2010), we consider their use appropriate for this analysis. Forest expansion is a gradual process influenced by long-term land-use and demographic changes, rather than short-term fluctuations. The forest and land cover maps used (1999–2017) represent cumulative changes

over several decades, making the socio-economic context from the early 2000 s a reasonable approximation of the prevailing conditions during most of the forest expansion period. Normalising or interpolating these variables would have introduced further uncertainty, given the lack of consistent time-series data at the municipal level.

2.3. Data analysis

Our objective was to compare the factors driving the expansion of black locust and native trees on a national scale. We began by identifying areas where both native trees and black locust had an equal opportunity to afforest land made available by land use abandonment. Given that some native tree species, under suitable ecological conditions, will always be present and capable of colonising abandoned lands, we focused on identifying regions where black locust was already present or potentially present in neighbouring areas, ensuring its spread was not constrained by distance or physical barriers.

To identify those regions, we grouped municipalities into geographically compact clusters. Geographic data were processed to calculate distances between municipality centroids and define spatial weights based on neighbourhood relationships. A Frobenius distance matrix was used to quantify dissimilarities in forest expansion, forming the basis for hierarchical clustering using Ward's method. Municipalities were then partitioned into four clusters, reflecting patterns of f_{rob} . Neighbourhood constraints were incorporated into the clustering process to account for spatial dependencies, balancing within-cluster homogeneity with spatial continuity. This approach allowed clusters to include municipalities without significant values of f_{rob} if they were adjacent to municipalities with high expansion, addressing the key question of why neighbouring municipalities might exhibit very different levels of forest expansion. The analysis was conducted using the R package ClustGeo (Chavent et al., 2018).

Then, we used logistic regression to model the probability that $f > 0$ for a given municipality, i.e., $p = \Pr\{f > 0\}$, and beta regression to model the mean value of f for municipalities with $f > 0$, i.e., $E(f|f > 0)$. Beta distribution describes continuous random variables that fall naturally between 0 and 1, such as proportions. The approach used consists of two stages: the first stage seeks a binomial model addressing whether f is zero or positive; if $f > 0$, the second stage is initialised to address the conditional distribution of f .

The decision to employ this approach rather than a standard linear model can be explained by the following reasons. The variable f (particularly f_{nat}) exhibits many zeros, needing the use of a two-part model, specifically the hurdle binomial-beta model, to address both zero and non-zero values. The first component, which is discrete and binary $\{1, 0\}$, is naturally suited to binomial modelling. The second component, being a fractional variable, is better modelled by a beta distribution, which does not rely on the normality assumption required by linear models. Then, logistic regression is used to describe the

Table 1

Summary statistics for response variables used in the analysis across 1,493 municipalities in Italy. Variables include temperature (bio1), rainfall (bio12), continentality (tconmean), farm size (numazr), railway density (lenferr), population density (popde), road density (lenroadr), landscape diversity (shdi), dispersed settlement (popdi), urbanization (urbr), and mean income (redre). The table reports the mean, standard deviation (SD), minimum (Min), and maximum (Max) values, with units specified for each variable.

Acronym	Name	Mean	SD	Min	Max	Units and explanation
bio1	temperature	11.4	1.6	-1.2	14.1	$^{\circ}\text{C}$ (mean annual temperature)
bio12	rainfall	961.0	163.0	692.0	1394.0	mm (mean annual rainfall)
tconmean	continentality	19.8	1.1	14.2	22.6	$^{\circ}\text{C}$ (difference July-Jan mean temperatures)
numazr	farm size	7.0	8.7	0.0	131.3	ha (mean farm size)
lenferr	railway density	0.1	0.18	0.0	1.43	km/100 ha (railway density)
popde	population density	336.0	450.0	5.0	6931.0	residents/ km^2 (population density)
lenroadr	road density	2.1	0.92	0.06	8.22	km/100 ha (road density)
shdi	landscape diversity	1.28	0.40	0.0	2.31	Shannon index (landscape diversity)
popdi	dispersed settlement	0.21	0.21	0.0	0.95	proportion (dispersed settlement)
urbr	urbanisation	0.15	0.21	0.0	1.0	proportion (urbanisation)
redre	mean income	10684.0	1793.0	3683.0	21117.0	€/inhabitant (mean income)

probability that a municipality with given properties will have $f > 0$, while beta regression with a logistic link function was employed to evaluate the mean value of f , $E(f)$, when $f > 0$. Additionally, to account for the non-linear relationships between f and the environmental variables, we incorporated a generalised additive structure into the link functions. The estimation process is facilitated by an equation that allows for the separate fitting of a binomial-GAM to $1|f > 0$ and a beta-GAM to $f|f > 0$, as detailed in the [Supplementary materials](#). This approach enables the calculation of point estimates and confidence intervals for each process feature independently of the others.

As a standard diagnostic for binomial regression, we used the area under the curve (AUC) to evaluate the model's ability to discriminate between municipalities, indicating the potential for forest expansion to begin. AUC values range from 0 to 1, with 0.5 indicating random guessing and 1 indicating perfect discriminatory power. To assess the predictive ability of the binomial models, cross-validation was performed by dividing the municipalities into two subsets, with models first fitted to a training subset comprising 75 % of the dataset. This procedure was repeated multiple times using different data splits. Then, the resulting mean AUCs were compared to the AUC from the original model. For the beta model, cross-validation was less relevant since its focus is on explaining variations in cover within already established areas. Its complexity is managed through internal penalization (REML), making further validation unnecessary for this context.

The two dependent variables were spatially autocorrelated. We modelled spatial autocorrelation by including latitude and longitude of the municipality centroids as a smoothed, interaction term, representing spatial patterns in the data. In this way, the residuals are more likely to be independent random variables and therefore not violate the assumptions of the inferential procedure. The smooth splines were treated as random effects with a power exponential correlation function with range estimated from the data according to the method of [Kammann and Wand \(2003\)](#). In this way we accounted for non-linear phenomena related to adjacencies not directly controllable, before making inference about the other explanatory variables. Municipalities were weighted proportionally to the inverse of their size.

The last analysis dealt with the importance of municipality characteristics. Broadly speaking, the shape and steepness of the regression curves obtained with the previous explained methods could serve as indicators of each predictor's relative influence on f . A more formal approach to evaluate the significance of these characteristics is to use the Wald test statistic, T_{kj} , to assess the significance of the j_{th} predictor in model M_k for $k = 1, 2$, while accounting for the other predictors. As a result, only variables that are significant in one or both models are retained. As explained in the [Supplementary materials](#), the sum $T_{1j} + T_{2j}$ represents the test statistic for assessing the significance of the j_{th} predictor across both processes combined. Specifically, this statistic tests the hypothesis that the j_{th} predictor has no influence on the probabilistic threshold above which the forest expansion process can begin, or on the mean value of f if the forest expansion process has already started. Municipality characteristics were then ranked according to the value of this test statistic minus the test degrees of freedom.

Further details about the analyses can be obtained in the [Supplementary materials](#).

3. Results

3.1. Geographical clustering

The patterns of forest expansion in Italy are shown in [Fig. 1](#). Native trees species expanded over abandoned land use in every mountainous area of Italy, from the most north-western regions to most southern Sicily. Black locust invaded abandoned agricultural land mainly along the Prealps and the foothills of the northern Apennine.

Following the pattern of distribution of forest expansion by black locust in Italy, we identified four clusters of municipalities, one of which, coloured in light blue ([Fig. 2](#)), groups municipalities where black locust woodlands are absent or are too isolated to form clusters ([Fig. 3](#)). The municipalities included in the analyses are therefore those belonging to the clusters number 2–4. Further details on the statistical analysis are reported in the [Supplementary materials](#).

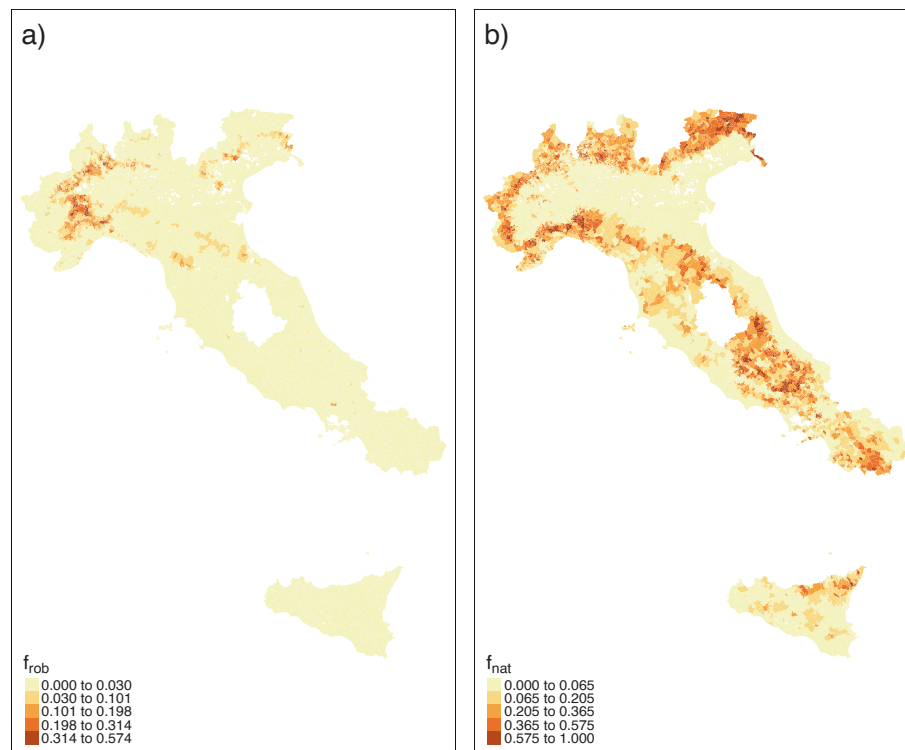


Fig. 1. Forest expansion by black locust (f_{rob}) (a) and by native trees (f_{nat}) (b) in the Italian municipalities where data were available ($n = 6,316$).

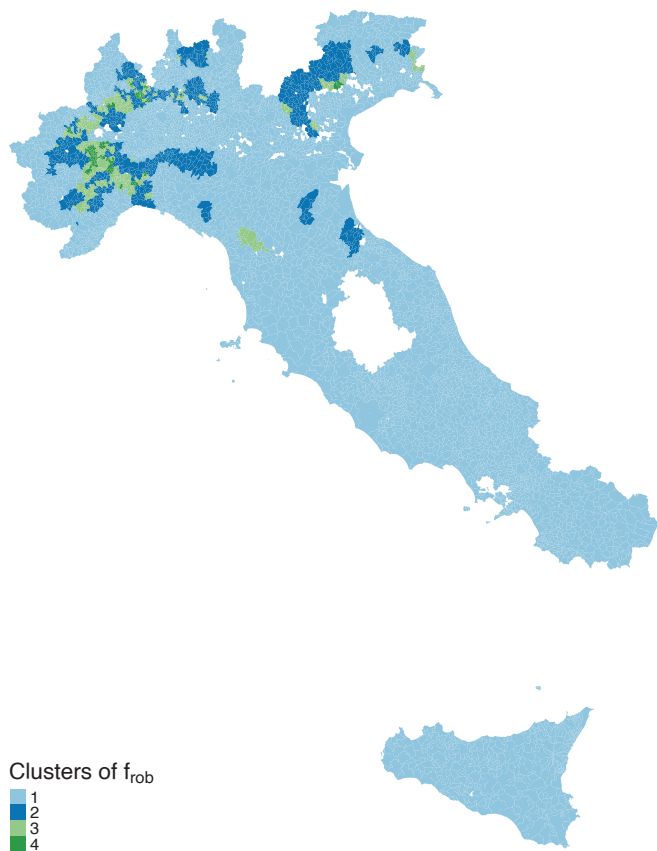


Fig. 2. Municipalities clustered based on forest expansion by black locust (f_{rob}) and geographical proximity in the Italian municipalities where data were available ($n = 6,316$).

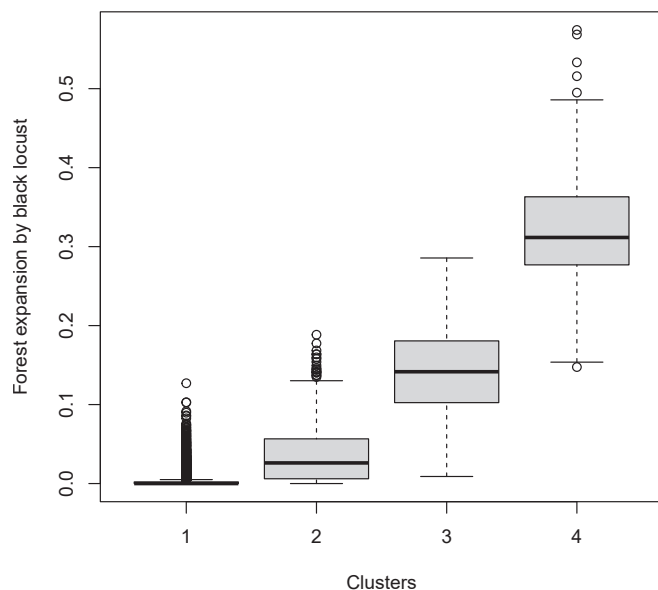


Fig. 3. Forest expansion by black locust (f_{rob}) in each cluster of Fig. 4.

3.2. Modelling invasive and native tree forest expansion

3.2.1. Probability of initiating non-native and native tree forest expansion

We first fit a Binomial Generalized Additive Model (GAM) with a logistic link to the $1|f > 0$ responses, denoted as model M1 (with separate models for “nat” and “rob”). The sample size for this analysis was

1,493. Approximately 58.8 % of the variability in $1|f_{rob} > 0$ was explained by model $M1_{rob}$, a measure adjusted to account for the number of regression parameters included in the model. The AUC for $M1_{rob}$ was 0.91, indicating a high level of discriminatory power.

Spatial patterns, represented by the geographical coordinates of the municipality centroids, were highly significant in all models. These patterns were modelled through an interaction term, with graphical representation as contours showing different levels of the interaction effect, where the x-axis represents latitude and the y-axis represents longitude. However, due to the complexity of interpreting these graphs and since our analysis did not focus on the spatial distribution of the interaction effects, we have decided not to report them.

Temperature, continentality, landscape diversity, and road density were identified as significant predictors ($p < 0.05$). Apart from landscape diversity, which had an effective degree of freedom equal to 1, these predictors exhibited non-linear relationships. The other characteristics were either not significant or only marginally significant ($p < 0.1$).

Fig. 4 shows the estimated probability (with 95 % confidence intervals) that f_{rob} is greater than zero. Each panel varies one significant municipal characteristic while holding all other variables constant at their median values. Only the range of each explanatory variable between the 0.1st and 99.9th percentiles are plotted, excluding values below or above this range to improve readability and focus on the central trends. For example, in the temperature panel (bio1), the estimated probability that a municipality with the characteristics $x_1 \equiv (\text{bio1} \equiv 9, \text{bio12} \equiv 936.5, \text{tconmean} \equiv 20.1, \text{shdi} \equiv 1.31, \text{popde} \equiv 578, \text{numazr} \equiv 4.69, \text{urbr} \equiv 0.05, \text{popdi} \equiv 0.14, \text{redre} \equiv 10,628, \text{lenroadr} \equiv 2.02)$ will have non-zero black locust cover is 0.90, with a 95 % confidence interval of (0.40, 0.99). In contrast, the probability at another point x_2 , which is identical to x_1 except that bio1 equals 6 instead of 9, is 0.01, with a 95 % confidence interval of (0.00, 0.29). In other words, the likelihood of having black locust cover drops drastically, by 90 times, when bio1 changes from 9 to 6, regardless of whether the other municipal characteristics are set to their median values or any other fixed values (Fig. 5).

Temperature displays a sigmoidal relationship with the probability of $f_{rob} > 0$, where probabilities increase sharply around 5 °C and then plateau at 10 °C. Road density shows a decreasing trend in the probability of $f_{rob} > 0$ at both very high and very low values. Landscape heterogeneity exhibits a slight increase in the probability of $f_{rob} > 0$, while continentality, expressed as the mean difference between July and January temperatures, shows a dramatic decline in the probability of $f_{rob} > 0$ with differences higher than 17 °C.

In all these characteristics, the level of uncertainty in the estimates of the response is high, at least in some portions of the ranges.

The cross-validation of $M1_{rob}$ resulted in a mean AUC of 0.85, which is only 0.06 less than the AUC obtained from the model fitted to the entire dataset, confirming the strong predictive ability of $M1_{rob}$.

The same procedure was applied also to the $1|f_{nat} > 0$ responses. Model $M1_{nat}$ explained approximately 57.9 % of the variability in $1|f_{nat} > 0$, with an AUC of 0.88, indicating a high level of discriminative power. The significant characteristics ($p < 0.05$) were temperature, rainfall, population density, dispersed settlement and landscape diversity.

The probability of $f_{nat} > 0$ shows a clear declining trend after 10 °C of temperature. The fluctuations in rainfall suggest no distinct relationship with the probability of $f_{nat} > 0$, except for a noticeable decrease below 800 mm, which also comes with high uncertainty. While a clear negative trend of f_{nat} with increasing population density is observed between the minimum values and approximately 500 residents/km², at higher values, the curve appears to exhibit a U-shaped trend. However, the wide confidence intervals, particularly at extreme values, hinder its predictive reliability. In contrast, dispersed settlement displays a consistent upward trend in the probability of $f_{nat} > 0$ although with uncertainty, and landscape diversity demonstrates a strong positive

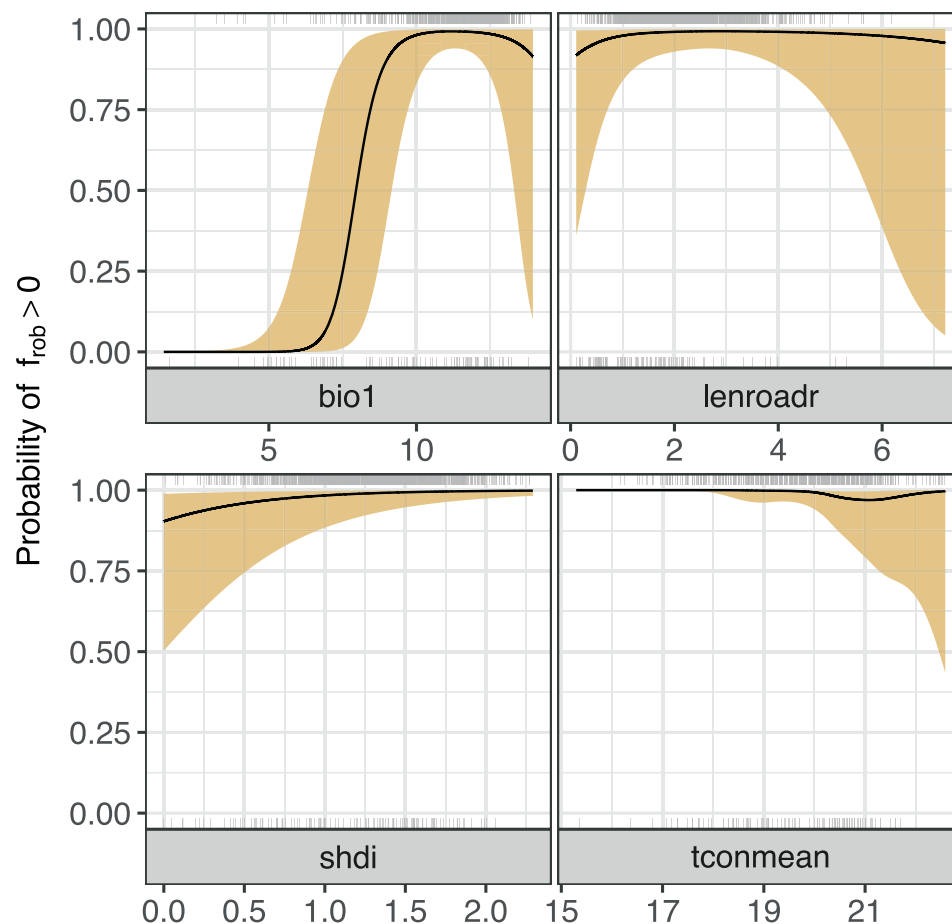


Fig. 4. Fitted probability curves for the four municipality characteristics indicated in the labels (bio1 = temperature, lenroadr = road density, shdi = landscape diversity, tconmean = continentality). In each panel, the black solid line represents the estimated probability of $f_{rob} > 0$ while varying only one municipality characteristic and holding other characteristics fixed at their median. The shaded areas depict 95 % confidence intervals. Data points (1 if $f_{rob} > 0$ and 0 otherwise) are laid out in the background. Only the characteristics that were significant according to the model M_{1rob} are reported.

relationship, continuously increasing the probability of $f_{nat} > 0$ throughout (Fig. 5).

The mean AUC values of the cross-validation of the predicting ability of M_{1nat} yielded 0.86, confirming its predictive ability.

3.2.2. Determinants of non-native and native tree spread

A beta-GAM was fitted to the $f|f > 0$ responses, referred to as model M_2 (with separate models for nat and rob). The sample sizes for M_{2rob} and M_{2nat} were 1,377 and 672, respectively, after excluding responses that were exactly zero.

Model M_{2rob} accounted for 53.0 % of the variability in $f_{rob}|f_{rob} > 0$, indicating a high level of discriminatory power. All climatic variables, along with landscape diversity, road density, urbanisation, dispersed settlement, and farm size, were statistically significant and exhibited non-linear relationships with $f_{rob}|f_{rob} > 0$.

Fig. 6 presents the estimated average of $f_{rob}|f_{rob} > 0$ with 95 % confidence intervals, varying one significant predictor while holding all other predictors fixed at their median values. Temperature exhibits significant uncertainty below 4 °C and a peak around 11–12 °C. Rainfall shows a general decreasing trend as its amount increases, albeit with local fluctuations. Similarly, continentality displays a fluctuating pattern, with uncertainty narrowing in the mid-range (17–20 °C), where the trend becomes more stable and consistently negative. Overall, the trends of these three variables suggest that the climate sensitivity of black locust is variable and only partially predictable. Farm size displays a downward trend, indicating that f_{rob} decreases as farm size increases. In contrast, both road density and landscape diversity exhibit a positive

trend, suggesting a distinguishable increase in f_{rob} as these variables rise. Dispersed settlement, apart for a weak decline at the lowest values, presents a rather flat pattern without a clear pattern, like urbanisation.

Model M_{2nat} accounted for 50.4 % of the variability in $f_{nat}|f_{nat} > 0$, indicating a strong discriminative power. Temperature, railway density, farm size, landscape diversity, and population density were statistically significant predictors ($p < 0.05$), with landscape diversity and population density exhibiting linear relationships with the response. Fig. 7 presents the estimated average of $f_{nat}|f_{nat} > 0$, along with 95 % confidence intervals, as each significant predictor is varied while holding all other predictors fixed at their median values.

Temperature shows a clear declining trend in f_{nat} for values above 9 °C. Railway density exhibits no distinct trend until it exceeds 0.5 km/100 ha, after which it shows an increase, albeit with high uncertainty. Farm size initially shows a negative trend at lower values but, beyond approximately 20 ha, displays a consistent upward trend in f_{nat} . Population density, on the other hand, shows a modest negative trend. In contrast to farm size, landscape diversity demonstrates a strong and consistent negative relationship, with f_{nat} continuously decreasing as landscape diversity increases.

3.2.3. Importance of the municipality characteristics

We now turn our attention to the importance of municipality characteristics. Municipality characteristics were ranked according to the value of the test statistic T_{kj} minus the test degrees of freedom. This ranking is reported in Fig. 8 and Fig. 9 for each part of the model respectively for f_{rob} and f_{nat} and it quantitatively confirms what has been

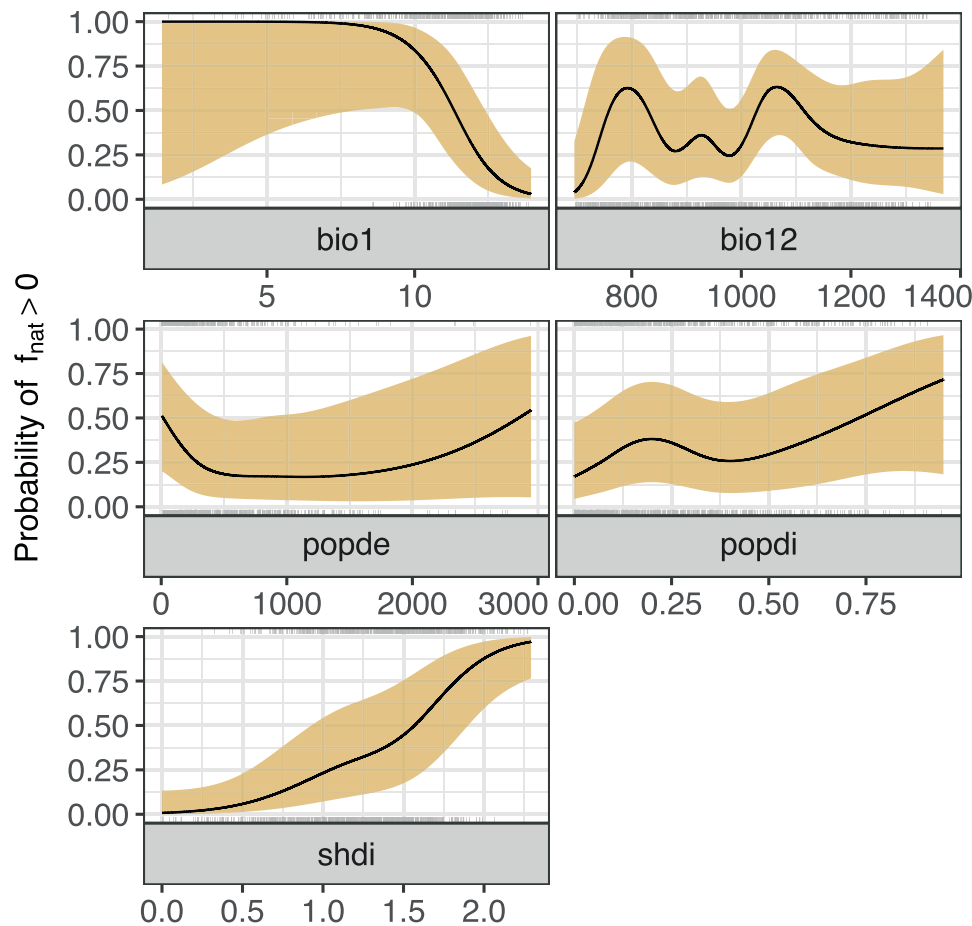


Fig. 5. Fitted probability curves for the five municipality characteristics indicated in the labels (bio1 = temperature, bio12 = rainfall, popde = population density, popdi = dispersed settlement, shdi = landscape diversity). In each panel, the black solid line represents the estimated probability of $f_{\text{nat}} > 0$ while varying only one municipality characteristic and holding other characteristics fixed at their median. The shaded areas depict 95 % confidence intervals. Data points (1 if $f_{\text{nat}} > 0$ and 0 otherwise) are laid out in the background. Only the characteristics that were significant according to the model $M_{1\text{nat}}$ are reported.

more qualitatively illustrated in the previous figures.

Regarding f_{rob} , we found that the spatial patterns, as described by the geographical coordinates of the municipalities' centroids, are by far the most influential factor. In contrast, dispersed settlement, road density, and urbanisation played less significant roles. The test also suggests that while temperature and continentality had a greater impact on determining the probability of black locust initiating the forest expansion process (i.e., whether f_{rob} is 0 or not), landscape diversity and farm size were more important where $f_{\text{rob}} > 0$.

Regarding f_{nat} , landscape diversity, together with spatial patterns and temperature, is the most influential factor in determining the probability of native trees initiating the forest expansion process. This is like what we have found for black locust, but here the relevance of landscape diversity is even greater. However, for native trees, its influence diminishes once the expansion process has begun. Continentality has no discernible role. Population density consistently exhibits a medium-level influence across all models, while dispersed settlement only affects the initiation phase. Railway density and farm size are moderately influential only where $f_{\text{nat}} > 0$.

4. Discussion

We aimed to disentangle and compare the socio-economic, landscape, and climatic factors predicting whether, and to what extent, agricultural lands have experienced forest expansion by invasive black locust versus native trees, from the late 1930s to the present, at the municipal scale, across the entire Italian territory. Our analysis

considered not only socio-economic factors directly tied to monetary values but also demographic and land use variables, which are influenced by the broader regional socio-economic system. We hypothesised that forest expansion by both native and black locust trees involves two distinct processes: the first determining a probabilistic threshold beyond which trees can establish and develop, and the second influencing the extent of cover once colonisation has begun.

The results confirm that the forest expansion by black locust exhibits a non-linear relationship with municipal characteristics. This non-linearity is reflected in the skewed nature of the cover data, which can manifest through threshold effects, saturation points, and complex interactions between variables. Using hurdle models, we explored the relationship between black locust cover and municipal characteristics, ranking these factors based on their influence while addressing non-linear relationships. This approach, extended to native tree expansion, highlighted complex interactions between socio-economic factors and landscape dynamics during land abandonment and colonization. Similar statistical methods have even been applied to vastly different fields, such as the evolution of the universe (Hattab et al., 2019).

Our analysis reveals that both spatial patterns and climatic conditions influence forest expansion by black locust and native trees, though their relative importance differs. For black locust, spatial patterns, represented by the geographical coordinates of municipalities, had the highest influence, as indicated by the top-ranked test statistic (Fig. 8), followed by temperature and continentality. In contrast, for native trees, landscape diversity and temperature were more influential (Fig. 9), and spatial patterns played a more moderate role in initiating the

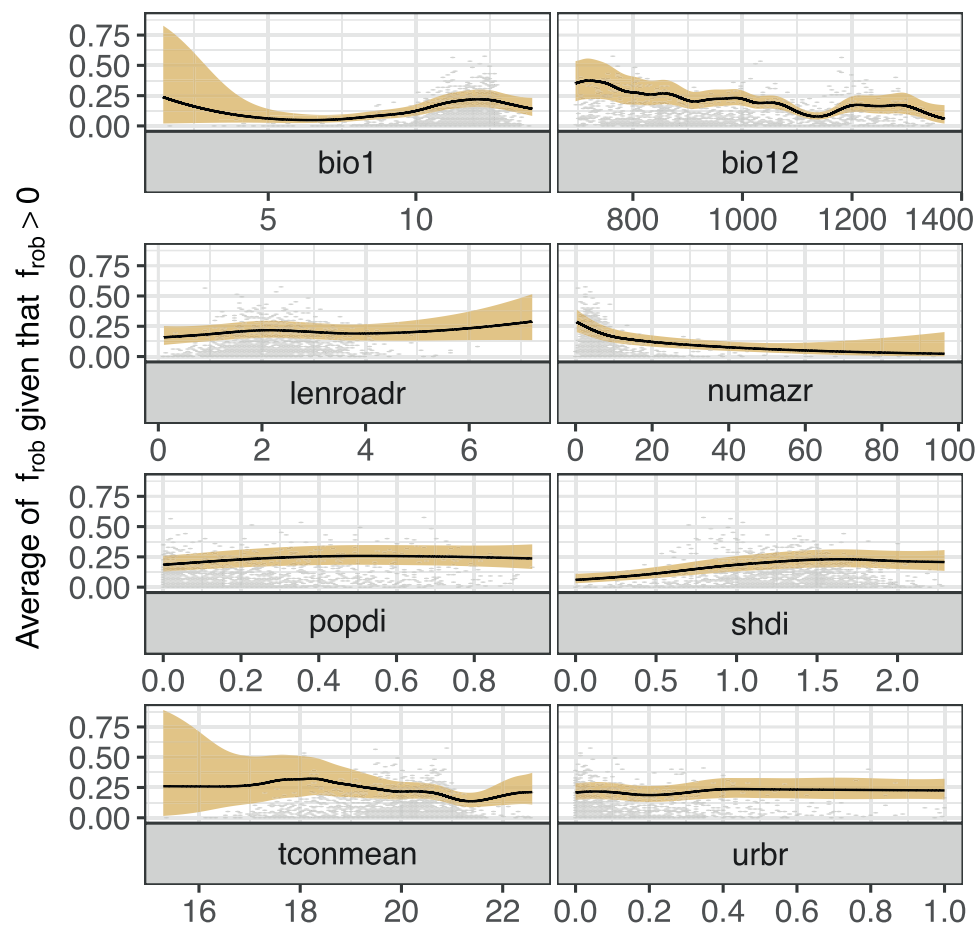


Fig. 6. Estimated mean curves of f_{rob} when $f_{\text{rob}} > 0$ for the significant municipality characteristics indicated in the labels (bio1 = temperature, bio12 = rainfall, lenroadr = road density, numazr = farm size, popdi = dispersed settlement, shdi = landscape diversity, tconmean = continentality, urbr = urbanization). In each panel, the black solid line represents the estimated mean while varying only one characteristic and holding other characteristics fixed at their median. The shaded areas depict 95 % confidence intervals. Data points are laid out in the background.

colonisation process. This suggests that while spatial clustering is key to black locust expansion, native tree colonisation is more closely linked to environmental conditions and landscape composition.

This finding aligns with previous studies that emphasise the importance of spatial configuration in invasive species spread (With, 2004), particularly for species like black locust where long-distance spread by natural means is not very common and the heavy seed is mainly dispersed by gravity and wind in the vicinity of the mother tree (Vítková et al., 2017). In contrast, native trees, which are already present in the landscape, do not face the same spatial constraints, reducing the relative importance of spatial patterns for the beginning of the forest expansion.

Our findings indicate that landscape diversity, temperature, and rainfall significantly influence the establishment and growth of both black locust and native trees, although the fluctuating local pattern of climatic variables in the first seems to confirm its highly variable climate sensitivity (Klisz et al., 2021). This highlights the diverse environmental conditions that facilitate forest expansion and the importance of landscape structure in managing tree cover dynamics. However, landscape diversity has contrasting effects on forest expansion: it positively influences the initial establishment of native trees but hinders their further expansion in favour of black locust, which thrives in more diverse landscapes. This pattern, as observed by Kotowska et al. (2022), may arise because heterogeneous landscapes contain more features that facilitate black locust spread, such as increased wildland–urban interfaces (Gavier-Pizarro et al., 2010).

Landscape diversity plays contrasting roles in forest expansion by native trees and black locust. For native trees, higher landscape diversity

increases the probability of establishment, likely due to the availability of ecotones, marginal patches, and remnant features that facilitate natural regeneration. However, once native expansion proceeds—particularly in farmlands dominated by permanent grasslands and pastures—landscape diversity tends to decline. This pattern suggests that diversity is more likely a consequence than a cause of expansion: as native forests gradually coalesce, the mean patch size increases, open areas shrink, and overall heterogeneity diminishes (Sitzia et al., 2010). This dynamic is supported by evidence from the Alps, where landscape diversity, calculated via the Shannon-Wiener index, decreases as forest cover becomes dominant (Tasser et al., 2024). In contrast, black locust tends to expand in more intensively managed landscapes, especially those dominated by arable fields, where its establishment introduces woody cover that increases land-cover heterogeneity. These divergent effects may also reflect temporal dynamics: native trees often expand earlier following abandonment, while black locust may establish later or persist in more fragmented, disturbed areas. Thus, the role of landscape diversity in forest expansion is context-dependent and may shift across successional stages or land-use legacies.

Forest expansion by native trees is initiated particularly in areas with very low density of population and dispersed settlement, an expected pattern obviously linked with abandonment of agriculture in marginal populated rural areas and the subsequent forest expansion (MacDonald et al., 2000). The initiation of forest expansion by black locust is facilitated by increased road density, a pattern consistent with the well-documented role of roads as vectors for invasive tree spread (Parendes and Jones, 2000). This is particularly true for black locust, as the

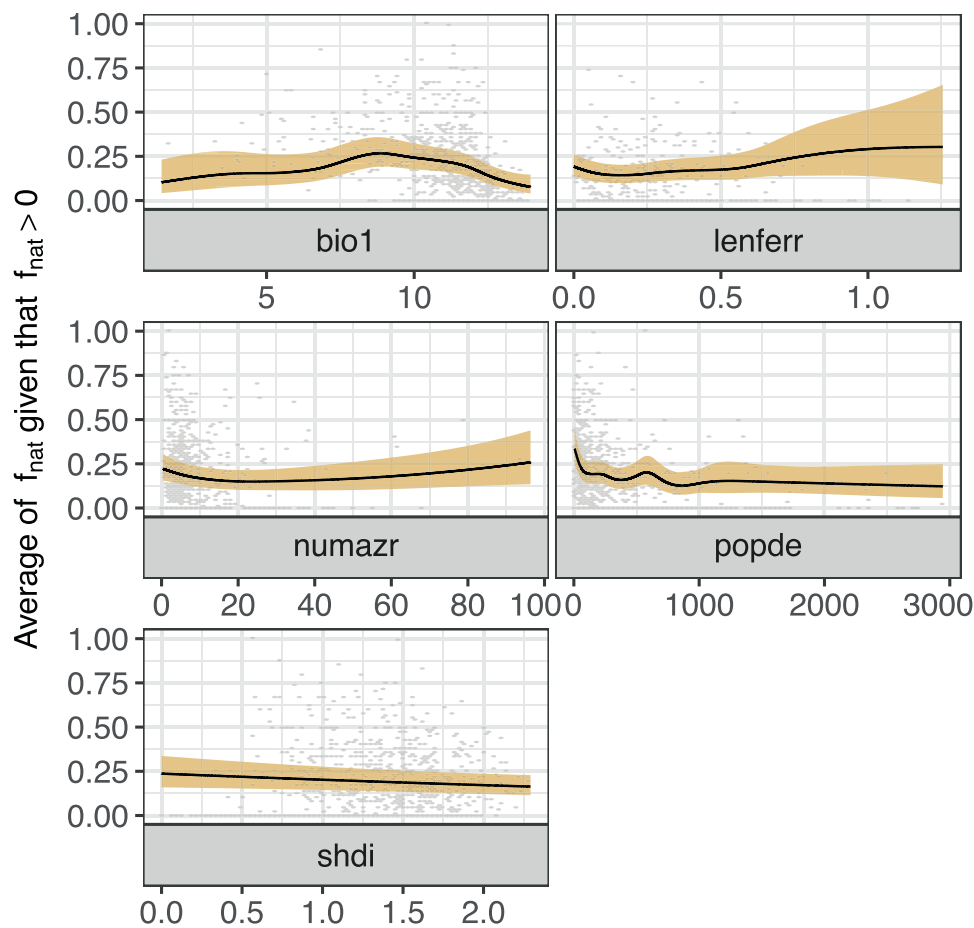


Fig. 7. Estimated mean curves of f_{nat} when $f_{nat} > 0$ for the significant municipality characteristics indicated in the labels (bio1 = temperature, lenferr = railway density, numazr = farm size, popde = population density, shdi = landscape diversity). In each panel, the black solid line represents the estimated mean while varying only one characteristic and holding other characteristics fixed at their median. The shaded areas depict 95 % confidence intervals. Data points are laid out in the background.

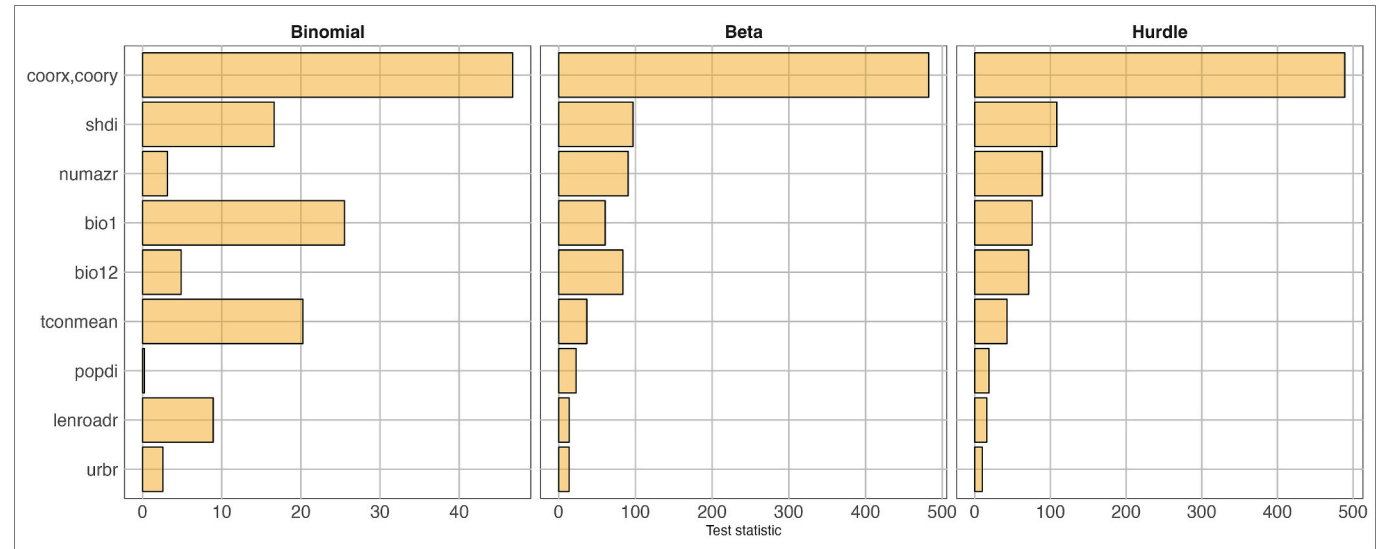


Fig. 8. Significant municipality characteristics (coorx,coory = geographical coordinates, bio1 = temperature, bio12 = rainfall, lenroadr = road density, numazr = farm size, popdi = dispersed settlement, shdi = landscape diversity, urbr = urbanisation) ordered according to the value of their test statistic minus the test degrees of freedom for each part of the hurdle model. Characteristics closer to the top on the rightmost panel have higher influence on f_{rob} .

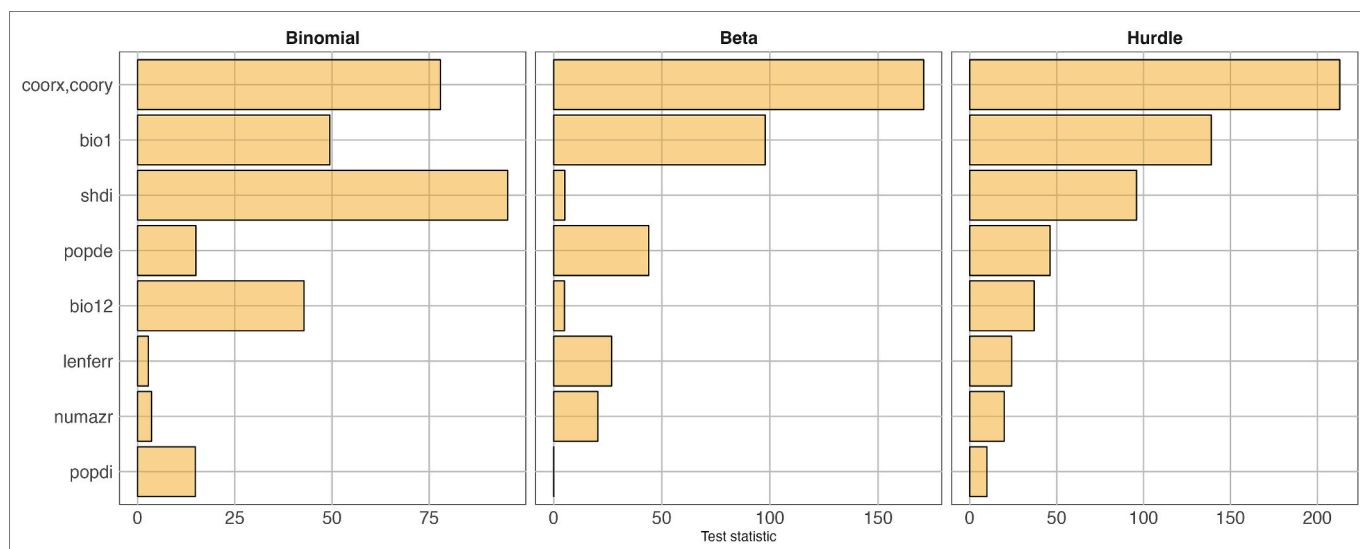


Fig. 9. Significant municipality characteristics (coorx,coory = geographical coordinates, bio1 = temperature, bio12 = rainfall, lenferr = railway density, numazr = farm size, popde = population density, popdi = dispersed settlement, shdi = landscape diversity) ordered according to the value of their test statistic minus the test degrees of freedom for each part of the hurdle model. Characteristics closer to the top on the rightmost panel have higher influence on f_{nat} .

recurrent cutting of roadside trees for safety reasons stimulates resprouting, driving new waves of expansion.

Forest expansion by either native or black locust trees decreases with increasing farm size up to approximately 20 ha. Beyond this threshold, larger farm sizes are still associated with reduced forest expansion by black locust but show an almost parallel increase in forest expansion by native trees. Farm size is positively correlated with field size (Clough et al., 2020), which may explain part of this trend. Smaller farms are often managed by older farmers. These farmers are more likely to abandon the smaller fields rather than the larger ones (Marini et al., 2011) due to their lower efficiency and productivity. This abandonment makes smaller farms more susceptible to natural forest expansion, including that driven by invasive trees (Guillermé et al., 2020), and highlights their vulnerability to reforestation processes (Orlandi et al., 2016). To better explain the trend beyond 20 ha, we verified that for $f_{nat} > 0$, permanent grasslands and pastures dominate across all farm sizes, increasing from 49.0 % in the 0–20 ha classes to 92–100 % in farms larger than 20 ha. This highlights 20 ha as a transition point where semi-natural agricultural lands become overwhelmingly dominant. Conversely, for f_{rob} , arable land dominates, rising from 42.6 % in the 0–10 ha class to 99.8 % in farms over 50 ha, while permanent grasslands and pastures decline from 38.1 % in the smallest farms to near-zero in those over 40 ha. These patterns suggest that intensive arable land management and reduced field edges limit forest expansion by black locust, explaining the monotonic negative relationship between f_{rob} and farm size as arable land dominance increases, especially on farms larger than 20 ha.

We anticipated that mean income and railway density would influence black locust distribution, given their historical role in supporting plantations for wood, honey production, and railway embankment stabilization. However, subsequent events, such as forest degradation during wartime and agricultural land abandonment, created further conditions favourable for black locust expansion. While railway density may have initially hindered native tree establishment, its role in spreading black locust now appears less significant. Historical plantations on railway banks are likely too temporally distant to impact current cover, which reflects the cumulative effects of long-term invasion rather than its initial drivers.

The role of income as a predictor of non-native species expansion, such as black locust, warrants further consideration considering socioeconomic transitions and the associated dynamics of rural economies.

Higher average incomes in rural areas may indicate a shift away from agriculture and deforestation towards a service-oriented economy, including tourism, as suggested by the environmental Kuznets curve framework (Tandetzki et al., 2024). According to this model, economic development initially leads to greater environmental pressures, such as land-use intensification, but beyond a certain income threshold, these pressures diminish as economies transition toward less resource-intensive sectors and prioritize environmental quality.

In the context of black locust expansion, increasing income could have dual and opposing implications: on the one hand, agricultural extensification or abandonment resulting from reduced economic dependence on farming could create opportunities for invasive species to colonize abandoned lands. On the other hand, higher income levels might also coincide with enhanced management and conservation efforts, potentially limiting the spread of invasive species.

Our results have several implications for spatial planning and invasive species monitoring. The contrasting expansion patterns of native trees and black locust suggest that land-use responses should be differentiated by context. For example, municipalities with high road density and fragmented landscapes may be more vulnerable to black locust spread and should be prioritised for surveillance or landscape connectivity planning. Conversely, areas dominated by permanent grasslands and small farms may offer better conditions for native forest recovery. The observed threshold effects of farm size further suggest that targeted policies could support spontaneous forest expansion or afforestation in certain land ownership structures. Finally, recognising that landscape diversity can facilitate either native recovery or invasive spread, depending on the successional stage, planners should evaluate land mosaics not only for their current configuration but also for their likely trajectories. This spatially explicit perspective could help integrate biodiversity conservation with long-term land-use scenarios in both rural development and invasive species strategies.

5. Conclusions

This study provides a comparative perspective on forest expansion by native and invasive trees, using the most widespread invasive tree species in Europe, *Robinia pseudoacacia*, as a model species. Using harmonised historical and recent forest maps across Italian municipalities, we showed that the probability and extent of forest expansion are shaped by different combinations of spatial, climatic, and land-use

factors, with divergent patterns between native and invasive trees.

Spatial configuration and landscape diversity were the most important predictors of black locust expansion, whereas native tree recovery was more strongly associated with environmental gradients such as temperature and rainfall, especially during the initial colonisation phase. Farm size emerged as a key socio-economic factor with opposite trends: native expansion was more likely in smaller farms but increased again above 20 ha, while black locust expansion declined steadily with farm size. In contrast, income and urbanisation had limited explanatory power, suggesting that landscape structural, rather than economic, features shape these dynamics.

Our findings demonstrate the value of applying a two-part hurdle modelling approach to disentangle establishment from expansion processes, while accounting for non-linearities and spatial dependencies. This framework can be adapted to study other widespread tree species, both native and invasive.

Finally, the municipal scale proved useful for integrating climatic, landscape, and socio-economic information. These results offer a spatially explicit basis for anticipating where native forest recovery is most likely and where invasive tree spread may require closer attention, particularly in fragmented or infrastructure-rich areas. Future planning efforts could benefit from incorporating these predictors into monitoring, early detection, or land-use zoning strategies to support biodiversity and ecosystem services over the long term.

6. Declaration of generative AI in scientific writing

During the preparation of this work, the main author, Tommaso Sitzia, used ChatGPT to improve sentences already written by drawing inspiration from suggestions for improvement. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Tommaso Sitzia: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thomas Campagnaro:** Writing – review & editing. **Marco Ciolli:** Writing – review & editing. **Davide Pettenella:** Writing – review & editing. **Laura Secco:** Writing – review & editing. **Jacob C. Douma:** Writing – review & editing, Methodology. **Rafael S. de Souza:** Writing – review & editing. **Simone Iacopino:** Writing – review & editing, Supervision, Investigation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.113961>.

Data availability

The raw data and the R scripts required to reproduce the above findings are available on the GitHub repository of Tommaso Sitzia [<https://github.com/TommasoSitzia/frob>].

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