Exploring the multiple effects of the invasive alien black locust tree

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Valutazione dei molteplici effetti della robinia,

un albero esotico invasivo

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A mio nonno Vincenzo,

per avermi insegnato a navigare tra le onde del mare e della vita …

Summary

Black locust (*Robinia pseudoacacia* L.) is one of the most widespread invasive alien tree species in Europe and throughout the world. Its spread has been favoured by its ecological attitudes and economic relevance, with positive and negative implications. The aim of this thesis was to further develop knowledge on the black locust's ecological and socio-economic drivers. A stand, landscape and national scale were considered. At the stand scale, ecological impacts on the plant community were assessed through a comparative approach, based on a sample of pairs of woodlands, invaded or non-invaded by black locust. A focus on a sample of three types of landscape (rural, riverine and urban) allowed black locust impacts to be compared across different environmental contexts. A second focus on a sample of three European cities (Berlin, Padova and Roma) allowed the impacts of both black locust dominance and urban matrix properties to be investigated across urban environments at different latitudes. Socio-economic drivers were investigated at a national scale in Italy, linking these factors with changes in both land cover and black locust distribution. Knowledge on the drivers of black locust spread and its effects on natural resources is deepened, offering insights into a desirable trade-off between biodiversity conservation and black locust socio-economic significance at multiple scales and contexts.

Riassunto

La robinia (*Robinia pseudoacacia* L.) è una delle specie arboree aliene invasive più diffuse in Europa e nel mondo. La diffusione di questa specie è stata favorita dalla sua amplitudine ecologica e dai suoi diversificati interessi economici, determinandone conseguenze positive e negative. Lo scopo della tesi è di approfondire le conoscenze sui fattori ecologici ed economici che hanno causato e caratterizzano la sua distribuzione. Sono state prese in considerazione diverse scale di studio, una scala di popolamento, una di paesaggio e una nazionale. A scala di popolamento, sono stati valutati gli impatti ecologici sulla comunità vegetale seguendo un metodo comparativo, basato su un campione di coppie di boschi, invasi o meno dalla robinia. È stato condotto un confronto degli impatti di robinia in diversi contesti ambientali mediante un approfondimento su un campione di tre tipi di paesaggio (rurale, fluviale e urbano). Un secondo approfondimento su un campione di tre città europee (Berlino, Padova e Roma) ha permesso invece di indagare gli impatti della copertura di robinia e delle proprietà della matrice urbana in contesti urbani a latitudini molto diverse. I fattori socio-economici sono stati indagati al livello nazionale italiano, collegandoli con i cambiamenti della copertura del suolo e della distribuzione della robinia. Le conoscenze sulle cause della diffusione della robinia e dei suoi effetti sulle risorse naturali vengono approfondite offrendo spunti di riflessione su un auspicabile bilanciamento tra conservazione della biodiversità e valorizzazione socio-economica di questa specie, a molteplici scale e contesti.

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Scientific names of plant species are reported according to Portal to the Flora of Italy (2019).

1. Introduction

Robinia pseudoacacia (black locust, Figure 1) is one of the most widespread alien plant species in Europe (Lambdon et al. 2008) and the world (DeGomez and Wagner 2001). It is the third most widespread tree, after poplars and eucalypts, in productive plantations of the world (Merzeau and Demené 2007). It was brought into Europe in the early 16th century by Jean Robin (Cierjacks et al. 2013). It is a pioneer forest species with fast growth and a prompt vegetative reproduction, is drought tolerant and adaptable to different site conditions and climates (DeGomez and Wagner 2001). Thanks to the rapid growth rate and adaptability to several soil types and acidity (Cierjacks et al. 2013), it competes successfully with several species, particularly shade-demanding trees (Motta et al. 2009). In Italy, the area covered by black locust is around 230,000 hectares, which includes *Ailanthus altissima* (tree of heaven) woodlands (Tabacchi et al. 2007). Many reasons exist for studying this species, which are the justification for the objectives of this thesis, as described in the following chapters.

Figure 1. A botanical illustration of *Robinia pseudoacacia* by Allegri (1941). 1. flowering branch; 2. isolated flower, seen from the front; 3. isolated pistil without stamens; 4. flower without corolla; 5. different elements of the corolla; 6. branch with legumes ; 7. detail of the fruit (legumes); 8. detail of bark on an adult tree; 9. cross section of the trunk; 10. detail of black locust wood.

1.1. Background and justification

Since its introduction, black locust has been much appreciated as an ornamental plant, so has spread in parks and gardens. Since being introduced, besides urban forestry, other uses have been made, such as honey production and forage for goats or cattle together with culinary use. It is also an easy source of good firewood, cut frequently thanks to its ability to sprout vigorously. Black locust has thus become an integral and distinctive component of the European landscape (Vítková et al. 2017).

Despite being part of the landscape and of folk uses, black locust is a widespread invasive alien species in the European Union, according to the definition given by the recent European Regulation on invasive alien species (Sitzia et al. 2016a). Its invasive behaviour has been documented even in its continent of origin, North America, outside its natural range (Richardson and Rejmánek 2011). In the alien context, black locust grows in a wide array of environments from natural sites to anthropogenic disturbed areas such as roadsides and transportation networks (Cabra-Rivas et al. 2016). Abandoned fields and disused factories, which expand in times of economic crisis, and also marginal lands are suitable for black locust, which colonizes bare soils and grasslands and forms new woodlands (Trentanovi et al. 2013).

Alien species invasion is considered a growing threat to the delivery of ecosystem services and native species diversity. This threat to biodiversity is the most detrimental consequence associated to many non-native species in Europe (DAISIE 2009). However, invasive species may also bring benefits to local people (Bardsley and Edwards-Jones 2006). That is the case for black locust, reported as a threat to biodiversity (Matus et al. 2003, Benesperi et al. 2012, Trentanovi et al. 2013), but also as an economically important multipurpose tree (Cierjacks et al. 2013). According to the European Environmental Agency (Scalera et al. 2012), black locust is affecting ecosystem services while providing additional ones. For this reason, it requires an approach that considers all its widespread effects, both negative and positive, as suggested by Vítková et al. (2017).

Studies concerning black locust impacts on biodiversity have led to contrasting results (Cierjacks et al. 2013). Black locust potential effects raise concern, particularly since this tree, together with the tree of heaven, is the most reported invasive alien tree in protected riparian and oak-dominated forest habitat types (Campagnaro et al. 2018a). Among the ecological impacts caused by black locust stands, nitrogen increase may impede native plant community return and ecosystem function (Rice et al. 2004). This is likely to cause a long-

lasting impact, even with short periods of black locust canopy cover. However, black locust woodlands hosting elderberry in the understory have been reported as food habitats for several bird species (Cierjacks et al. 2013).

Black locust stands can provide an array of ecosystem services in urban settings and are considered novel ecosystems (Sitzia et al. 2016b), well adapted to urban conditions such as high pollution and heat islands. In certain cases, depending on context and habitat, the same aspect could be either a problem or a benefit. Soil nitrogen increasing, for example, makes black locust an effective plant to restore disturbed soils (Bolat et al. 2015). It is thus evident that, due to the wide variety of both positive and negative implications, a cost-benefit balance, even if not easy to assess, represents a key point to guide management decisions (De Wit et al. 2001, Vilà et al. 2010).

Because of their complex and various effects on society and the economy invasive alien species should be considered a socio-economic problem (García-Llorente et al. 2008) and should be tackled with a multidisciplinary approach. Therefore, public consultation could offer insights into people's opinions and perceptions of non-native species, which need to be considered before acting (Maes et al. 2012). Despite the importance of this aspect, public attitudes towards invasive alien species are still poorly investigated, probably because of the difficulty in measuring social impacts (García-Llorente et al. 2008, Pejchar and Mooney 2009) and due to the broad range of stakeholders. Economic and ecological impacts need to be properly assessed together with social impact to maximize benefits and minimize costs. The two-sided effects resulting from invasive alien species spread has often led to conflicts over removal and management (Dickie et al. 2014).

Nevertheless, a stratified approach that includes tolerance in areas for black locust products and wise management at high value sites is still recommended and needed (Vítková et al. 2017).

1.2. Objectives

The general aim of this thesis is to deepen the current knowledge on black locust effects on forest habitats and to assess the socio-economic drivers that may have fostered the spread of this invasive tree in Italy. To achieve this general objective, we conducted a multi-scale study with a multiple context research that touched different scientific fields. The objectives of the thesis can be summarized in four main parts as follows.

First part of the thesis gives a brief literature review on the effects of black locust on forest habitats concerning plant community and soil changes and on the socio-economic conditions that have fostered black locust spread. This provides an entry for the next chapters.

The objective of the second part is to improve the knowledge of black locust effects on understory plant diversity and soil microfauna involved in biochemical cycles among three different landscapes of northern Italy. To meet this objective, we applied a paired sampling method of paired plots invaded and non-invaded by black locust in rural, riverine and urban landscapes. We also tried to attain a second objective, to understand whether black locust woodlands distribution in riverine habitats is influenced by river geomorphological variables. We explored possible links on this matter on black locust stands along the Piave River, north-eastern Italy.

The objective of the third part is to analyse potential effect of the urban matrix properties and black locust canopy on understory composition in three cities along a latitudinal gradient, by applying the same sampling design used in the Italian landscapes. Paired plots were surveyed in Berlin and in two Italian cities: Padova and Roma.

The objective of fourth and last part is to understand whether black locust spread and distribution within the Italian territory is related to specific socio-economic conditions. Study areas related to each part of the research are presented in Figure 2 (next page).
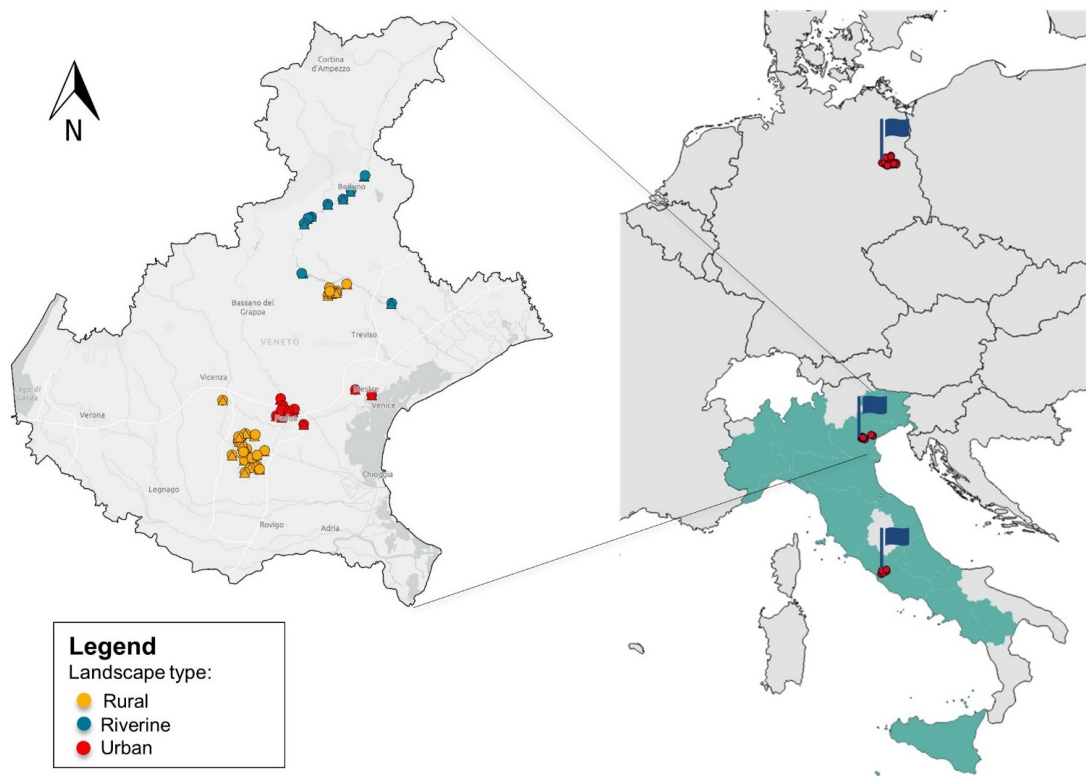
Figure 2. A schematic map showing different study areas related to the different part of the thesis. Veneto Region (on the left) with location of paired plots in the three landscape types. Blue flags (on the right) showing location of paired plots in three European cities (Berlin, Padova and Roma) and light blue Italian regions representing the study area of fourth part of the thesis.

1.3. Effects of black locust: a review

In the following sections a literature review of the known drivers and effects of black locust, as related to the thesis objectives is provided. Major effects on plant communities, soil, and potential uses, as well as a focus on riverine and urban environments, are presented, providing a framework for the next chapters.

1.3.1. Effects on plant communities and soil

Pure and mixed black locust stands have been quite well studied. First interest has been focused on economic uses of the species while attention to its ecological impact has only arisen recently (Vítková et al. 2017). One of the first studies reporting effects of black locust on other species was presented by Chapman (1935), who described effects on tree species growing next to black locust plantations. Reporting increases in soil total nitrogen content associated with an increment in mean heights and diameters for the other tree species in the plantation, Hruška (1991) warned that reforestation with black locust will drive floral and structural instability and reduce resistance to other alien species. Several examples of

black locust stands that host synanthropic and ruderal species are available in the literature. Hruška (1991) noted an increase in nitrogen demanding species of Slovakia black locust reforestations while black locust stands for honey production host trampled sites linked species pointing out a rather strong human disturbance.

Figure 3. Black locust stand with understory layer dominated by the nitrogen demanding bramble shrub at Volpago del Montello, Italy (photo by S. Iacopino).

Nitrogen demanding and ruderal species presence was closely positively correlated in poor sandy soil plots. Therefore, in young secondary woodlands communities on poor soils the strong divergence in composition may be due to availability of both nitrogen and light (Dzwonko and Loster 1997, Corenblit et al. 2014). Staska et al. (2014) studied variations in plant diversity among age and density gradients of black locust stands in floodplain forests in Eastern Austria without detecting significant differences. Some nitrogen demanding species gained abundance along one of these two gradients and some others along the other one.

A wide range of outcomes have been reported but the general statement «black locust reduces biodiversity» is not supported by ambiguous and controversial scientific results (Cierjacks et al. 2013, Vítková et al. 2017). However, pure and mixed black locust stands are characterized by markedly dissimilar plant communities compared with forests dominated by local woody species: a divergence described by several phytosociological associations (Vítková and Kolbek 2010).

These dissimilarities in species composition are mainly driven by changes in availability of soil nutrients and light according to Vítková and Kolbek (2010). Indeed,

nitrogen demanding and shade-tolerant species are the most favoured under black locust stands in Central Europe, *Alliaria petiolata*, *Anthriscus sylvestris*, *Chelidonium majus*, *Galium aparine*, *Sambucus nigra* and *Urtica dioica* are examples (Hruška 1991, Dzwonko and Loster 1997, Vítková and Kolbek 2010).

Several studies have been undertaken in central Europe to describe black locust communities and their different syntaxonomical units. However, as already said, these attempts to describe black locust impacts on plant communities' biodiversity have led to contrasting results. On the one hand, some studies presented negative impacts on plant communities' diversity. In riparian areas of Greece, black locust stands showed a clearly distinct species composition compared to non-invaded stands (Vasilopoulos et al. 2007). Benesperi et al. (2012) reported not only a shift in species composition but also a reduction in plant richness comparing black locust and native forests of the Northern Apennines. A homogenization of plant forest communities and the lack of many native forest dry tolerant and acidophilus species emerged from this case study. Other studies detected a homogenization of the tree canopy and understory species together with an increase and dominance of nitrophilous and ruderal species linked with an increase in soil nitrogen content (Hruška 1991, Dzwonko and Loster 1997). Secondary forests growing on northern Italian grasslands and recently abandoned cultivated areas have been split into three groups characterized by the occurrence of species indicative of (a) nitrogen-rich, (b) true forest and (c) open habitat conditions, and species replacement being the prominent process structuring plant communities β-diversity (Campagnaro et al. 2018b). Finally, the new alliance *Lauro nobilis–Robinion pseudoacaciae* all. nova hoc loco of the order *Chelidonio–Robinietalia pseudoacaciae* Jurko ex Hadac et Sofron 1980 and class *Robinietea* Jurko ex Hadac et Sofron 1980, with two new associations: *Melisso altissimae–Robinietum pseudoacaciae* ass. nov. hoc loco and *Rubio peregrinae–Robinietum pseudoacaciae* ass. nov. hoc loco is proposed to describe the black locust woodlands of the peri-Adriatic sector of the Mediterranean basin (Allegrezza et al. 2019).

Trentanovi et al. (2013), comparing black locust stands and native silver birch stands in Berlin urban habitats, found α-diversity values significantly lower in black locust stands. Moreover, black locust stands revealed a higher homogeneity of the non-native species pool in the same study.

On the other hand, examples of not significant differences of the understory plant species have been reported by studies in secondary stands (Sitzia et al. 2012a) and riparian forests (Akatov et al. 2016), but significant differences of tree layer. Von Holle et al. (2006)

argued that black locust facilitates invasion by other non-native species into naturally invasion-resistant systems.

Another important aspect related to alien dominance is the resilience of the system, or its capability to quickly recover the ecosystem functions and species composition. Benesperi et al. (2012) point out that mature stands do not recover the plant species diversity that is lost by the replacement of native forests by black locust. According to Vítková et al. (2015), spontaneous succession from black locust plantations towards natural communities is a slow process, but it is also true that, as already mentioned in the previous section, forest management and agricultural practises can be very effective in this sense (Motta et al. 2009, Benesperi et al. 2012).

Despite the scenario described in the literature there are still no elements to affirm that black locust stands affect native species richness or cover both directly and indirectly (Vítková et al. 2017). For this reason, further research is needed also considering that black locust is among the most reported invasive alien trees in important Natura 2000 forest habitat types (Campagnaro et al. 2018a). Moreover, these context-dependent outcomes explain the difficulty in making any general observations and show the necessity to study black locust impacts with multiple contexts research.
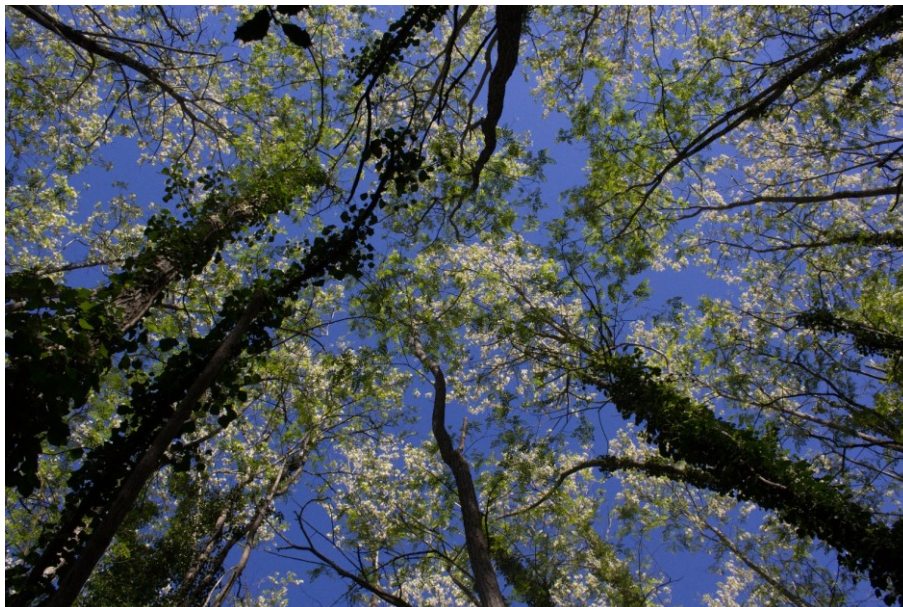

Figure 4. Black locust canopy at the beginning of the vegetative period (spring) during flower blooming (photo by S. Iacopino).

In addition, black locust dominance is also related to alteration of biochemical soil cycles and it has therefore often been charged with changing soil conditions. Substantial alteration of soil properties caused by the nitrogen fixation has been described. Increase in

total soil nitrogen is well documented. Rice et al. (2004) found soil nitrogen concentrations up to three times higher in black locust stands in comparison with nearby nutrient poor pine-oak stands, thus involving higher soil nitrogen mineralization rates.

Moreover, the nitrogen content was shown to increase with black locust density and stand age (Staska et al. 2014). The same pattern was found for nitrate and carbon, but not for total C/N ratio. The same results are provided by the American study of Eaton and Farrell Jr (2004) who also detected an increase in litter and soil pH. Among soil alterations, Wei et al. (2009) reported a decrease in total phosphorus. Furthermore, black locust flowers and leaf litter are subject to fast decomposition that considerably increases the presence of membrane phosphorus in the soil. The rapid nutrient cycle occurring in black locust stands might be the key factor that help this tree to survive in poor soil environments (Lee et al. 2011). As claimed by Dzwonko and Loster (1997), both plant biodiversity and soil alteration may be affected by black locust dominance and the alteration of soil properties might act as an important driver of plant community change as in the case of allelopathic substances of bark and roots that may inhibit growth of plant seedlings (Waks 1936, Nasir et al. 2005). Higher soil carbon/nitrogen (C/N) ratio and available phosphorus (P) have been associated with black locust stands, while higher soil phenols associated with native tree stands. These environmental effects resulted in differences in understory flowering periods, reproduction types, life forms. Moreover, by adopting a functional traits perspective rather than species-level investigation, Sitzia et al. (2018b) found more evident effects on plant functional trait composition.

Few studies have been conducted on microbial communities in black locust dominated stands (Ferrari and Wall 2008, Zhang et al. 2016). Among soil microorganisms, one promising example of indicator is represented by ammonia-oxidizing archaea (AOA) (Leininger et al. 2006, Stevanato et al. 2016) but often overlooked when assessing impacts of black locust on soil cycles (Medina-Villar et al. 2016, Lazzaro et al. 2018). Therefore, further research is required to deepen the knowledge about black locust impact on soil cycles and biodiversity.

1.3.2. A focus on representative types of forest landscapes

Following the objectives of the second and third part of the thesis, a description of the potential drivers and constraints to black locust development and spread is provided here. Given that the objectives involve black locust being studied in three different types of landscape (rural, riverine, urban), these are used as distinctive frameworks in the presentation

of the current knowledge. In each landscape, different dynamics of ecological connectivity are expected, as well as various black locust stands native counterparts. Connectivity is expected to follow an increasing gradient from urban to rural landscapes, while the riverine landscape shows a distinct pattern that is related to periodic floods (Moffatt et al. 2004). In the study areas, black locust woodlands tend to be mostly adjacent to chestnut (*Castanea sativa*), willows (*Salix alba*, S. *eleagnos*) and black poplar (*Populus nigra*), or broadleaved mixed woodlands, in the rural, riverine, and urban landscapes, respectively.

1.3.2.1 Rural landscape

In Italy, forests dominated by chestnut are frequently managed with coppice system (Manetti et al. 2017), whereas high forest stands are very limited. Chestnut-dominated forests are one of the protected habitat types listed in Annex I of Habitat Directive (92/43/EEC) and part of the Natura 2000 Network, the most important European Union program for the protection of habitats and species (Maiorano et al. 2007). Each habitat type is recognized by a four-digit code, for example chestnut-dominated forests are coded 9260.

The ecology of chestnut tree is very similar to that of downy oak (*Quercus pubescens* subsp. *pubescens*) regarding temperature range needs. It is mesophile and prefers an average annual temperature between 8 and 15 °C and an average annual rainfall of more than 600 mm (Bernetti 1995). It does not tolerate summer drought very well, which should not last for more than one - two months; during the foliation period the chestnut tree requires continuous water availability. Spring and autumn frosts are also not well tolerated. Chestnut tree has medium needs in terms of light, it tolerates enough shade at the seedling stage while it prefers isolation and abundant light for a sustained development and rich fructification. In Veneto region this tree occurs from 400 m to about 1000-1200 m a.s.l. (Masutti and Battisti 2007). The habitat type 9260 in Veneto is widespread in the foothills of the Alps, up to the outermost edge of the Dolomites. In the Euganean area and the Montello hills, included within the rural landscape framework, it is mainly found on slopes facing north or east (Figure 5). On these slopes and in deep soil stands with cooler conditions and greater water availability, chestnut woodlands are populated by species characteristic of mesophilic forests. It is possible to find chestnut woodlands on south-facing slopes where chestnut trees are associated with markedly thermophilic species.

Figure 5. Black locust stands cover most of the Euganean Hills, where one the studies presented here was conducted (from Sitzia et al. (2018a), photo by G. Corradini).

Chestnut woodlands differ according to slope exposure and type of soil, but also according to the type of forest management. This results in different floral assemblages; therefore, to describe this type, a rather complicated syntaxonomic framework is necessary. Different management types correspond to different forest stand structures. In coppice woodlands, the tree layer consists only of chestnut trees and the herbaceous undergrowth is monotonous. More complex structure chestnut woodlands are instead mixed and host a higher plant understory biodiversity. In general, chestnut can be accompanied by sessile oak, common hornbeam, wild service tree, manna ash and linden and the undergrowth can be enriched with geophytes and hemicryptophytes of interest, including, to name a few: *Epimedium alpinum*, *Allium ursinum*, *Erythronium dens-canis* and *Cardamine pentaphyllos*. Mixed chestnut woodlands are of some naturalist interest, including their fauna (Masutti and Battisti 2007). The regular coppice management favours ecotonal species, while aged or abandoned stands, which contain large individuals and abundant deadwood, represent a suitable habitat for xylophagous insects and woodpeckers. In addition to woodpeckers, the aged chestnut woodlands can be a suitable habitat for other birds, such as *Phoenicurus phoenicurus* (common redstart), *Erithacus rubecola* (European robin) and *Phylloscopus collybita* (common chiffchaff), which find a rich source of xylophagous insects in the dying plants. In autumn, chestnut trees are an important source of food for mammals such as rodents and wild boars and for birds such as jays (Masutti and Battisti 2007). Finally,

chestnut forest has a high pollen and nectar production, which makes chestnut a plant with excellent melliferous potential.

According to the reports of the botanist Augusto Béguinot, for a long-time black locust has occurred as a sporadic species in the outer Alps, confined to the driest slopes, along hedges and railway escarpments (Béguinot 1909). Today, however, black locust is, without doubt, the exotic species that most affects the north-eastern pre-Alpine Italian floral landscape. Among the invasive exotic plants, it is commonest and most abundant species. For example, the most frequent type of woodland in the Euganean Hills area is black locust, covering 2,080 ha (Sitzia et al. 2010).

Black locust tree frequently occurs in the basal part of the hills and in the areas between farmland and spontaneous vegetation. It typically forms narrow vegetated strips that climb up gullies. Black locust scrub can commonly be found within chestnut and oak stands, on plots that were once cultivated. Indeed, black locust participation in chestnut woodlands is found especially in the most disturbed areas, those covered by degraded chestnut woodlands, a fact already documented in the middle of the last century (Susmel and Famiglietti 1968).

Too frequent intermediate cuttings favour black locust at the expense of native tree species. The marked aggressiveness of black locust and its clear competition with other species are mainly due to its remarkable ability to reproduce vegetatively, especially in the early stages of colonization. It is therefore favoured by coppicing. Black locust has a broad ecological value, yet still avoids dry soil conditions; its ability to modify plant composition and structure of the tree layer and herbaceous undergrowth, as well as the biogeochemical cycles of the soil is known (Sitzia et al. 2018b) (Figure 6).
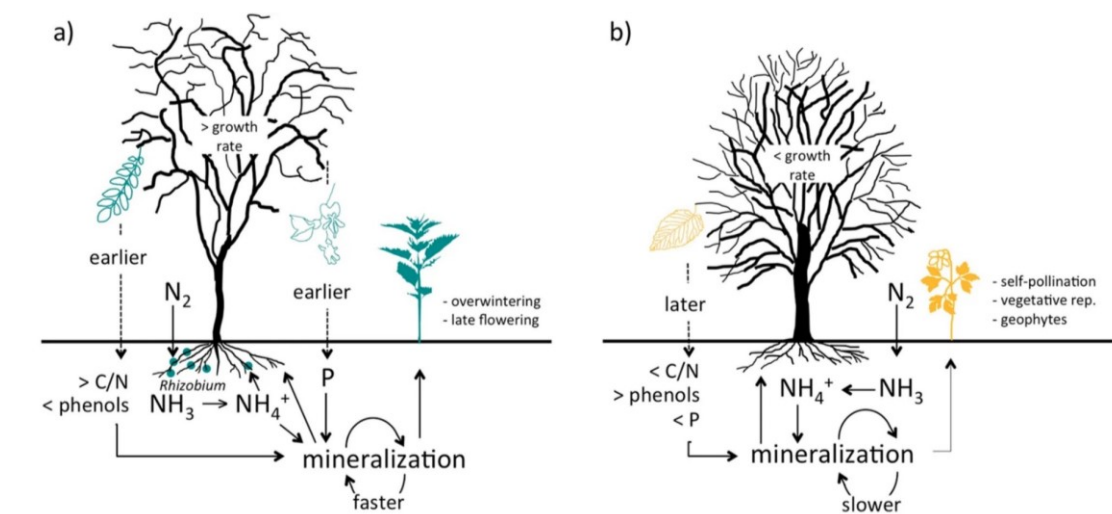

Figure 6. The relationships between black locust (a) and native tree (b) canopy dominance, environmental variables and plant trait composition from Sitzia et al. (2018b).

1.3.2.2 Riverine landscape

Rivers represent a significant corridor of spread for invasive species. The natural disturbance regime makes rivers highly prone to invasion by alien species (Mortenson and Weisberg 2010). The arrival of non-native species may be fostered by floods (Dyderski et al. 2015). An alteration of the regime can result in a river more prone to invasion. Indeed, human pressure in a riverine context may facilitate the establishment of alien species. Flow alteration often corresponds to the spread of invasive plants and animals in a riparian environment (Nilsson and Svedmark 2002, Richardson et al. 2007). Hood and Naiman (2000) suggested that water flow, flood frequency and magnitude and water availability from the water table are the three main factors influencing invasibility of rivers.

From the cited American case study of Mortenson and Weisberg (2010) it emerged that river regulation does not always translate into an increase in invasive species cover. Rivers more vulnerable to invasions are those with larger drainage area and low flow variability but the species life-history traits are more determinant on alien species expansion than river regulation.

A conceptual model proposed by Corenblit et al. (2014) describes how the presence and richness of native and alien species in riparian ecosystems is regulated by the balance among extrinsic and intrinsic factors, hydrogeomorphic disturbance and competition. Ecosystem engineers, by modifying habitat conditions, may alter this balance, thus influencing alien species success in a riverine context. Thus, in complex riparian ecosystems all these combined effects influence the resistance to invasion by alien species.

Therefore, according to Corenblit et al. (2014) this resistance to invasibility is likely to be affected by the combined effects of multiple native and exotic ecosystem engineer species forming a functional group enhancing the biogeomorphic succession. For example, tree and herb layers of the alder community have a key role in preserving the riparian forest from the invasive tree *Acer negundo* (boxelder maple) (Saccone et al. 2013).

Riverine forests are not immune from black locust invasions (Motta et al. 2009, Vítková et al. 2017). The important spread of black locust has been attributed to excessive sediment trapping by dams and to black locust plantations on hillslopes of the catchment of a Japanese river (Akamatsu et al. 2011). In another words, these factors can be defined as alteration of river dynamics and high propagule pressure. In this way, alteration of river dynamics may promote black locust expansion in higher floodplains. In accordance with this Dyderski et al. (2015) argued that river regulation could foster the colonization of mid- and

late-succession stage alien species given that riparian vegetation changes (in this direction) were observed after the Polish Warta River was regulated by the creation of a big reservoir dam.

Most alien woody species observed by Dyderski et al. (2015) were boxelder maple, green ash and black locust. Thus, the marginalization of river flows may be a driver together with high propagule pressure. Marginalization can translate into a reduction in frequency and magnitude of natural disturbances. A weakening of natural disturbances, extended over time, might cause black locust to invade formations of the more pioneer poplars and willows. Little research has been conducted on the relationships between river dynamics and black locust expansion. The influences of river dynamics on black locust expansion and vice-versa black locust impact on the river dynamics are less explored and insufficiently understood. However, the increase in riparian black locust woodlands in Japan might cause a decrease both in magnitude and frequency of natural river disturbances. Consequently, black locust may represent a threat to Japanese riverine landscape diversity in the near future (Maekawa and Nakagoshi 1997).

Considering the growing presence of this species in Alpine riverine environments, such as the Piave and Brenta rivers (Sitzia et al. 2016d), a better understanding is required to assess how and which river dynamics are more prone to black locust development in riverine ecosystems.

1.3.2.3   Urban landscape

The size of urban areas is increasing globally. This trend is affecting biodiversity with an unprecedented intensity (Marzluff 2001, Kowarik 2008, McKinney 2008). Loss of habitat types and species is therefore expected and has been observed worldwide. In particular, specialists are outcompeted by generalist species. This is due to a combination of factors, of which urban climate and soil are the major determinants. Soil nitrogen, phosphorus, and contaminants are relatively higher in urban than in other soils (Pouyat and McDonnell 1991, Morillo et al. 2007). Air temperature is usually higher than in suburban and rural environments. Economic activities are a constant driver of exotic species introduction, which cannot be controlled, being inherit to the urban setting dynamic (Dehnen-Schmutz et al. 2007, Essl et al. 2011). As a consequence, urban floras show a high rate of exotic species up to 60%, at both the city (Pyšek 1998) and community scale (Kowarik 2008). Moreover, an increasing proportion of alien species has been explained by an increasing intensity of human impacts (Kowarik 2008).

Ecosystem function is therefore transformed, and novel ecosystems develop. One of the main effects of urbanization is flora homogenization. However, one important question is whether the dominance of an alien tree vs. a native tree may act as a filter to such factors and hence enhance the homogenization effect. Results are different and contrasting.

Black locust, like other alien tree species, may act as an ecosystem transformer (Richardson and Rejmánek 2011). For example, in Berlin its canopy has been regarded as the main parameter for homogenization. The high contribution of the proportion of built-up area to homogenization, in the native species group, may indicate dispersal limitation that can lead to reduction of the species pool in plots that are located in highly urbanized surroundings (Trentanovi et al. 2013). Variables which have been found to affect plant species richness include road and railway density (Sitzia et al. 2016b). However, a limited relationship may exist between explanatory variables and plant richness, which strengthens the discourse that the city is an integrated ecosystem (Rebele 1994); whereas it is not possible to define one variable in particular that is affecting species richness. There is a degree of chaos theory involved, promoting heterogeneity. Richness is a result of complex interactions of abiotic and biotic processes at different scales (Werner 2011). Studies conducted in single cities are common, but syntheses among several cities are still lacking. It is therefore relevant to compare different cities along latitudinal gradients.

1.3.3. The role of socio-economic activities on black locust spread

The economic importance of black locust is proved by the array of uses made throughout the world. Black locust is the second most planted woody species worldwide (Vítková et al. 2015). In the whole planet, the area of black locust plantations took just 20 years (1958-1978) to increase from 337,000 ha to 1,890,000 ha. The largest plantations are in South Korea, Hungary, Romania, former Soviet Union and France (Cierjacks et al. 2013). In Italy, pure or mixed stands of black locust are not negligible, covering 230,000 ha (Sitzia 2014).

In Europe, black locust is extensively naturalized, it occurs in 42 countries (Sitzia et al. 2016c), with Hungary having the biggest extent of black locust forests (400,000 ha) (Sitzia 2014). In this country, black locust has been an important forest tree species used to produce firewood, fodder, poles and props. It was also planted for soil protection, slope stabilisation, honey and timber production (the latter limited to best sites). Black locust woodlands cover almost a quarter of all the forested area in Hungary (Rédei et al. 2008) as a result of the post-WWI national afforestation programme in which black locust was widely used (Vítková et al.

2017). Afforestation projects also occurred in north-eastern Italy (Friuli Venezia Giulia) after both WWI and WWII. In the same Italian region, black locust has been favoured next to vine-growing areas since posts of this tree are very efficient for vine support (Del Favero et al. 1998). In Japan it is very highly valued for honey production and half of the honey produced nationally is provided by black locust plantations (Morimoto et al. 2010). In the same country black locust has been used widely for revegetation purposes on denuded slopes (Akamatsu et al. 2011). In China black locust value was so widely recognized that, currently, among introduced tree species plantations in the country, black locust cover the biggest area. Furthermore, these plantations are expected to increase for the implementation of soil and water conservation programmes (Yanhui 1992). The number of current and potential timber uses is very wide, including fence posts, boatbuilding, flooring, furniture, mine timbers, railway sleepers, turned objects, and veneer (Sitzia et al. 2016c). Black locust use in forest plantations and agroforestry practices is also reported in the North-West and Central Himalayas by Swamy et al. (2002). In India, the tree has been used in social-agroforestry programmes and for landslips reclamation, denuded hills and wastelands. In the same country, it is also used widely as a source of fodder for cattle, so that a thornless variety has been developed. Black locust was widely planted in parks and gardens thanks to its urban stress resistance and ornamental beauty.

Given the wide variety of uses and the remarkable number of countries in which the tree has been exploited, the role that humans have played in fostering black locust spread and establishment is clear. Hence, socio-economic factors have significantly influenced the widespread distribution of this invasive tree. Considering the broad ecology of this tree, it is likely that socio economic factors have played a relatively greater influence than environmental factors (Maráková et al. 2016). Indeed, Essl et al. (2011) claim that, on broad spatial scales, the influence of climate and geography are overwhelmed by human activities in species invasion processes.

Landscape management, use of the species and agricultural practices had and still play a key role in guiding black locust spread and establishment. The abandonment of open areas such as arable fields, meadows and grasslands has significantly guided black locust intense invasion in these environments. The detrimental effects of farmland abandonment have been reported and rural activities abandonment has been linked to loss of landscape heterogeneity (Grau et al. 2003). For example, Maráková et al. (2016) presented the case of Slovakia as an area subject to a dramatic landscape structure change due to abandonment of traditional agricultural activities and the intensification of agriculture practices.

Abandonment of agricultural activities caused the greatest land cover change in Slovakia, favouring a vegetation succession with many non-native species. Hence, black locust occurrence was mainly influenced by rural landscape abandonment and by afforestation programmes from 1949 to 1986 (Maráková et al. 2016). In that case study, changes in black locust occurrence were analysed regarding the influence of land cover change. Half of the agricultural areas managed in 1949 are now dominated by black locust but this expansion may be partly encouraged by human introduction of the species to stabilize slopes and by the subsequent forest use of the tree. According to the authors, in the studied area, black locust was relatively more influenced by anthropogenic interventions and applied management rather than by environmental factors. These aspects have also been documented in the Italian context (Sitzia et al. 2012a, Sitzia et al. 2016a). Good agricultural practices can thus help in controlling black locust spread. The presence of cultivations (e.g. orchards, vineyards or fields) surrounding black locust stands is considered a very efficient biological barrier since these elements of the rural landscapes are capable of both vegetative and generative reproduction (Vítková et al. 2017).

Beside agricultural practices, forest management can surely affect the fate of this species in exotic woodlands. As a light-demanding species, black locust requires disturbances that create gaps in the canopy (e.g. after trees die, fire, windthrow or forest management) (Vítková et al. 2017). Hence, light-abundant sites are favourable. Results from the study of Motta et al. (2009) suggested that the best way to tackle black locust colonization is by avoiding disturbances, since the natural suppression by local species will gradually regain space. Of course, this way is in contrast with the multipurpose economic interest linked to the species. Harvesting is often the main factor in preserving black locust cover. In their riverine study, Höfle et al. (2014) observed that black locust growth rate was higher in plots where management was permitted than in those with restrictions. Cases of coppice management of other forest types have been reported to promote black locust entrance. Radtke et al. (2013) showed that traditional coppice management drives black locust and tree of heaven into the deciduous forest of Southern Switzerland. So, management practices need to be adjusted according to research outcomes.

Figure 7. Black locust expanding in riparian woodlands close to the Piave River at Pederobba, Italy (photo by S. Iacopino).

Staudhammer et al. (2015) suggested that the identification of socio-ecological indicators is important in developing an effective landscape scale management to control invasive species. At the same time, the authors argued that land use and socioeconomic indicators can be used as efficient predictors of invasive woody plants occurrence.

However, there are few studies aimed at investigating links between invasive woody plants and socio-economic factors in the literature.

2. Methods

This thesis involved multiple scale studies: at stand, landscape and national scale. At the stand scale, ecological impacts on the plant community were assessed through a comparative approach, based on a sample of pairs of woodlands, invaded by black locust or not (the second hereafter also called "native stand"). A focus on a sample of three types of landscape (rural, riverine and urban) allowed black locust impacts to be compared across different environmental contexts. We also included soil sample collection to observe microbiological effects on soil cycles. In addition, in the riverine landscape we surveyed geomorphological variables. A second focus on a sample of three European cities (Berlin, Padova and Roma) allowed the impacts of both black locust dominance and urban matrix properties to be investigated across urban environments at different latitudes. Finally, at the Italian national scale, socio-economic drivers were investigated, linking these factors with changes in both land cover and black locust distribution.

Table 1. Number of sampling pairs for each part of the thesis and study areas. Each pair consists of an invaded by black locust plot and a plot non-invaded. Paired plots from the urban landscape type coincide with paired plots in the study area of Padova for assessing urban land patterns. Paired plots from the rural landscape type and from Euganean hills partly coincide.

Thesis part	Study area	Sampling pairs (no.)
Landscape types	Rural	28
	Riverine	9
	Urban	10
Focus on Euganean hills	Euganean hills	16
Urban land patterns	Berlin	34
	Padova	10
	Roma	5

2.1. Study areas

2.1.1. Native and black locust stands in three different landscapes

Comparison among stands invaded by black locust and not is investigated among three northeastern Italian landscapes: rural, riverine and urban. A brief description of the study areas in the three landscapes is provided in the next pages and paired plots are shown in Figure 2 (§ 1.2).
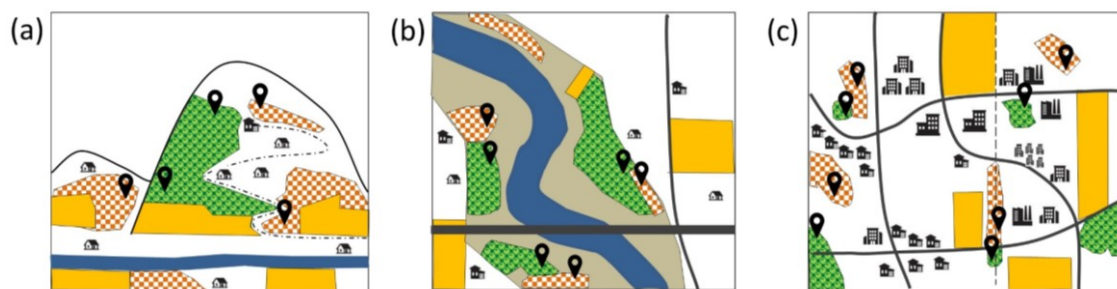

Figure 8. Schematic representation of the three landscape types: rural (a), riverine (b) and urban (c).

2.1.1.1 Rural landscape

In the rural landscape, paired plots were selected in the foothills of the Eastern Alps within the Mediterranean Mountains environmental zone (Metzger et al. 2005). Forest plots surveyed are located in hilly areas in the provinces of Padova, Treviso and Vicenza.

Most of the stands are located within the Euganean Hills, a hilly area of volcanic origin, well isolated in the surrounding alluvial plain between the Adige and Bacchiglione rivers and south-west of the city of Padova. The hills are of modest height, just over 600 m a.s.l. for Monte Venda. The Euganean Hills cover about 15,000 hectares, the hills and part of the surrounding valleys are part of the Natura 2000 network and fall within Special Protection Area (SPA) IT3260017. They form a complex landscape that is considered a biodiversity hotspot. In the Euganean Hills black locust was particularly favoured for a series of social-environmental factors and black locust woodlands are nowadays the most common (Sitzia et al. 2010).

The rural landscape includes Montello, a large morainic hill in the northern Venetian plain, lapped to the north and east by the Piave River. Montello covers about 6,000 ha. It is of very modest height with a maximum of 369 m a.s.l. and a mean of 200, 100 m higher than the surrounding plain. Historically most of the area of Montello was covered by oak-dominated forest while today nearly 60% is covered by forest, 90% of which is dominated by black

locust interspersed by oak-dominated patches. These formations are mainly coppiced for firewood production (Nascimbene et al. 2015).

2.1.1.2 Riverine landscape

In the riverine landscape, pairs of invaded plots by black locust and non-invaded plots within native stands were surveyed along the Piave River. The Piave River is one of the most important rivers of north-eastern Italy. From its source at 2,037 m a.s.l. in the eastern Italian Alps to the Adriatic Sea, the river flows for 222 km. Its drainage basin has an area of 4,022 km^2 and is largely composed of sedimentary rocks. With regard to its morphology, the river is divided into three reaches: upper, middle, and lower. In the upper reach, the river has a quite narrow channel. In the middle reach, the river forms a wide and multithreaded channel pattern (from Longarone to Ponte di Piave). The lower course is the most impacted by man and has been artificially straightened (Surian 1996).

Figure 9. Location of Piave River and Veneto Region, north-eastern Italy (on the left) and a picture of Piave River close to Belluno (on the right - photo of Flymee drone).

The history of this river is characterized by centuries of conflicting water uses; however human exploitation of water resources increased drastically in the last century. A series of dams and reservoirs were built along its main stream and most important tributaries from 1930 to 1950 (Picco et al. 2016). Nowadays there are 13 major reservoirs along the river, mainly used for hydropower production. Reservoir operations and related management is strongly affecting the temporal evolution of discharge. Thus, the natural streamflow regime is impacted by dam-induced alterations shaped by the dynamic water exploitation system in the river basin (Surian 1996). Study sites were selected in the middle reach that has a wider

and multi-thread channel pattern. The middle reach extends for 117 km from Longarone (BL) to Ponte di Piave (TV). The upper part of Piave River basin was subjected to natural and artificial reforestation after WWI. While recently, several areas in the basin are characterized by forest stand ageing and expansion due to abandonment of forest management (Sitzia et al. 2012b).18 paired plots were selected and surveyed along the river stretch between Ponte nelle Alpi (BL) and Cimadolmo (near Ponte di Piave, TV) between May and September 2017.

2.1.1.3   Urban landscape

Paired plots of invaded and non-invaded stands by black locust in the urban landscape of Veneto Region were selected in the city of Padova. Padova is located in the centre of Veneto Region within the metropolitan area that includes Padova, Venezia and Treviso (Calafati 2013). It is a municipality of 93 km^2 with 210,000 residents (Comune di Padova 2017). The territory of Padova has a sub-Mediterranean climate with annual precipitation of 846 mm and mean annual temperature of 12.9 °C. Within the city, built-up settlements is the dominant land use followed by areas mixed with agricultural uses. Woody vegetation is barely represented as land cover and mainly limited to riverbanks (ARPAV 2013). In addition to the paired plots from the urban context of Padova there were two pairs from Venezia mainland.

2.1.2. Urban land patterns and black locust effects in three cities

This part of the thesis encompasses three European cities at different latitudes: Berlin (52°31'N), Padova (45°24'N) and Roma (41°53'N).

Berlin, the capital city of Germany, has a population of 3.5 million and covers an area of 892 km^2. It is a green city in which green spaces and water bodies cover 41% of the total area: among which forests cover 17.5%. Built-up areas cover 48% and streets 11% (Kowarik 2019). Within the complex matrix of Berlin, spontaneous urban woodlands develop on debris and gravel and are often dominated by native birch tree and the alien black locust tree (Trentanovi et al. 2013).

Padova is the second city studied in this part of the thesis. A description of this study area is provided above (§ 2.1.1.3). Paired plots from Padova are the same as those surveyed and used in the comparison of the three landscapes of northern Italy.

Roma, the capital city of Italy, is located in the centre of the country. It has a key biogeographic location and a transitional climate; sub-Mediterranean climate conditions are

recorded with a moderate drought in the summer period (Blasi et al. 1999). The municipality of Roma covers an area of nearly 1,287 km^2 and has almost 2.9 million residents (Ufficio di Statistica di Roma Capitale 2017). The municipal area consists of an inner artificial matrix and an outer agricultural matrix. The artificial matrix is permeated by agricultural areas till the historical centre. The surrounding agricultural matrix contains quite a number of scattered settlements and even some large suburbs (Capotorti et al. 2013). Spontaneous potential vegetation mainly includes deciduous or mixed oak woodlands. Climate conditions are less favourable for black locust thus limiting presence of black locust-dominated woodlands around the city of Roma relative to the other two cities considered.

Figure 10 Pictures depicting the three landscapes: rural (a), riverine (c) and urban (e) and landscape related examples of sites invaded by black locust (b,d,f) (photos by S. Iacopino and from Google maps (e)).

2.1.3. Socio-economic and black locust distribution patterns in Italy

The fourth part of this thesis is aimed at improving the knowledge on black locust spread and distribution in relation to specific socio-economic conditions within the Italian territory. The study area for this part of the work coincides with the national scale of Italy. Nevertheless, some Italian regions were excluded due to accessibility limits and not suitable classification systems of regional forest maps. Regions not considered are: Valle d'Aosta, Puglia, Calabria, Umbria, Sardegna, Trentino-Alto Adige. Given forest distribution data available and suitable for this study, it was possible to cover 73% of the whole Italian territory. However, given that, in the excluded regions (other than Umbria) survivability is assessed mainly as negligible (de Rigo et al. 2016), we covered nearly the entire national territory climatically suitable for black locust. Regional forest type maps used in the study are shown below (Figure 11).
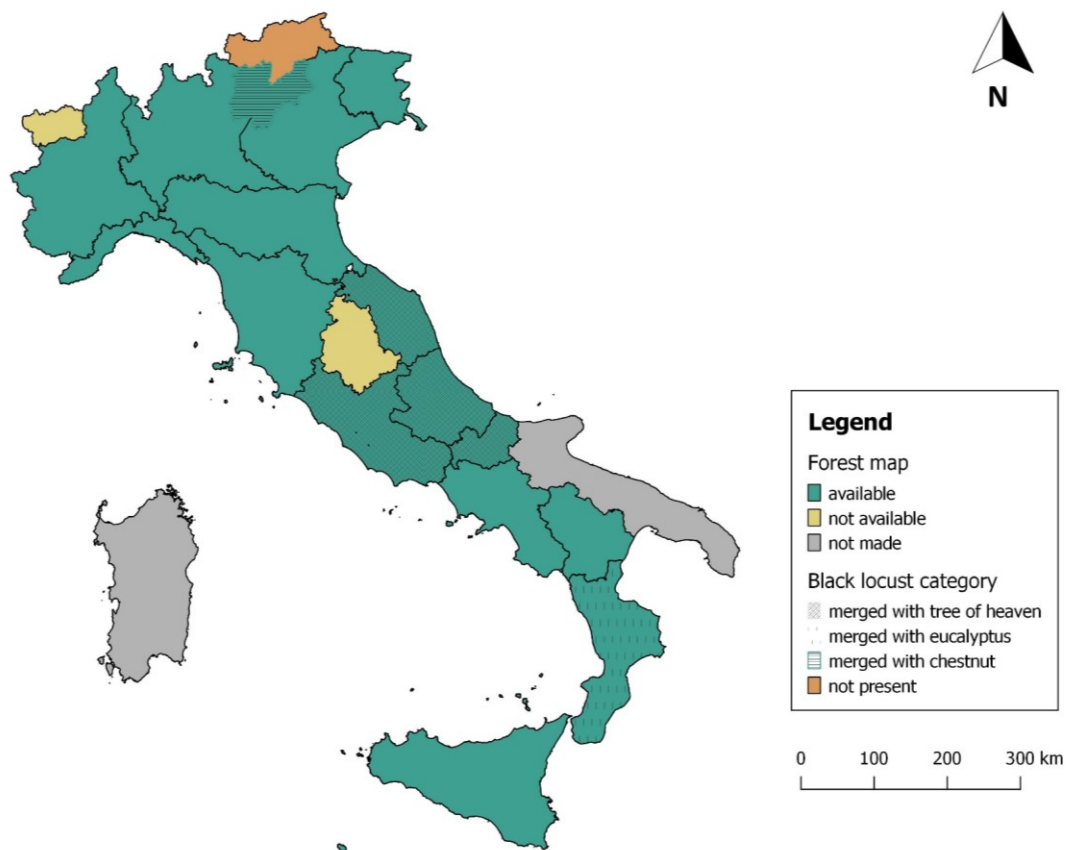
Figure 11. Accessibility of forest type maps (colours) for Italian regions and categorization system of black locust (texture) when including other forest types in addition to black locust category.

2.2. Data collection and analysis

2.2.1. Native and black locust stands in three different landscapes

2.2.1.1   Sampling design

A commonly applied method to investigate effects of alien species invasion is comparing invaded sites to nearby non-invaded sites (Vanderhoeven et al. 2005, Hejda et al. 2009). This approach, suggested by Walker and Smith (1997), is a proxy to measure impacts driven by an invasive species when is not possible to survey the same site before, during and after the invasion occurs. We applied the paired comparison method on invaded vs. non-invaded sites by black locust tree to detect changes in understory plant communities due to dominance of the invasive alien tree. The presence of neighbouring invaded and non-invaded stands was investigated in GIS environment (QGIS Development Team 2018). The process was eased by consulting regional forest type maps of Veneto Region (Del Favero 2006); however, in the urban context of Padova, a more intense effort was necessary to identify stands that were not mapped. First step was the identification of potential black locust stands, then a paired native stand was chosen within a 500 m radius. A minimum distance of 1 km between plots of different pairs was respected. Plots are sited at least five metres from forest edge to avoid ecotone and disturbance effect within the plot. Each plot is square and has a surface of 100 m^2 as suggested by Wheater et al. (2011).
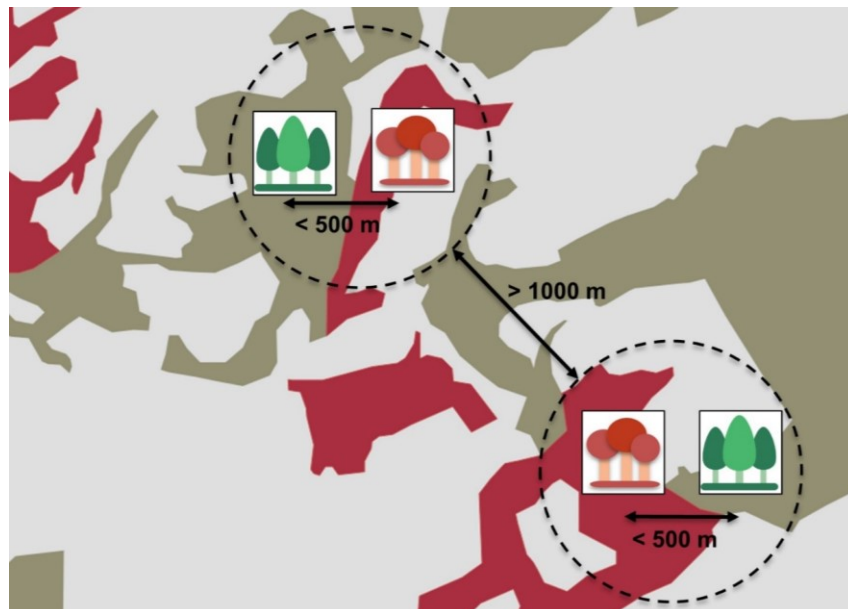

Figure 12. Graphic illustration of the paired sampling design. Each pair includes a native tree-dominated stand and a black locust-dominated stand. Plots of each pair were less than 500 m apart and more than one km apart from other pairs.

This paired comparison sampling method was already applied for seeking black locust impacts on local woodlands (Sitzia et al. 2012a). The maximum distance between stands of the same pair is respected to obtain comparable stands in terms of land-use type and disturbance regime. The minimum distance of 1 km between stands of different pairs is kept avoiding spatial autocorrelation effects. Sampling design is graphically described in Figure 12 (previous page).

2.2.1.2 Stand structure and plant surveys

Following the above-described sampling design, a total of 94 paired plots of black locust and native woodlands were surveyed in the three landscapes of north-eastern Italy. Prior to the surveys, selected plots were verified in the field. With a visual assessment, plots of same pairs were selected with comparable stand age and structure. Nevertheless, in the urban landscape due to the irregularity of stand structure it was not always possible to select pair members with similar stand characteristics. In each 10 x 10 m^2 paired plot, the structural parameters commonly used in forest surveys were measured. Each tree (diameter at breast height (DBH) $\geq$ 5 cm) was identified at species level and DBH and height were recorded. Floral surveys were conducted within the squared plot in collaboration with expert botanists. Plots belonging to same landscape were surveyed by the same botanist to ensure equal sampling effort. Each vascular species was identified and assigned to cover class according to Braun-Blanquet (1932) (Table 2). Cover class was referred to stand layers which are defined on the basis of plant height as follows: ground layer – species $\leq$ 1 m tall; shrub layer – species between 1 and 5 m tall; tree layer – species $\geq$ 5 m tall.

Table 2. Cover classes, relative percentage cover values according to Braun-Blanquet (1932) and transformation values according to Tüxen and Ellenberg (1937).

Cover class	Range of cover (%)	Transformation values
+	Few individuals	0.1
1	< 5	2.5
2	5 - 25	15
3	25 - 50	37.5
4	50 - 75	62.5
5	75 - 100	87.5

In each stand, three increment cores were collected from representative trees, the largest ones. CATRAS$^{©}$ program (Computer Aided Tree-Ring Analysis System) (Aniol 1983) was used to count number of rings in the laboratory. The volume of deadwood was

assessed recording length and diameter for all snags (diameter ≥ 3 cm), length and minimum and maximum diameter for logs and stumps. Volume of both live trees and snags (standing dead trees and broken-top snags) was calculated by applying the allometric equations available in Tabacchi et al. (2011). We applied the equation of the dominant tree species; where this was not possible, we used the general equation for other hardwoods. Volume equations have been commonly applied to calculate the volume of snags and standing deadwood (e.g. Goodburn and Lorimer 1998, Brunet and Isacsson 2009) as in our case. Volume of ground logs was calculated using the truncated cone formula.
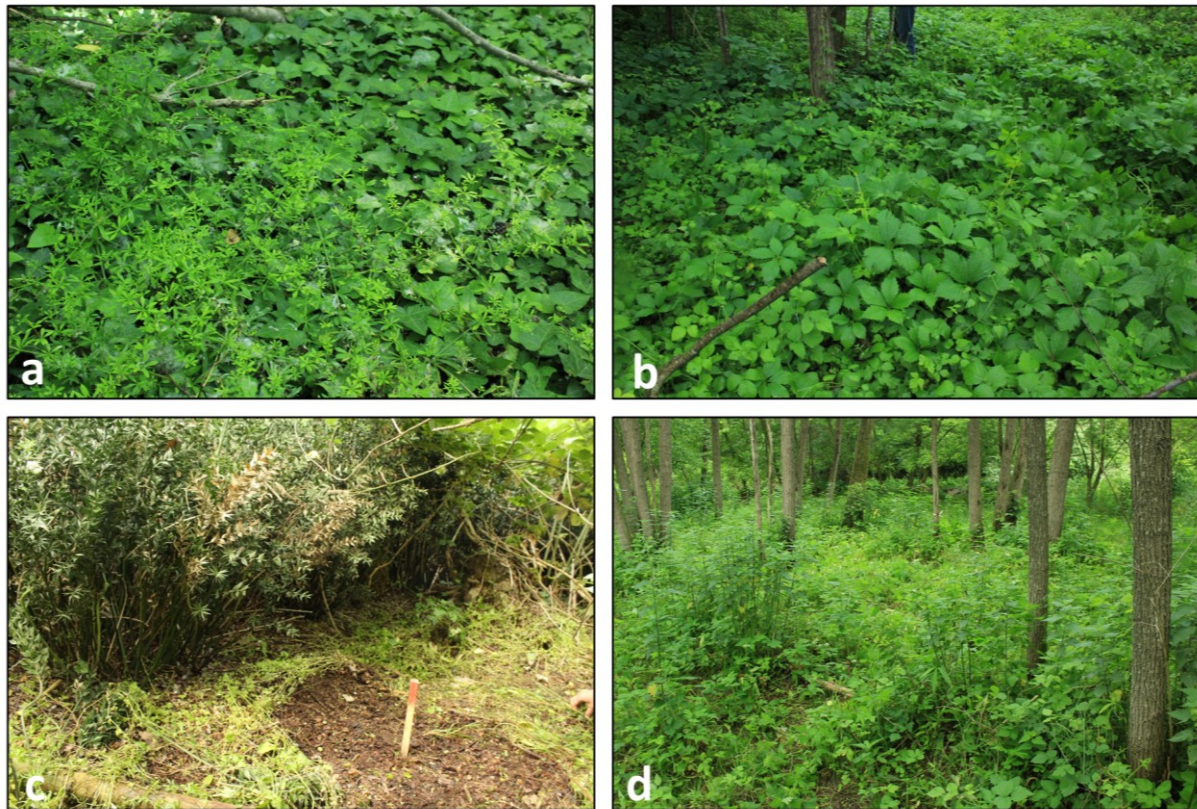
Figure 13. Examples of plants commonly found in the understory of black locust stands. a) Understory made by a carpet of the common *Hedera helix* with *Galium aparine*, annual herb found in nitrogen rich soils; b) A thick carpet of the exotic *Parthenocissus quinquefolia* was commonly found in the urban woodlands of Padova; c) *Ruscus aculeatus*, a shrub present in the understory of both native and black locust stands in Euganean hills; d) the typical understory of black locust stands formed by nitrophilous species, in the picture *Urtica dioica* and *Rubus caesius*. (photos by S. Iacopino)

2.2.1.3 Soil samples

In each plot, three soil samples were collected to study differences in the presence of ammonia-oxidizing archaea (henceforth abbreviated as AOA) community mainly related to nitrogen-fixation activities. Soil samples were taken from three representative spots within each stand. A soil corer of 1.5 cm diameter and 10 cm depth was used, litter was removed, and hollows avoided. After collection, tubes were kept open to let samples dry out at ambient temperature for 10-15 days. Dry soil samples are crushed, stones and other particles removed, and 0.4 g moved to Eppendorf centrifuge tubes for lab analysis. Quantitative Real Time PCR (qPCR) was performed to quantify the ammonia-oxidizing archaea gene (*amoA*) from the DNA extracted by soil samples. According to Zanardo et al. (2016), the gene is a reliable marker to detect AOA involved in nitrification. The process was performed in a Quantstudio 12K Flex Real Time PCR System using Power SYBR® Green PCR Master Mix and 384 wells plates (Applied Biosystems).

In qPCR, the target gene is amplified by gene-specific primers. Serial dilutions of determined amounts of plasmids with the target cloned gene allow a standard curve to be built that is used to quantify the gene copy number. qPCR is adjusted for a 10 ml volume reaction. This reaction mixture contains 5 ml Sybr Green mix, 0.2e0.5 mM of the forward and reverse primers, 0.6 mg/ml BSA, 1 ml of template DNA solution, sterile MilliQ water to reach the final volume. Inhibition effects of soil and co-extracted compounds were avoided and tested diluting the DNA extracted from soil samples 50 times. qPCR methodology is reported by Zanardo et al. (2016).

2.2.1.4 River geomorphic variables and black locust stands

In the paired plots of the riverine landscape of Piave River, together with the data already presented, we collected variables to describe geomorphological processes occurring in the surroundings of paired plots. In addition to the sampling design criterion already mentioned, sampling units in the riverine landscape were selected with a maximum 10 metres elevation above the active channel of the river (Google Earth) to ensure the influence of river dynamics. All sampling units along Piave River were identified in the middle reach, characterized by a multithreaded channel pattern (Surian 1996).

Granulometric analysis included measures of fine sediment depth and grain size determination. A small trench was dug down to the gravel layer in each plot. Depth of fine sediment till the gravel layer was measured. In plots featuring coarse sediments located less

than one metre in depth we measured the b-axes of 30 coarse elements to calculate the grain size distribution of gravel layer. We assessed elevation above the thalweg and active channel from Google Earth. Through the use of available aerial photos, we also calculated plot distances from the thalweg and active channel dating from 2015.

2.2.2. Urban land patterns and black locust effects in three cities

The methodology and sampling design applied for paired plots in the three landscapes (§2.2.1.1) were applied on paired plots established in Berlin and Roma. With the aim of analysing the potential different effect of urban matrix properties and black locust dominance on understory species composition in cities at different latitudes, data collection in urban stands of Padova was integrated with data from paired plots of Berlin and Roma for a total of 98 paired plots (68 in Berlin, 20 in Padova and 10 in Roma). Matched black locust and native stands in Berlin were surveyed by Trentanovi et al. (2013).

The fewer stands in Roma derives from the difficulties in finding stands according to the applied sampling design. To disentangle the effects of urban matrix properties on species composition we identified proportions of land use types in a joint area of two 500 m buffers following the method applied in Trentanovi et al. (2013).

Land use types for Berlin were retrieved from the official habitat map of the city (SenStadt 2008). Coherently with land use types categorization of Berlin, land use types were visually interpreted from recent aerial photos and manually reconstructed in GIS environment (QGIS Development Team 2018) for Padova and Roma.

In order to build environmental variables describing urban matrix properties, we identified proportions of urbanity, roads and railways within the joint area of two 500 m buffers from paired plots. We identified urbanity as the proportion of built-up area. In the case of Berlin urbanity was retrieved by subtracting road area from impervious surface.

Among the total number of sites surveyed in Berlin, we selected 46 paired plots removing the ones with lower or higher proportions of urbanity area than those recorded in Padova and Roma thus eliminating plots from urban areas with very dissimilar matrix connectivity.

2.2.3. Socio-economic and black locust distribution patterns in Italy

Distribution of native and black locust forest at the Italian national scale was built for two different periods: $t_1 = 1936$ and $t_2 \approx 2010$. The year for t_2 was chose as a standard, forest type maps were drawn up between 1998 and 2018.

Forest distribution at t_1 was retrieved from "Carta Forestale della Milizia Forestale del Regno d'Italia del 1936", 1936 Italian Kingdom Forestry map (henceforth as IKFM) (Figure 14). This map was the first homogenous and systematic cartographic document reporting forest extent and tree species composition for the whole Italian territory. IKFM forest classification was based on species composition and silvicultural system. Istituto Geografico Militare Italiano (IGMI) recently digitalized the map, also providing a raster format available in a WebGIS portal (Ferretti et al. 2018).
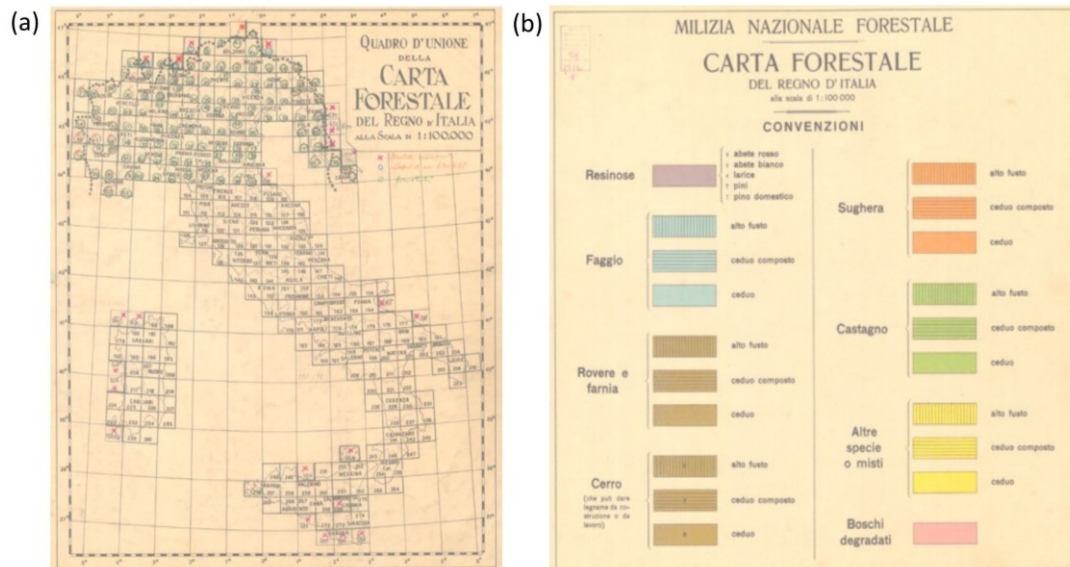
Figure 14. (a) IKFM sheets in the original index map and (b) IKFM original legend showing forest classification with main forest categories and treatments. Images from Ferretti et al. (2018)

1936 IKFM reports native forest categories. Black locust forest category is assumed not to be represented in 1936 in the Italian territory since this species was still scattered.

Forest distribution at t_2 was built from the most recent versions of regional forest type maps available (dated between 1998 and 2018). Those maps were retrieved from regional Geoportals or by requesting cartographic material from the Regions.

The regions for which we have obtained forest maps are as follows: Piemonte (Camerano et al. 2017), Liguria (Regione Liguria 2013), Lombardia (Del Favero 2002), Veneto (Del Favero 2006), Friuli Venezia Giulia (Del Favero et al. 1998), Emilia-Romagna (Baratozzi and Pattuelli 2002), Toscana (Arrigoni and Menicagli 1999), Marche (IPLA 2001), Abruzzo (Collalti et al. 2009), Molise (Garfì and Marchetti 2011), Lazio (Regione Lazio 2011), Basilicata (Costantini et al. 2006), Sicilia (Camerano et al. 2011).

Availability of maps and type of categorization for black locust woodlands is summarized in Figure 11 (see § 2.1.3).

To ensure a better correspondence of forest classification among t_1 and t_2, polygons referring to Mediterranean brushwood, shrubs, parks - gardens and short rotation systems categories were eliminated from each regional forest map when present. All the regional maps retrieved were merged into a raster to obtain a simplified classification with the following classes: native forest, black locust forest and no forest. Forest distribution maps of t_1 and t_2 were rasterized in a 10 m x 10 m grid. In order to allow a proper overlay of forest maps and to overcome a coordinates system shift of 1936 IKFM, number of 10 m × 10 m cells for each land cover class was transferred onto 1,000 m × 1,000 m grids for t_1 and t_2. Then, for t_1 and t_2 each 1,000 m × 1,000 m cell was assigned to the dominant land use class according to these criteria: t_1 land use class covering > 50% of the cell; t_2 land use class with higher number of 10 m × 10 m cells.

Thus, patterns of land cover changes from t_1 to t_2 were constructed at municipal level following the scheme represented in Figure 15. The main focus was on changes involving black locust forest category, specifically to 'robinia afforestation' (pattern A) and 'robinia replacement' (pattern B), so black locust spread into open habitats and colonization in native forests, respectively. The obtained 1,000 m × 1,000 m grid with patterns information was then crossed with the ISTAT 2011 municipalities boundaries vector file to count number of grid cells patterns for each municipality.

Municipalities not ecologically suitable for black locust were not considered in the following steps and data analysis. This distinction was made by means of the Maximum Habitat Suitability map (MHS, also known as survivability) of black locust (de Rigo et al. 2016, Sitzia et al. 2016c). We kept municipalities with survivability value higher than 0.5.
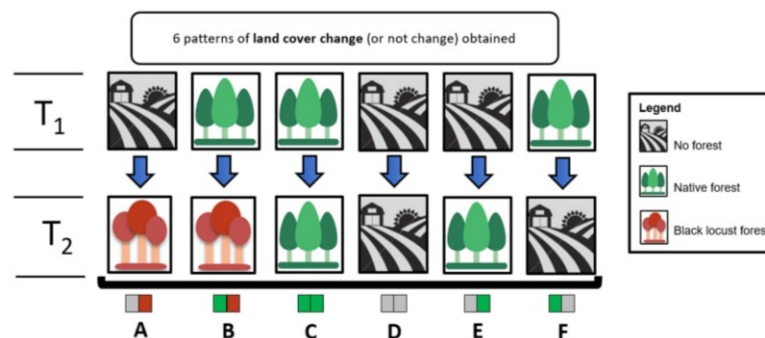

Figure 15. Scheme followed to calculate the combinations of patterns of land cover change from t_1 to t_2. Pattern A and pattern B represent 'robinia afforestation' and ' robinia replacement' respectively. Pattern E represents afforestation by native tree species.

Two literature-based socio-economic indices were applied to link municipalities features with black locust forest distribution and spread.

We applied the rurality/urbanity index (IRU) and level of per capita income and consumption in each municipality index (IRC) built by Anania and Tenuta (2006). IRU and IRC were built taking into account effective variables able to describe important elements of rurality/urbanity (Table 3) and wealth level (Table 4) of municipalities for IRU and IRC respectively.

Table 3. Variables used to build rurality/urbanity index (IRU). From Anania and Tenuta (2006). To check sources of variables see Anania and Tenuta (2006).

Variables	Description
Population density	Number of inhabitants / municipality area (km^2)
Weighting of people working in agriculture	Resident population working in agriculture / resident population aged over 14
Weighting of people working in public services	Resident population working in public services / resident population aged over 14
Level of urbanization	Urban surface (km^2) / land area (km^2)
Population dispersal	Resident population in settlements and scattered houses / resident population
Availability of living spaces	Surface area (m^2) of living units occupied by residents / resident population

Table 4 Variables used to build the index on level of per capita income and consumption at municipal level (IRC). From (Anania and Tenuta 2006). To check sources of variables see Anania and Tenuta (2006)

Variables	Description
Women's employment in non-agricultural jobs	Resident female population working in non-agricultural sectors / resident female population aged over 14
Unemployment rate	Unemployed active population / workforce
Big-engined cars	Number of cars owned by residents with a cylinder capacity exceeding 2000 cc per 1000 inhabitants
Consumption of electricity	Consumption of electricity for household and general uses (kwh) / users
Per capita income according to income tax	Taxable income (€) / resident population

2.3. Statistical methods

All statistics were performed with R software packages (R Core Team 2018).

β-diversity, measure of species composition dissimilarity among communities, was calculated with abundance and presence/absence data and evaluated with Bray-Curtis' index and Sørensen index respectively, two dissimilarities indices commonly applied to ecological data (Faith et al. 1987). Differences in species composition at stand scale were investigated and compared through a non–metric multidimensional scaling (NMDS). NMDS is a multivariate statistical tool often applied to describe species composition differences among different stands or environment conditions (Pyke et al. 2001, Della Bella et al. 2007). NMDS is effective for describing graphically composition differences between sampling units. This method requires a matrix with n rows of samples and p columns of variables. As already applied in Minchin (1987), using a similarity or dissimilarity matrix, this is turned into a n x n symmetrical matrix with pairwise distances among samples. The NMDS ordination is performed on this distance matrix. The arrangements of stands in the graph is based on rank order starting from higher similarity among samples to lower similarity among samples. In contrast with other ordination methods, NMDS calculates a limited number of axes chosen prior to the analysis. We applied NMDS to graphically compare understory species composition between stand types. NMDS was performed with 'vegan' package (Oksanen et al. 2019). ANOSIM (Analysis of Similarity) function of 'vegan' package was applied using dissimilarities matrices to verify similarity of species composition among stands invaded and non-invaded by black locust. This analysis returns an r value that ranges from -1 to 1 where value close to 0 indicate very similar groups, values close to 1 differing groups and values close to -1 indicate that dissimilarities are greater within groups than between groups. Groups are compared considering centroids and values dispersion around centroids.

To detect further differences among invaded and non-invaded stands indicator species were identified for each cluster group with the Indicator Species Analysis (ISA) and using indicator value (IndVal) method from 'indicspecies' package (De Caceres and Legendre 2009). For each species, IndVal combines specificity and fidelity to the sampling unit (specificity is the uniqueness to a determined sampling unit while fidelity is the frequency within that sampling unit) (Dufrêne and Legendre 1997). IndVal ranges from 0 (no indication) to 1 (maximum indication).

Permutation test for homogeneity of multivariate dispersions based on 999 permutations is performed to test statistical significance of β dissimilarity. We applied the

permutation test using the package 'vegan' (Oksanen et al. 2019) to test differences among landscapes and stand types adjusting for small and unequal samples. As suggested by Anderson et al. (2006), β-diversity can be measured as average dissimilarity from sampling units to their group centroid in multivariate space and visualized as β dispersion. The technique allows variances of beta dissimilarities to be visualized. We performed beta dispersion using the function 'betadisper' of 'vegan' package and tested statistical significance with permutational test of same package.

We also applied the recent zeta diversity (ζ) concept (Hui and McGeoch 2014) to quantify the variation in species composition of multiple combinations of stands within native and black locust stands groups to assess the different contribution of specialist and generalist species to biotic heterogeneity. ζ-diversity, a measure of compositional change in terms of similarity, is defined as the number of shared species by i number of sites, with i representing the ζ-order. The number of orders depends on sampling design. ζ_1 corresponds to number of species in one sampling unit, so coinciding with species richness of the plot and highest order at maximum is the total number of sites. Increasing orders of ζ-diversity capture a lower contribution of specialist species (specialists) and higher contribution of generalist, ubiquitous species (generalists) to compositional change (McGeoch et al. 2019).
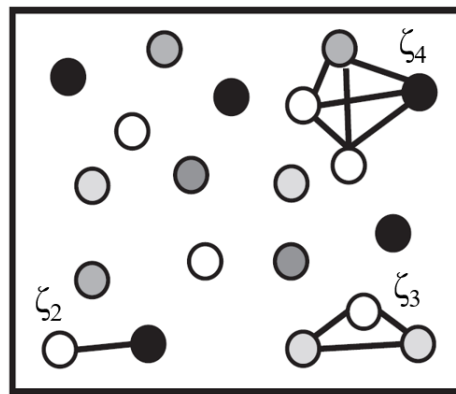
Figure 16. Scheme showing how sites are combined for the calculation of ζ-diversity at different ζ-orders with the nearest neighbour nondirectional scheme. Point shades represent hypothetically different environmental conditions. From McGeoch et al. (2019), modified.

Using 'zetadiv' package (Latombe et al. 2018), we plotted ζ-distance decay and ζ-decline. ζ-decay shows variation of ζ-diversity with increasing distance for considered ζ-order whereas ζ-decline quantifies how the number of shared species decreases with ζ-order. ζ-diversity was computed using nearest neighbour as sample selection scheme. Given that we applied a paired sampling method and differences in rates of decline are calibrated against distance, ζ-decline enables scale-specific comparisons of distance decay across stand types.

Moreover, to assess the relative contribution of environmental variables connected to ζ-diversity, we performed a multi-site generalised dissimilarity model (MS-GDM) for each stand type and landscape for orders ζ_2, ζ_3, ζ_5 for landscapes comparisons and orders ζ_2, ζ_3, ζ_4 for cities comparisons (Latombe et al. 2017).

Environmental variables contribution is graphically displayed with I-splines giving two useful pieces of information: (a) importance of each variable relative to others for the same ζ-order (in explaining ζ-diversity that is provided by the maximum value of the spline, (b) rate of compositional turnover and its change along the environmental gradient observed which is indicated by the variation in slope (Ferrier et al. 2007, Latombe et al. 2017).

In addition, we tested differences in both abundance and presence-absence of AOA between native and black locust stands. To test the statistical difference of AOA presence-absence we applied a binomial logistic regression, whereas AOA abundance differences were tested by a Poisson regression.

Lastly, we performed a binomial generalized linear model (binomial GLM) to test differences in geomorphological variables between invaded and non-invaded riverine plots. Grain size determination was not possible for plots with a fine sediment layer greater than one metre in depth. In those cases, not available values were replaced by the mean of grain size for the corresponding stand type.

We did not apply regression statistics to the fifth part of this thesis. We used descriptive statistics showing the distribution of Italian municipalities by socio-economic indexes classes. We considered the application of regression statistics less meaningful for this part given that we analysed the entire population of Italian municipalities in which black locust stands are mapped and not just a sample.

3. Results

3.1. Native and black locust stands in three different landscapes

We surveyed a total of 83 vascular understory species in the urban landscape, 99 in the riverine and 225 in the rural one. No significant differences emerged comparing α-diversity (species richness) of stands invaded and non-invaded by black locust in the three landscapes (Figure 17). The average number of species identified is not different in the two stand types.

Understory species composition of paired plots computed with Bray-Curtis dissimilarity is graphically plotted with a non–metric multidimensional scaling (NMDS) in Figure 18, showing black locust plots with red dots and native stands with black dots. Species composition (Bray-Curtis dissimilarity) is significantly different both between landscapes and stand types (ANOSIM; landscapes: R=0.322, p=0.001; stand type: R=0.1321, p=0.001). Plots belonging to different landscapes have distinct species composition with partial overlay of ellipses, however showing a certain variability of species composition within landscape. This variability is also shown in Figure 19 in which variance of β-diversity computed with Bray-Curtis dissimilarity is plotted distinguishing landscapes (a) and stands types (b) and plotting the considered group dispersion applying a Principal Coordinates Analysis (PCoA) to ordinate sites.

Differences in variance of β-diversity of stands by landscape is always significant (permutation test; p=0.001) except for urban against riverine landscape. Rural landscape exhibits a higher dispersion of plots with an average distance from centroid of 0.64 against 0.50 for urban plots and 0.51 for riverine ones.
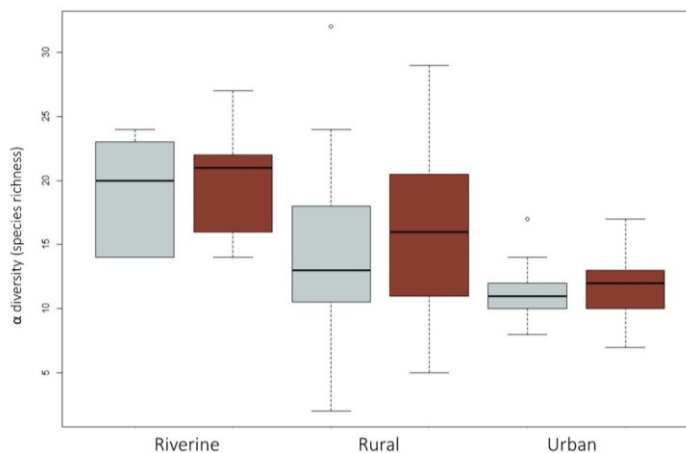
Figure 17. Species richness observed in native and black locust stands in the three landscape types. Grey boxplots represent values for native plots while red boxplots values for black locust plots.
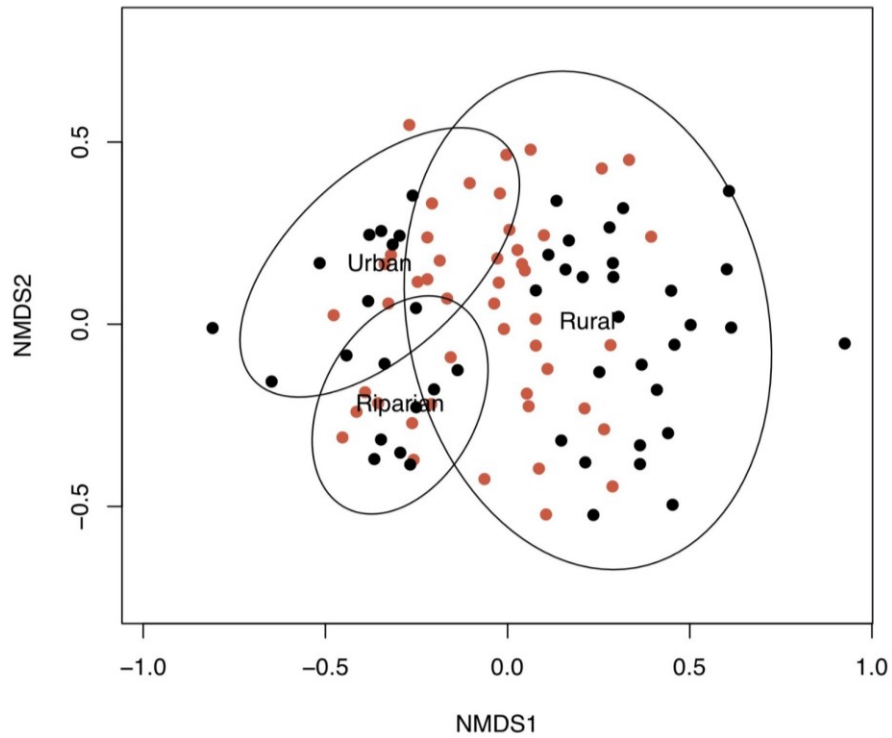
Figure 18. Comparison of understory species composition (Bray Curtis dissimilarity). Plots distribution according to NMDS analysis. Red dots are black locust woodlands, black dots are native woodlands. Ellipses display ordination of plots by landscape type (representing 95% CI around the centroid) (n=94).
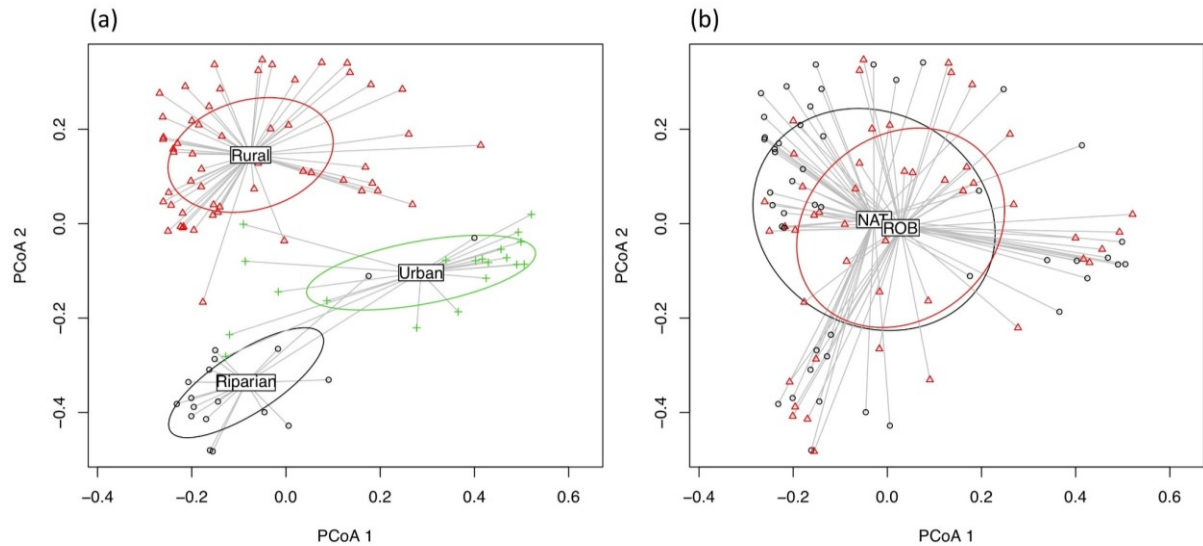

Figure 19. β dispersion plotted reducing the distances from Bray-Curtis dissimilarities to principal coordinates. β dispersions observed by landscape type (a) and by stand type (b): native (NAT) and black locust (ROB).

With the aim of observing and quantifying patterns in compositional change in the different landscapes of north-eastern Italy we used ζ-decay, one of the main applications of ζ-diversity. It represents the variation in the number of species shared with increasing distance between sites for a specific ζ-order. ζ-decay allows scale-specific comparisons of distance

decay because changes in rates of decline are adjusted against distance (McGeoch et al. 2019). Results of ζ-decay for each landscape type are plotted from Figure 20 to Figure 22. Significance of ζ-decay is expressed by regression slope. Results for ζ-decay in rural landscape show statistically significant regression slopes of ζ-diversity (GLM; $p<0.0001$) in both native and black locust stands for all ζ-orders plotted. Rate of compositional turnover is similar and over the same distances the average number of shared species does not vary between native and black locust stands from ζ_2 to ζ_5.

In riverine landscape, regression slopes of ζ-decay are statistically significant for all ζ-orders (GLM; $p<0.0001$) except in native stands for ζ_5. Compositional turnover has a similar rate in both native and black locust stands for ζ_2 and ζ_3. In ζ_3, both stand types lose shared species with increasing distance between sites, however, over 40 km, native stands still share 4 species on average while black locust stands have no more species in common. For ζ_5, for which contribution to ζ-diversity is higher from generalist species, ζ-diversity declines steeply in black locust riverine stands reaching zero shared species over distances of 30 km. In contrast, in riverine native stand of the same order, ζ-diversity is nearly stable.
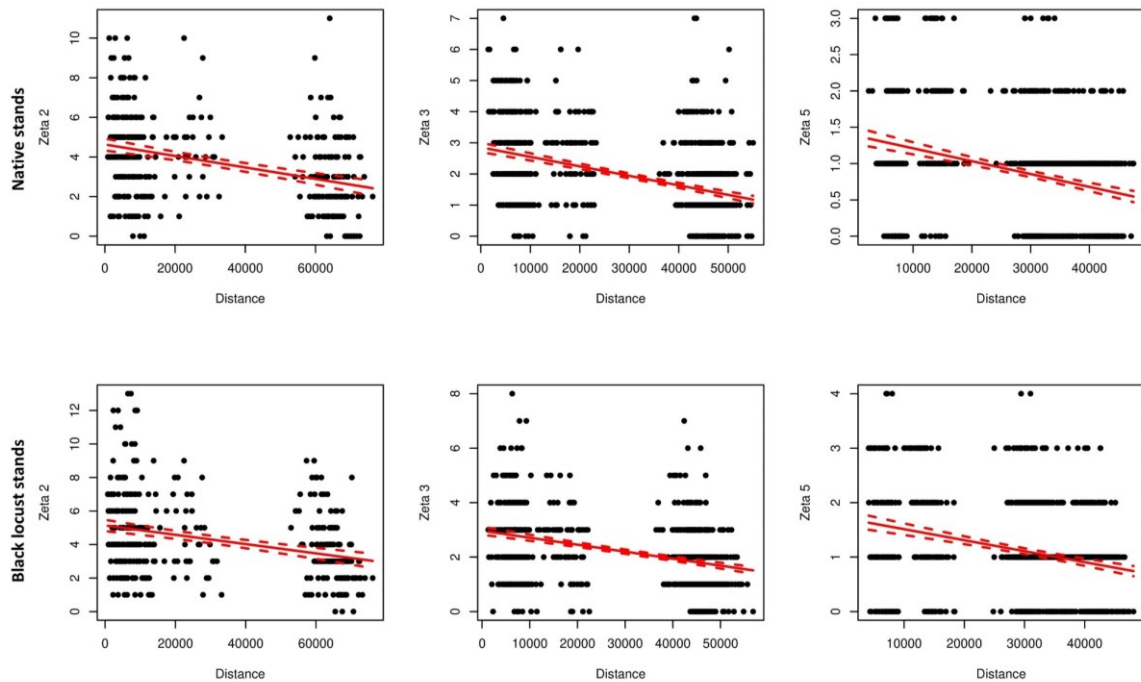

Figure 20. ζ-decay over distance for order $\zeta_{2,3,5}$ in native and black locust stands of rural landscape. ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen ζ-order. Dashed lines represent 95% confidence intervals.
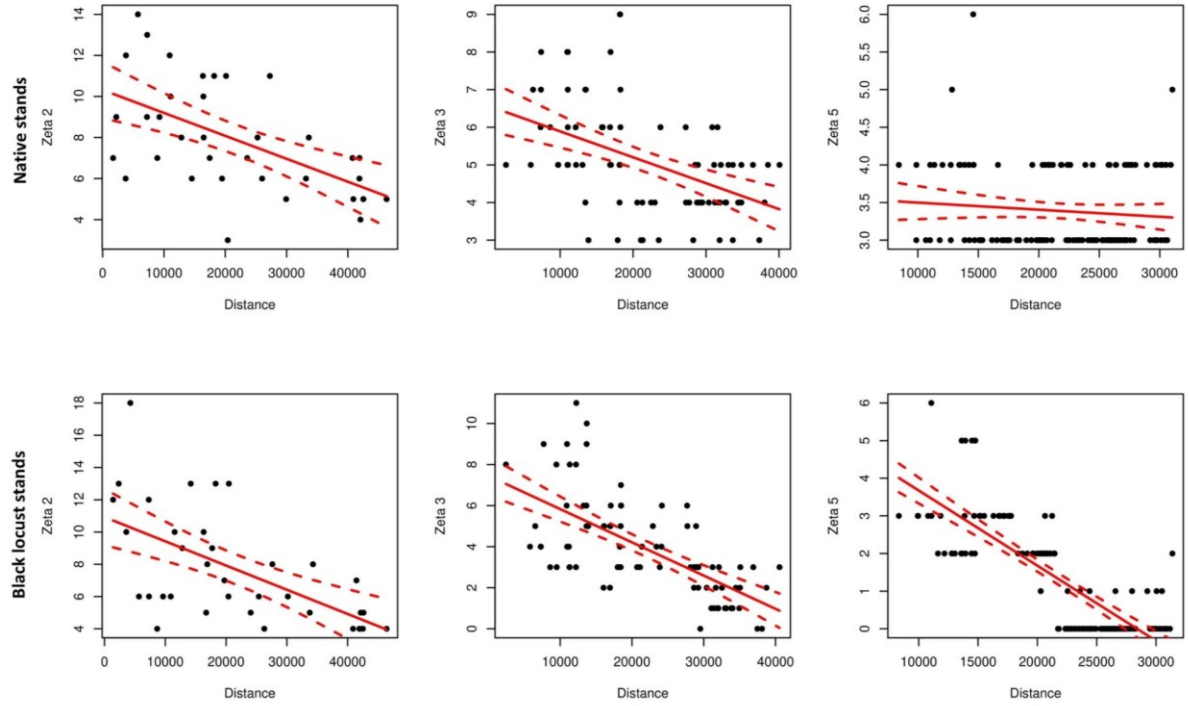
Figure 21. ζ-decay over distance for order $\zeta_{2,3,5}$ in native and black locust stands of riverine landscape. ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen order. Dashed lines represent 95% confidence intervals.
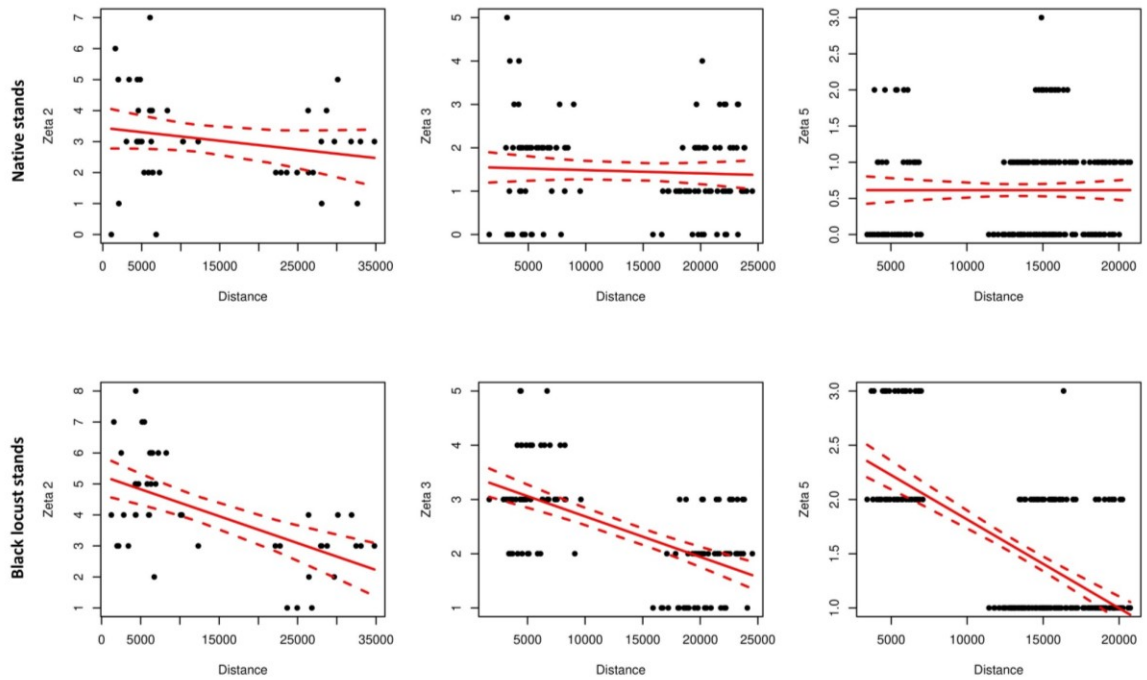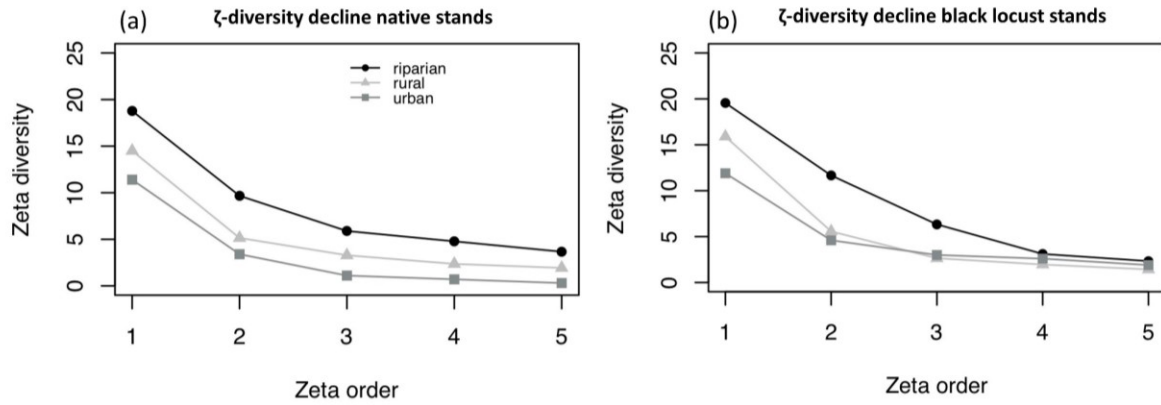

Figure 22. ζ-decay over distance for order $\zeta_{2,3,5}$ in native and black locust stands of urban landscape (Padova). ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen order. Dashed lines represent 95% confidence intervals.

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Figure 23. ζ-decline in native and black locust stands for the three studied landscapes. ζ-decline shows how ζ-diversity changes with the ζ-order.

To observe and visualize the relative contribution of environmental and stand structure variables explaining ζ-diversity we plotted I-splines-based MS-GDM (from Figure 24 to Figure 26). In all the different landscapes, I-splines show nonlinearities. This means, as expected, that rate of ζ-diversity, therefore of compositional turnover, changes along environmental gradients.

Observing I-splines in Figure 24, in the rural landscape, the most important variables influencing ζ-diversity of native stands are distance between sites, elevation, volume of logs and stand mean height. Elevation affects species turnover mainly from the lowest values to first increases of elevation. From lower to higher ζ-order the influence of elevation on species turnover increases indicating a greater effect on generalist species. Stand mean height shapes species turnover mainly considering specialist species where rate of compositional turnover is higher for lower and higher values of height. Moving to black locust stands in rural landscape, the main drivers of compositional turnover are distance between sites, stand mean height and slope. Stand mean height in black locust stands has different effects on ζ-diversity depending on ζ-order, however with all sets of sites considered the effect is more pronounced for variations of height in the lower part of its range.

Observing I-splines in Figure 25, for native stands in the riverine landscape the major drivers of species turnover are stand age, basal area and distance between sites. Stand age is the most important variable in influencing ζ-diversity for specialists (ζ_2), and this change is more important for the youngest surveyed stands while distance is the major driver of compositional turnover for higher ζ-orders. In black locust stands, major drivers of species turnover are, in order of importance, stand mean height, distance between sites and volume of logs. Stand mean height is the variable shaping most ζ-diversity for all orders with the rate of

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compositional turnover high next to highest values of stand mean height. Moreover, volume of logs shows a binomial effect on species turnover; presence or absence of deadwood on the ground results in a change of species composition.

Observing results for the urban landscape (Figure 26), in native stands the most important variables explaining ζ-diversity are basal area and volume of logs. Basal area shapes compositional change for all ζ-orders considered. Volume of logs displays effects on ζ-diversity only for ζ_5 where presence or absence of logs in stands results in two very different species compositions. Finally, ζ-diversity in urban black locust stands is mainly affected by distance, volume of snags and volume of logs.
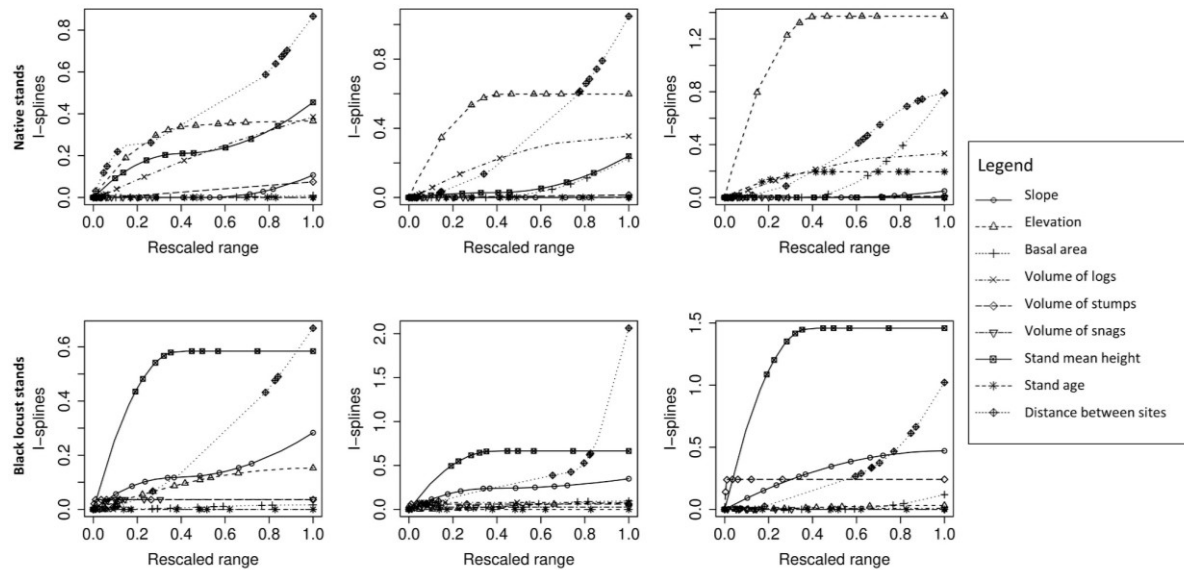
Figure 24. I-splines showing the contribution of environmental and stand structure variables to explaining ζ-diversity for $\zeta_{2,3,5}$ in paired plots of rural landscape. All variables are rescaled between 0 and 1 for comparison and visualization.

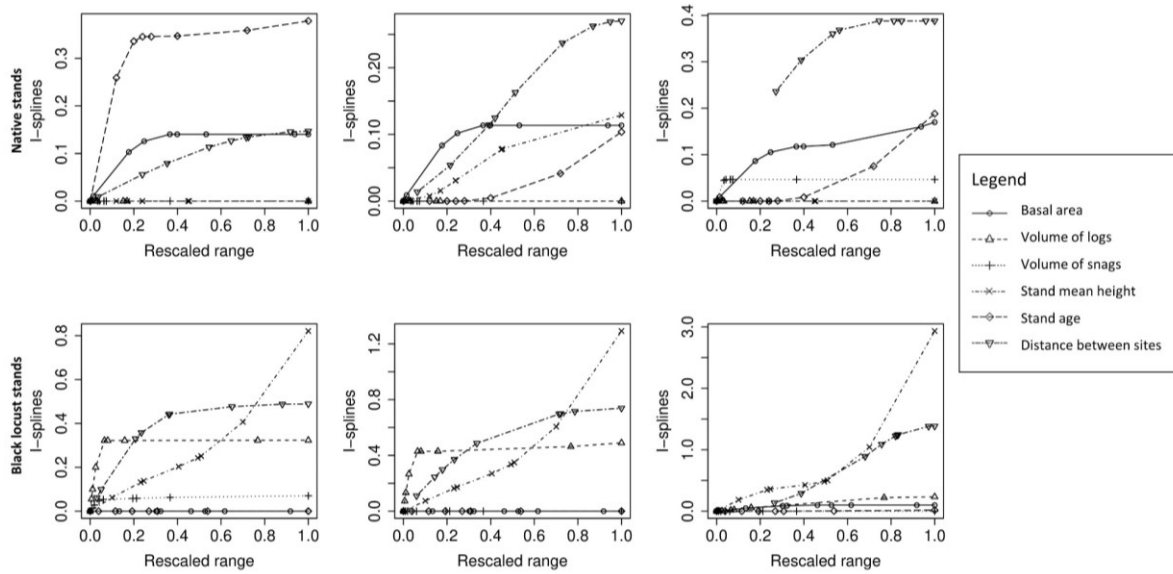**Figure 25. I-splines showing the contribution of environmental and stand structure variables to explaining ζ-diversity for ζ2,3,5 in paired plots of riverine landscape. All variables are rescaled between 0 and 1 for comparison and visualization.**
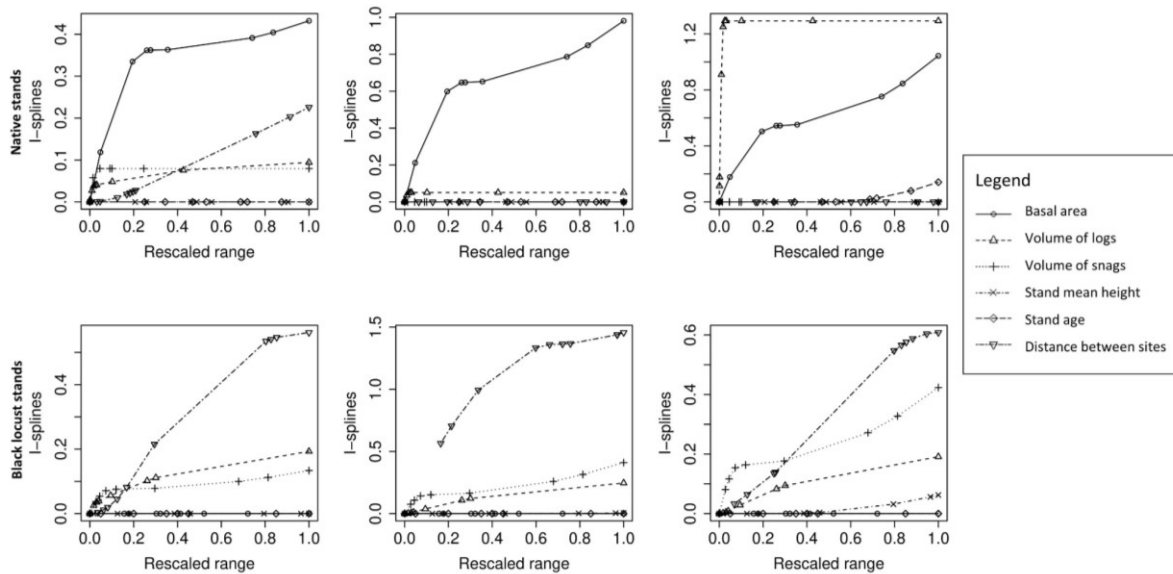

Figure 26. I-splines showing the contribution of environmental and stand structure variables to explaining ζ-diversity for ζ2,3,5 in paired plots of urban landscape (Padova). All variables are rescaled between 0 and 1 for comparison and visualization.

3.1.1. River geomorphic variables and black locust stands

We tested differences of geomorphological variables between invaded and non-invaded riverine plots. Differences in distance from thalweg between the two stand types resulted close to statistical significance (binomial GLM; p=0.181). In details, black locust woodlands along the Piave River were never found at a distance from thalweg smaller than 141 m. These values represent thresholds below which this alien species is not found in the Piave River floodplain. This result suggests that black locust stands did not occur in floodplain areas with frequent natural disturbances and is in line with black locust ecological requirements reported in the literature (Cierjacks et al. 2013, Vítková et al. 2015).
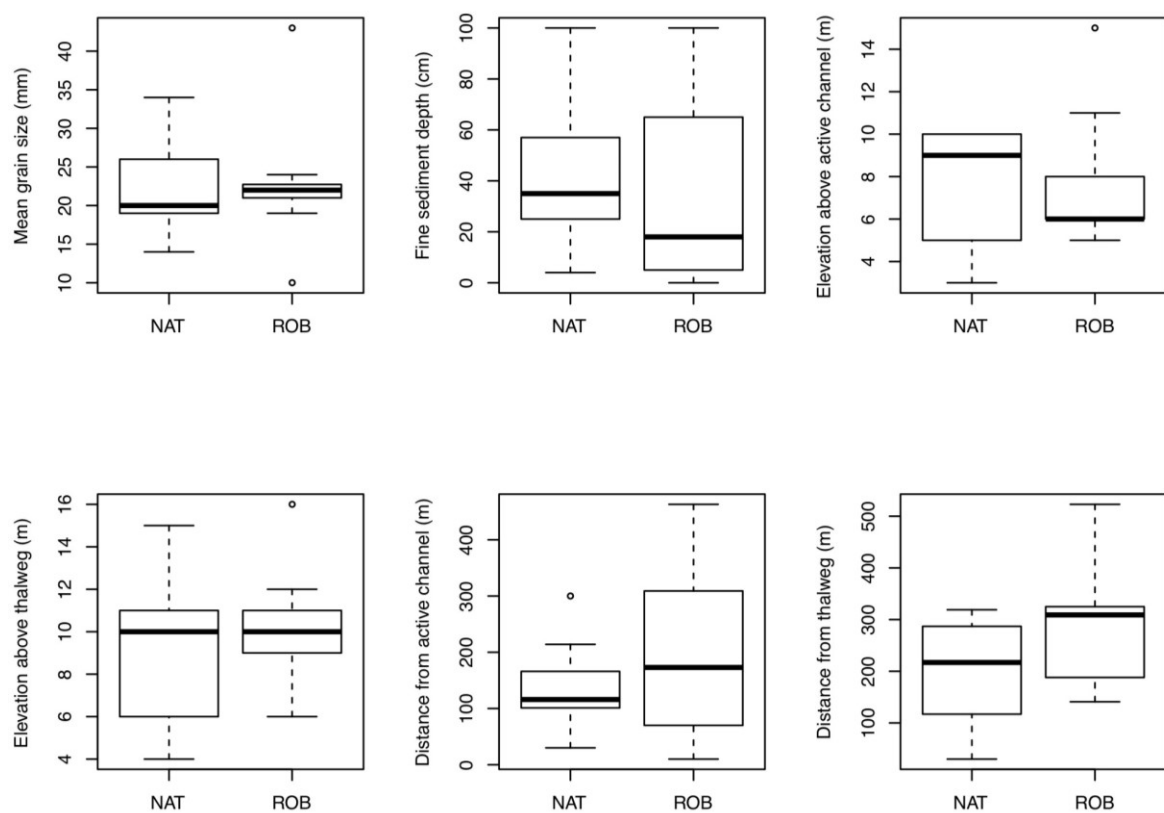

Figure 27. Geomorphological variables collected in the riverine landscapes and plotted for native (NAT) and black locust (ROB) stands.

3.1.2. Biochemical soil nitrogen cycle in black locust vs. native stands

We investigated whether AOA (ammonia-oxidizing archaea) differs in presence between native and black locust stands. We expected more abundant AOA in black locust stands due to nitrogen fixation associated with symbiotic rhizobia in black locust root nodules (Cierjacks et al. 2013). Distribution of values for both stand types were zero-inflated, so we accounted for zero-inflated distribution in binomial and Poisson regressions using 'zeroinfl' function of 'pscl' package (Zeileis et al. 2008, Jackman 2017). We recorded a significantly higher presence of AOA in black locust stands (binomial GLM; p=0.0357) (Figure 28).
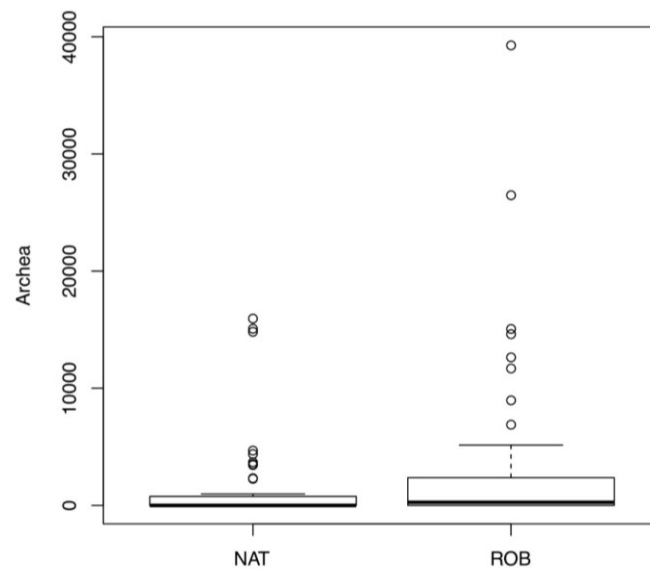

Figure 28. Abundance of ammonia-oxidizing archaea associated with nitrification cycling processes in native (NAT) and black locust (ROB) stands.

3.1.3. Chestnut vs. black locust woodlands in a rural area

A total of 133 vascular species were detected. Most of them were found in the ground layer: 130 species, 96 of which were in chestnut woodlands and 83 in black locust woodlands. Data analysis allowed the different plots to be represented in relation to species composition as already shown in § 3.1, determining the proximity of the composition to the characteristic one of habitat type 9260. The paired sampling comparison, when applied between plots related to habitats themselves, but subjected to different treatments, allows the effect of treatments on the number of characteristic and typical species of the habitat to be understood and to evaluate possible changes in the habitat structure and functions, as well as in its representativeness. A first result is the clear separation between the communities found in chestnut woodlands from those found in black locust (Figure 29A). This result confirms that the composition of chestnut woodlands differs from that of black locust woodlands, but at the same time shows a certain variability within the two woodland types. With regard to chestnut woodlands, composition differs in short rotation coppice stands from neglected coppice ones (Figure 29B). This result indicates that the difference in treatment generated by maintaining coppice management in chestnut woodlands results in a greater heterogeneity of flora. The abandonment of regular coppicing does not seem to have the same effect on black locust woodlands. Furthermore, the graphical comparison of α-diversity (species richness) makes it clear that there are no substantial differences between chestnut and black locust woodlands in the Euganean Hills (Figure 30A). This has already been found in secondary woodlands of Veneto Region by comparing black locust stands with a variety of native tree species stands (Sitzia et al. 2012a). If we consider the separation between the two different managements in chestnut stands (Figure 30B), no substantial differences are shown graphically. It seems, however, that the cessation of management results in a slight increase in species number in both woodland types. As expected, chestnut woodlands, whether or not they are still coppiced, host a higher number of characteristic and typical species than black locust woodlands (Figure 31). However, even black locust stands are not completely lacking these species, especially woody ones like *Sambucus nigra*. The number of characteristic species is higher in coppice woodlands than in neglected stands, but that is not true for typical species.
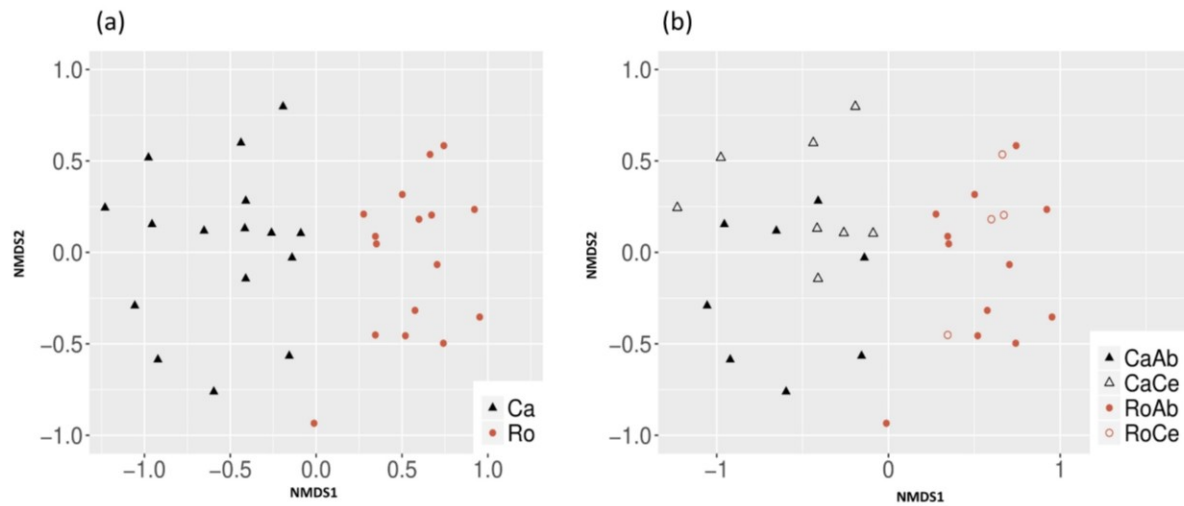
Figure 29. Comparison of understory vascular species composition. (a) Plant community ordination by stand type: plots of chestnut woodlands of habitat type 9260 (Ca - black triangles) and plots of black locust stands (Ro - red dots). (b) Plant community ordination by management status: neglected chestnut stands (CaAb – black triangles), chestnut coppice stands (CaCe – empty triangles), neglected black locust stands (RoAb – red dots) and black locust coppice stands (RoCe – empty dots) (n=32).
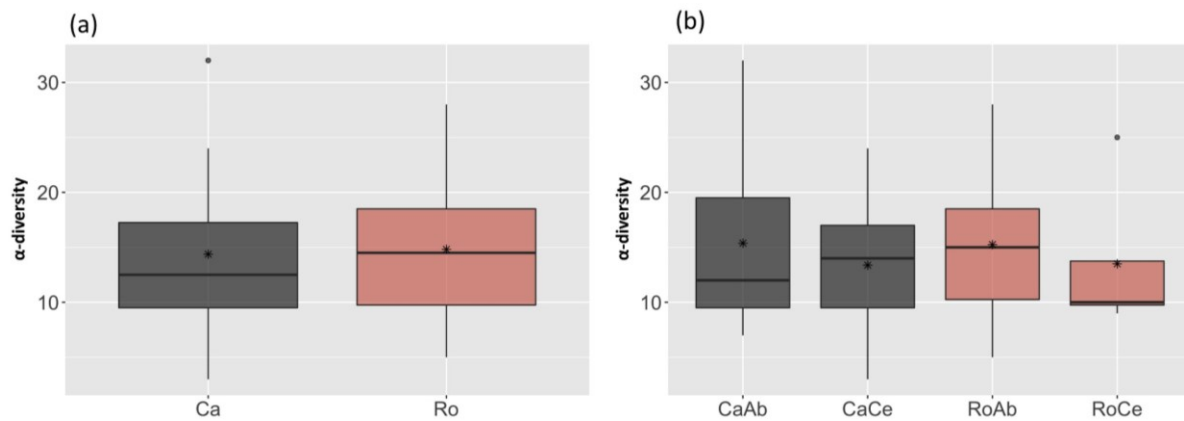

Figure 30. Comparison of α-diversity (species richness) (asterisk shows mean values). (a) Box plots showing α-diversity (species richness) variation across chestnut stands – habitat type 9260 (Ca – black coloured) and black locust stands (Ro – red coloured). (b) Box plots showing α-diversity (species richness) variation across neglected chestnut stands (CaAb), chestnut coppice stands (CaCe), neglected black locust stands (RoAb) and black locust coppice stands (RoCe) (n=32).
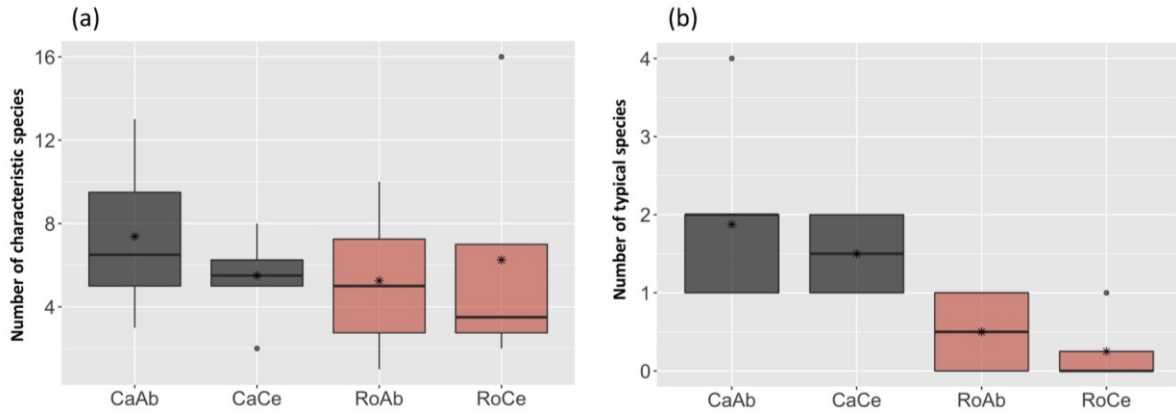
Figure 31. Comparison of the number of characteristic and typical vascular plant species of habitat type 9260 (asterisk shows mean values). (A) Box plot showing variation of the number of characteristic species (a) and typical species (b) of habitat type 9260 across neglected chestnut stands (CaAb), chestnut coppice stands (CaCe), neglected black locust stands (RoAb) and black locust coppice stands (RoCe) (n=32).

The difference between the groups shown graphically in the previous figures was deepened by searching for the indicator species of the two types of forest. The indicator species associated to chestnut woodlands, in addition to chestnut, are *Fraxinus ornus* and *Pteridium aquilinum* subsp. *aquilinum*, which are also associated with management abandonment. These species are mentioned among those characteristics of habitat type 9260. The indicator species associated to black locust woodlands, in addition to black locust, are *Crataegus monogyna*, *Lamium orvala*, *Sambucus nigra*, *Rubus ulmifolius* and elm (*Ulmus minor* subsp. *minor*). Elderberry and elm are also species indicating aged coppice, while black locust and *Symphytum officinale* are indicators of fully developed coppice. In addition to the typical and characteristic species, alien species may be used as indicators of forest or habitat conditions. Inside the forests surveyed, whether they are chestnut or black locust trees, there are few alien species. Furthermore, it is clear that coppicing does not lead to an increase in alien species within habitat type 9260 (Figure 32).

We also observed the variation of deadwood volume in chestnut and black locust stands. We found a higher presence of deadwood in the chestnut woodlands compared to black locust woodlands (Figure 33A). When comparing deadwood volume in neglected and coppiced chestnut stands, the total amount of deadwood was greater in the sites no longer managed compared to those still coppiced (Figure 33B).
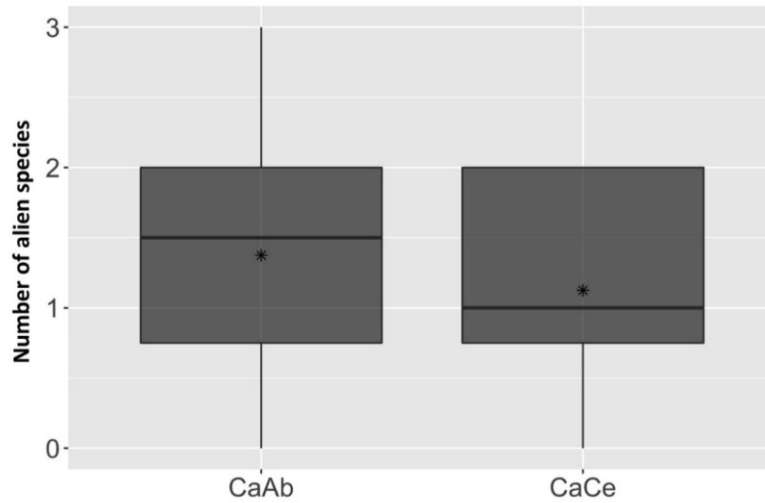
Figure 32. Variation of the number of alien species in neglected chestnut stands (CaAb) and regularly coppiced chestnut stands (CaCe) (n=16) (asterisk shows mean values).
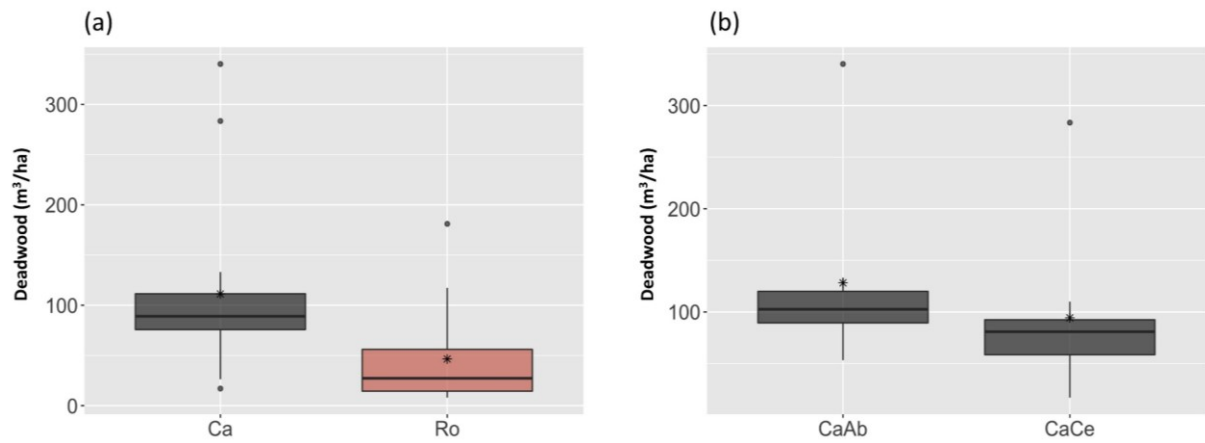

Figure 33. Comparison of total volume of deadwood (asterisk shows mean values). (a) Variation of total volume of deadwood in chestnut (Ca) and black locust stands (Ro); (b) variation of total volume of deadwood in neglected chestnut stands (CaAb) and in regularly coppiced chestnut stands (CaCe).

3.2. Urban land patterns and black locust effects in three cities

In this chapter we present results from the third part of the thesis with the aim of observing the potential effect of urban matrix properties and black locust canopy dominance on understory composition in three European cities: Berlin, Padova and Roma. We surveyed a total of 218 understory vascular species in Berlin, 83 in Padova and 91 in Roma. Among these three cities, we only recorded a significant difference of α-diversity (species richness) between native and black locust stands in Berlin; native stands in Berlin host a higher number of species than black locust stands. Instead, no differences of α-diversity were recorded in Padova and Roma between the two stand types (Figure 34).

We observed variation of pairwise β-diversity (Bray-Curtis dissimilarity) among plots from three different combinations of sites according to stand type (Figure 35). We thus considered the following groupings: *natnat*, combinations between native stands; *robrob*, combinations between black locust stands and *natrob*, combinations between different types of stand. This approach aims at verifying whether β-dissimilarities differ significantly among native stands, black locust stands or between different woodlands. In other words, to verify whether plant composition varies more, therefore if composition is more heterogeneous within one of the two woodland types or comparing the whole set of plots within each city. We tested differences of β-dissimilarity between groupings by Tukey contrasts; difference is close to statistical significance only comparing *natnat* against *natrob* combinations in Berlin (p=0.0782). This highlights that on average β-dissimilarities are higher when comparing native stands with black locust stands rather than a comparison between native stands.

We applied a binomial general linear model to test which environmental variables influence species richness in all plots. City and stand type were taken as random factor in the model. Considering all cities together black locust dominance significantly influences the number of species, while basal area has a weak effect on species richness. Black locust dominance effect is most likely driven by the difference among black locust stands and native stands in Berlin.
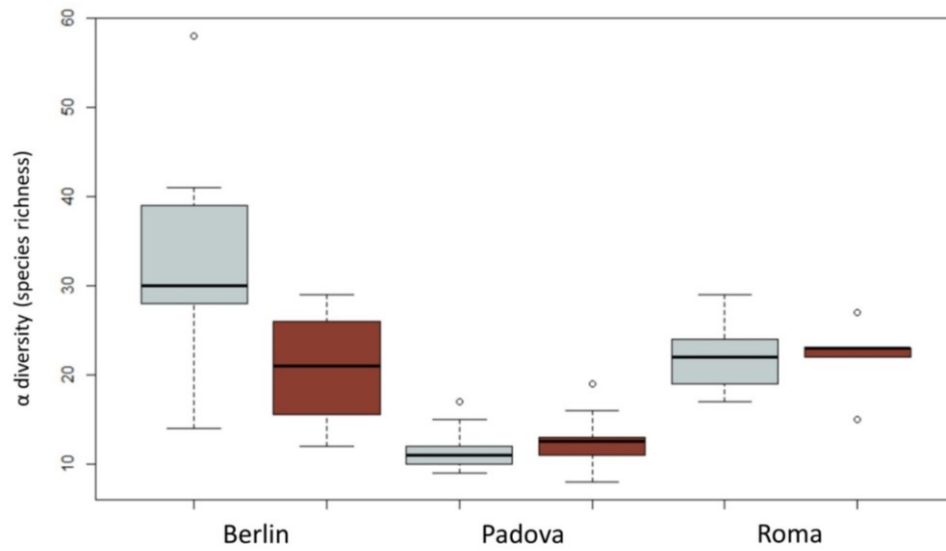
Figure 34. α-diversity observed in native and black locust stands in the three cities. Grey boxplots represent values for native plots while red boxplots values for black locust plots. Mean number of species: Berlin native: 32.17±2.1; Berlin black locust: 20.57±1.2; Padova native: 11.50±0.8; Padova black locust: 12.6±1; Roma native: 22.2±2.1; Roma black locust: 22±1.9.
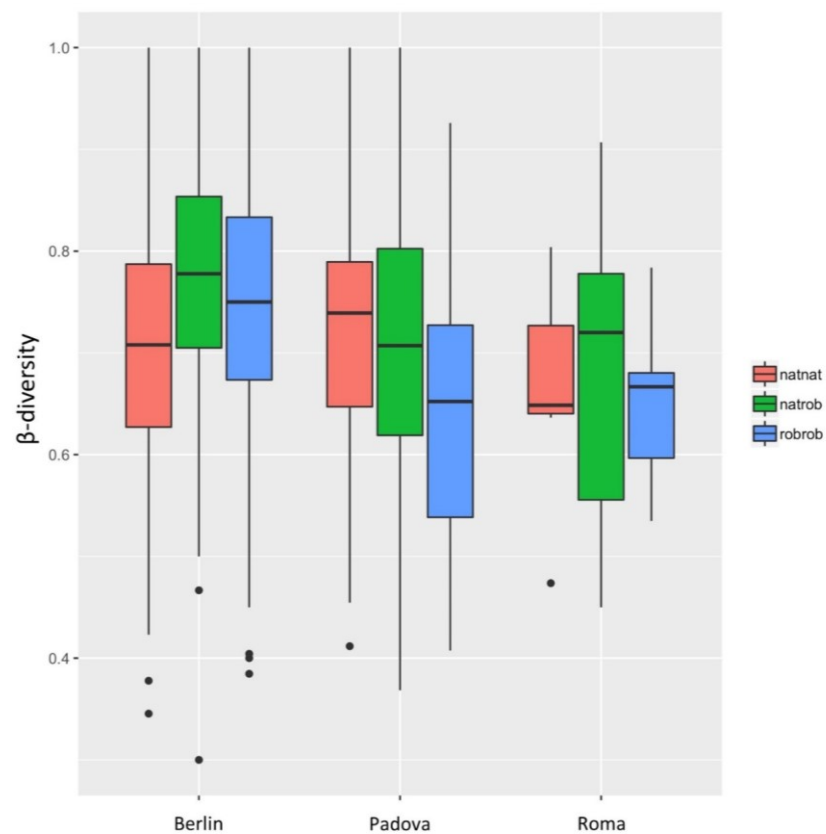

Figure 35. Boxplot of β pairwise dissimilarities in the three cities observed by combinations of stand type. natnat: native vs. native; natrob: native vs. black locust; robrob: black locust vs. black locust.

Comparison of understory species composition (Figure 36) shows that each city has a distinct species composition. Results are similar considering both Bray-Curtis dissimilarity (a) and Sørensen dissimilarity (b).

Figure 36. Comparison of understory vascular species composition. (a) Comparison of understory vascular species composition of native (black dots) and black locust stands (red dots) applying Bray-Curtis dissimilarity (species abundances) (a) and Sørensen dissimilarity (species presence-absence) (b). Ellipses display ordination of plots by cities (representing 95% CI around the centroid). (c) Ordination of most common understory species.

To observe patterns of compositional change, we used zeta distance decay (ζ-decay), one of the main ζ-diversity applications. ζ-decay measures variation in the number of species shared with increasing distance between sites. ζ-order provides the number of sites taken in the ζ-diversity calculation. The higher the order, the higher is the contribution of generalists to compositional change and, on the contrary, the one from specialists is more reduced. Regression slope is statistically significant (GLM; $p < 0.0001$) in black locust stands in both Berlin (Figure 37) and Padova (Figure 38) for all ζ-orders indicating a variation of ζ-diversity with increasing distance between sites. Instead, this is not true for native stands, which show more stable values of ζ-diversity for all ζ-orders in Berlin and Padova. In Roma (Figure 36) we found a wide dispersion of ζ-diversity values over distance for both native and black locust stands thus not allowing any clear pattern of compositional turnover to be described.

Indeed, black locust stands show a steeper ζ-decay over distance than native stands in both Berlin and Padova. In Padova the rate of ζ-decay is more pronounced in black locust stands. Species composition of black locust stands in the urban matrix of Padova seems more dynamic with variation of an environmental gradient. In both stand types of Roma, we

recorded wide changes of ζ-diversity across different combinations of stands, however these changes do not show correlation with distance between sites.
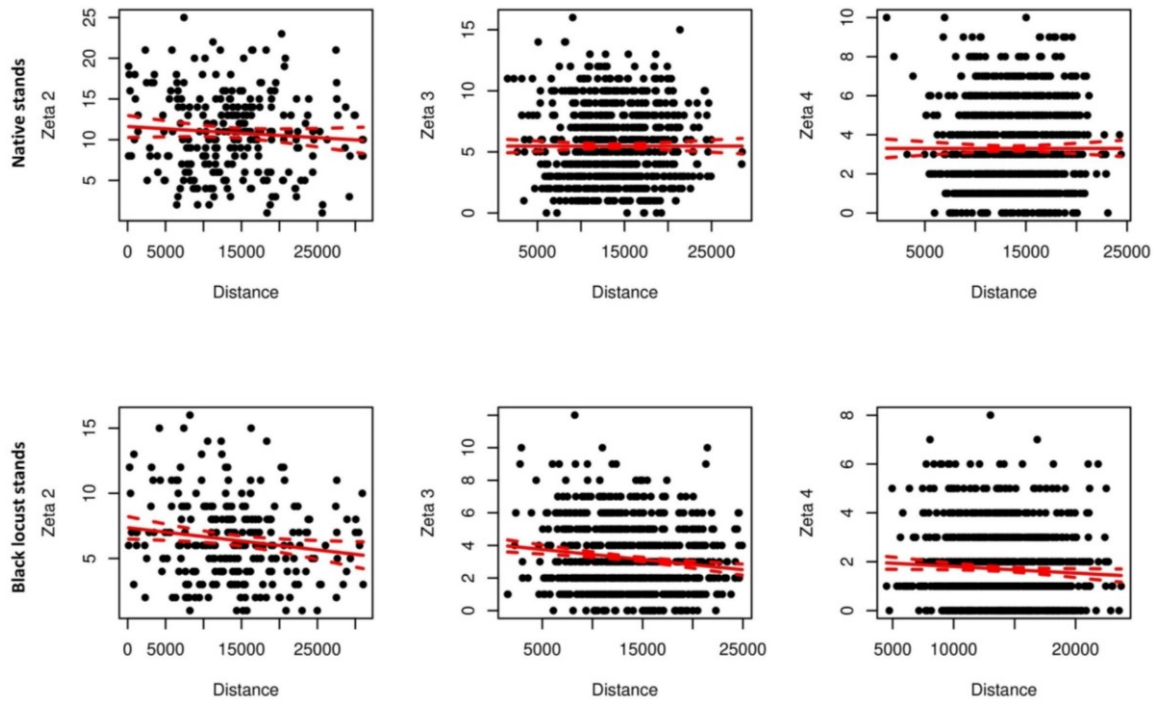

Figure 37. ζ-diversity decay over distance for ζ-order ζ2-4 in native and black locust stands of Berlin. ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen ζ-order. Dashed lines represent 95% confidence intervals.
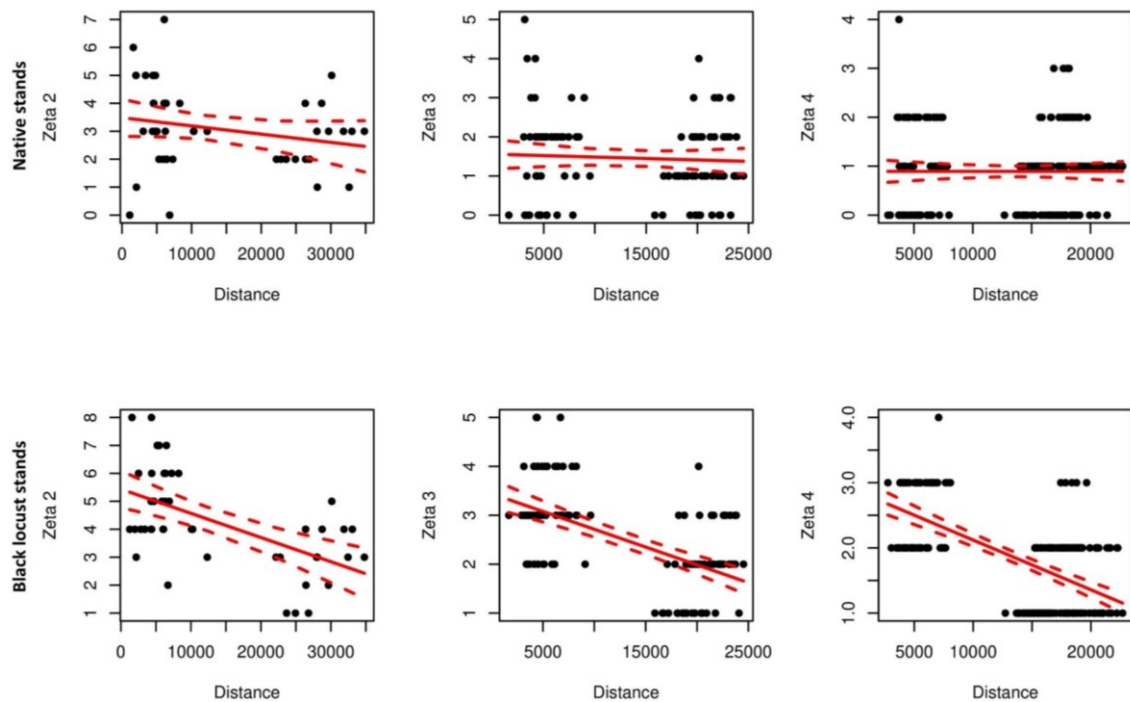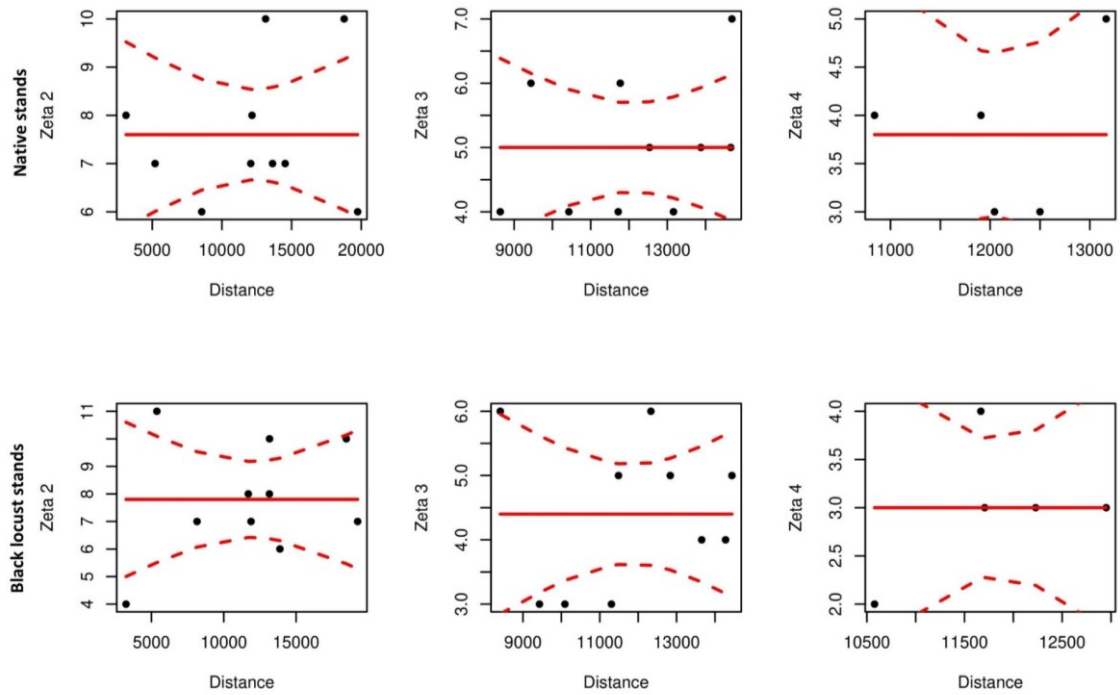

Figure 38. ζ-diversity decay over distance for ζ-order ζ2-4 in native and black locust stands of Padova. ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen ζ-order. Dashed lines represent 95% confidence intervals.

Figure 39. ζ-diversity decay over distance for ζ-order ζ2-4 in native and black locust stands of Roma. ζ-decay shows variation in number of shared species with increasing distance between sites considered by the chosen ζ-order. Dashed lines represent 95% confidence intervals.

Together with ζ-decay, another main application of ζ-diversity is ζ-diversity decline, showing the variation of ζ-diversity with increasing ζ-orders (Figure 37).

ζ_1 corresponds to mean α-diversity of plots so the average number of species per plot; it is evident that Berlin, Padova and Roma hosts a different number of species in native stands. This difference affects the rate of decline moving from ζ_1 to ζ_2.
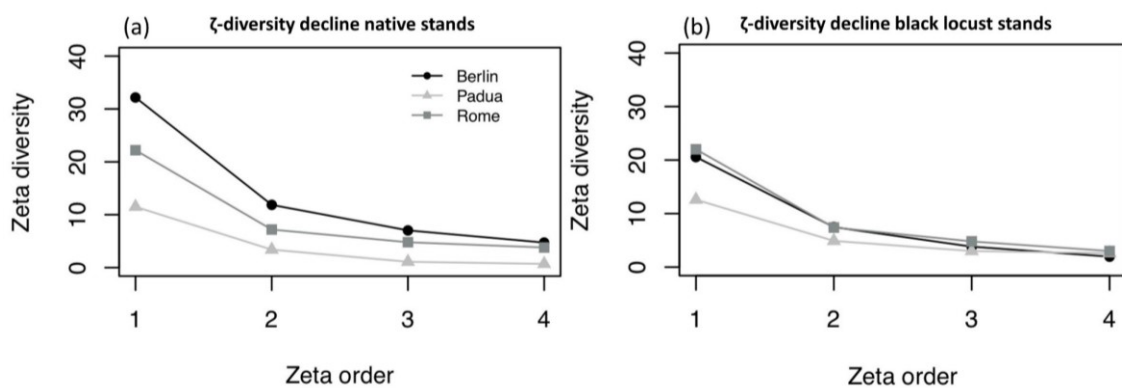

Figure 40. ζ-diversity decline in native and black locust stands for the three studied cities. ζ-decline shows how ζ-diversity changes with the ζ-order. ζ1 corresponds to α-diversity of plots showing average number of species.

Observing the contribution of environmental variables in explaining ζ-diversity (next figures), we see that in native stands of Berlin major drivers of species turnover are urbanity, stand mean height and road area.

Urbanity is the most important variable in influencing ζ-diversity, especially for specialists, and its effect is more important with lower proportions of built-up area. Black locust stands in Berlin are still influenced by urbanity but stand mean height and road area reach higher values. The same variables in different stand types display different patterns of effects on compositional turnover.

In Padova, road area is the environmental variable with strongest influence for native stands. Road area still shows an effect on compositional turnover in black locust stands but with a lower incidence. Analysing influence of environmental variables, none of the variables taken into consideration showed an effect on species composition in Roma.
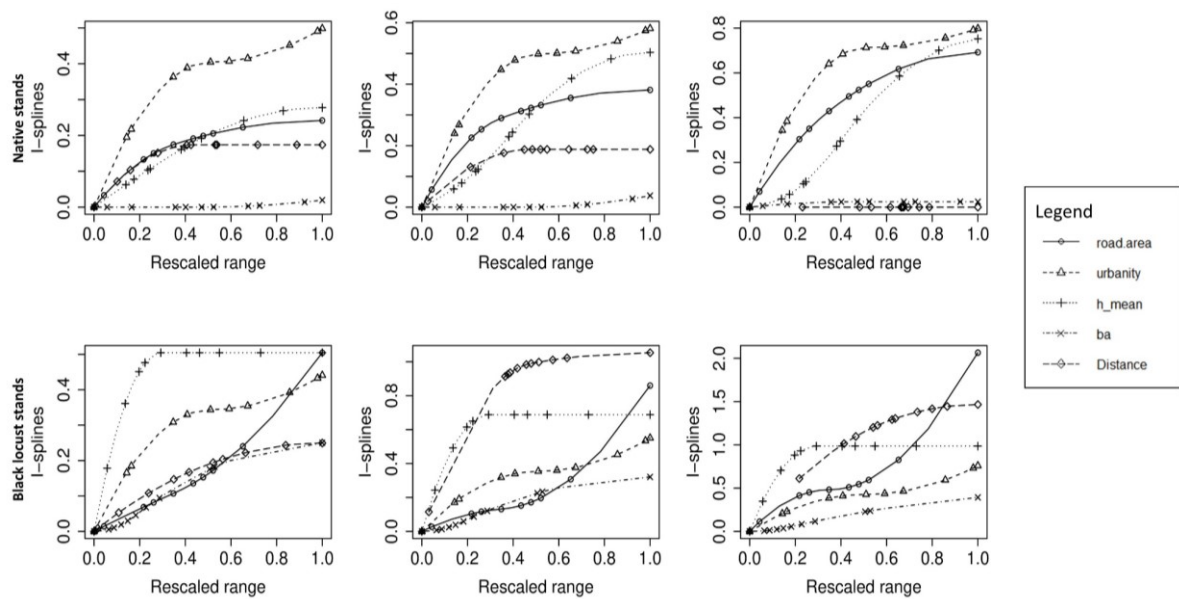

Figure 41. I-splines showing the contribution of environmental and stand structure variables to explaining ζ-diversity for ζ2,3,5 in paired plots of Berlin. All variables are rescaled between 0 and 1 for comparison and visualization.

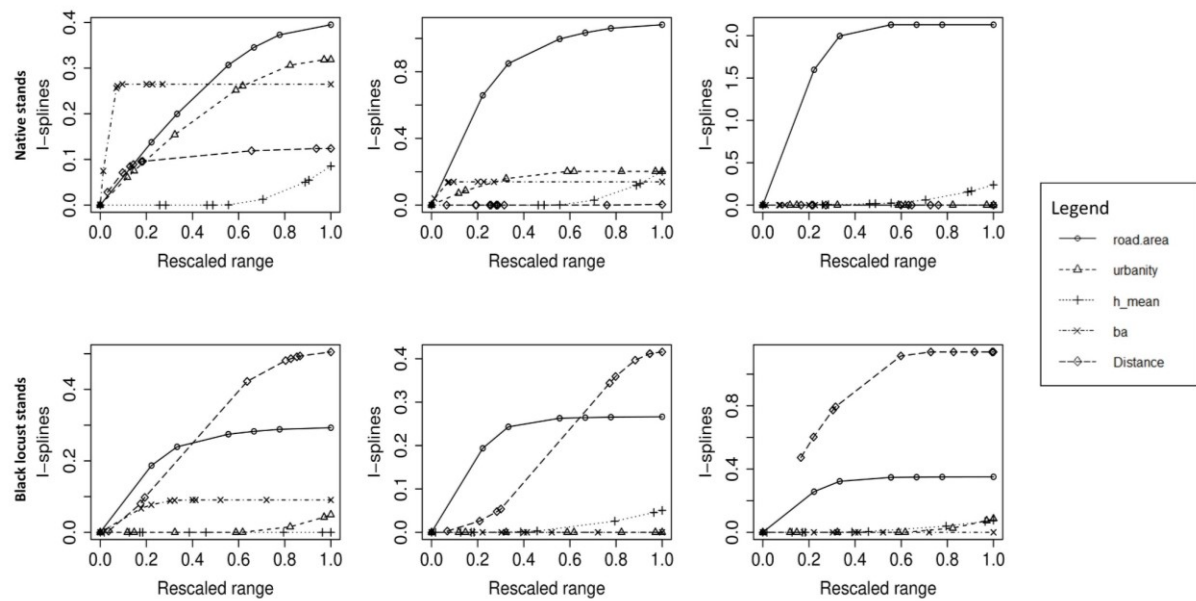**Figure 42. I-splines showing the contribution of environmental and stand structure variables to explaining ζ-diversity for ζ2,3,5 in paired plots of Padova. All variables are rescaled between 0 and 1 for comparison and visualization.**

3.3. Socio-economic and black locust distribution patterns in Italy

To meet the objective of the fourth part of the thesis, we investigated black locust distribution and socio-economic patterns at Italian national scale.

A first result of this part of the work is represented by detailed national distribution of black locust that has been retrieved from collection of the most recent regional forest type maps (Figure 43). Black locust woodlands and plantations occur mainly in northern part of the country. As clearly displayed on the map, Lombardia, Piemonte, Veneto and Emilia-Romagna host the largest extension of this forest type. In fact, black locust forest is mostly found in northern and central Italy and particularly in the north-west.
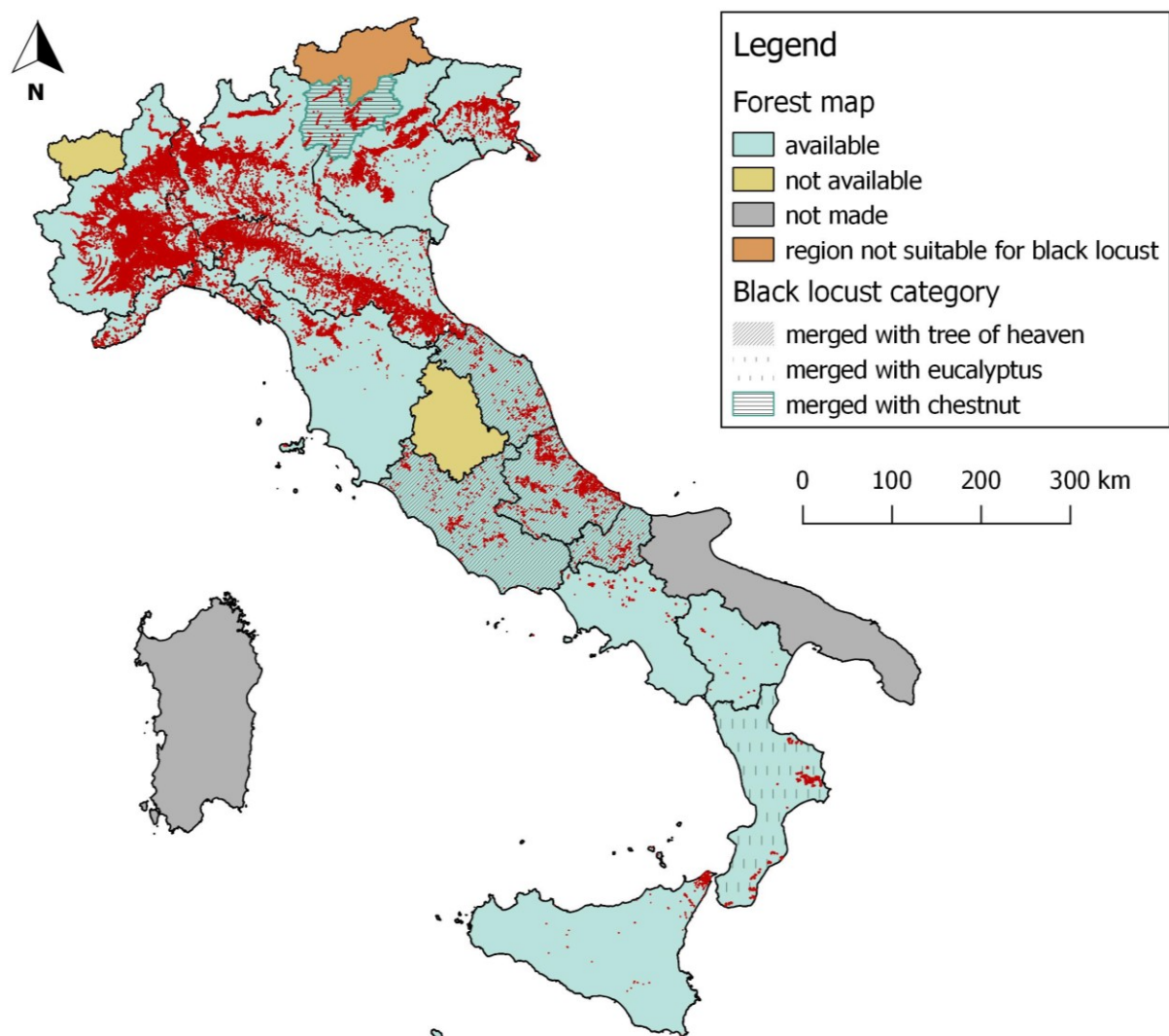

Figure 43. Map showing polygons (red coloured) of black locust woodlands. This information was extracted from the forest type maps of Italian regions. Edited in GIS software (QGIS Development Team 2018). For the following regions forest type maps were not available: Puglia, Sardegna, Umbria, Valle d'Aosta. Due to forest type categorization system applied we did not consider the following regions for data analysis: Calabria and Trentino-Alto Adige.

We found that in 307 municipalities black locust spread over at least 1 km^2 compared to 1930s (t_1). Moreover, in 11 Italian provinces there are municipalities in which the spread of black locust has increased on more than 20% of the municipal territory, among which Asti with 39 municipalities, Varese with 18 and Alessandria with 13. In the table below, the 10 municipalities with highest frequencies of cells assigned to black locust spread are listed, 7 municipalities out of 10 are located in Piemonte region.

Table 5. Table showing the 10 municipalities with highest frequencies of 1x1 km grid cells assigned to black locust spread (both 'robinia afforestation' and 'robinia replacement').

Municipality	Region	Grid cells of black locust spread	Proportion of municipality area assigned to black locust spread (%)
Asti	Piemonte	22	14.7
Volpago del Montello	Veneto	16	37.2
Borgo d'Ale	Piemonte	11	27.5
San Damiano d'Asti	Piemonte	11	21.6
Gattinara	Piemonte	10	31.2
Montafia	Piemonte	10	62.5
Gavi	Piemonte	10	21.3
Pistoia	Toscana	10	4.2
Coreglia Antelminelli	Toscana	9	17
Roasio	Piemonte	8	28.5

We observed frequencies of black locust land change patterns from t_1 to t_2 at municipal level, thus 'robinia afforestation' and 'robinia replacement' by class of IRU (rurality/urbanity index) (Figure 44) and IRC (level of per capita income and consumption) (Figure 45). Indexes details are provided in § 2.2.3. We found that in rural municipalities (class 2 - IRU) 'robinia afforestation' was relatively more represented than 'robinia replacement'. Whereas, moving toward middle situations along a rurality-urbanity gradient 'robinia replacement' showed relatively more importance for class 4 (so weakly urban municipalities). In addition, with regards to municipalities classification based on income and consumption level, both 'robinia afforestation' and 'robinia replacement', mostly occurred in municipalities with income level from very high to middle-low (class 1 to 4 - IRC). This was not true for native forest expansion patterns that were also in relation to the poorest municipalities of the country (class 5 and 6).
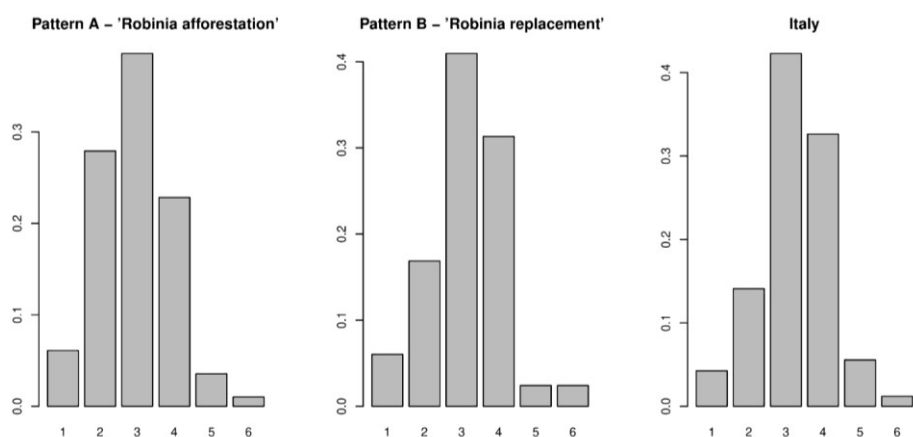
Figure 44. Proportions of municipalities in which 'robinia afforestation', 'robinia replacement' occurred and proportions of all Italian municipalities (Italy) by the six classes of the rurality/ urbanity index (IRU).

IRU classes: from 1 for extremely rural to 6 for extremely urban.
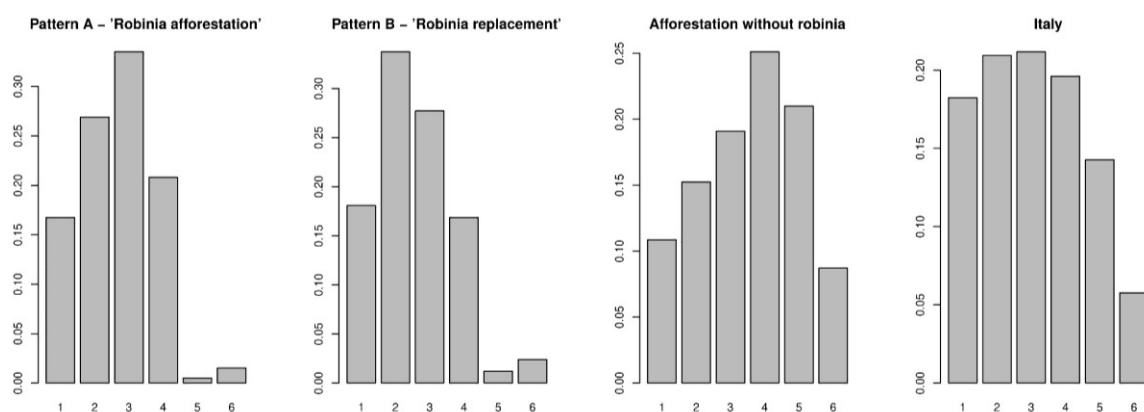

Figure 45. Proportions of municipalities in which 'robinia afforestation', 'robinia replacement' occurred and proportions of all Italian municipalities (Italy) by the six classes of income and consumption index (IRC).

IRC classes: from 1 for very high income to 6 for very low income.

4. Discussion

The aim of this thesis was to deepen the current knowledge on black locust effects on forest habitats and to assess the socio-economic drivers that may have fostered the spread of this invasive tree in Italy.

In this chapter, the extent to which the thesis responds to the gaps associated with existing research is presented, following the same sequence of topics that has been followed in the presentation of the results.

4.1. Native and black locust stands in three different landscapes

Prior work has documented the differential response of plant composition which may be provoked by black locust canopy depending on the characteristics of the surrounding land use patterns. Trentanovi et al. (2013), for example, reported that black locust stands found in a big city showed lower α-diversity and higher homogeneity of non-native species pool than in native stands. However, in a rural land use pattern, those differences are less marked (Sitzia et al. 2012a). This response is therefore mediated by complex mechanisms of propagule availability and ecological connectivity which is usually lower in urban than in rural areas. In fact, species composition and richness in forest ecosystems are highly sensitive to landscape configuration (Honnay et al. 2002). However, current landscape properties are not always able to explain variations on plant composition. Lindborg and Eriksson (2004) pointed out that variation of plant species could be more shaped by historical landscape connectivity than by present-day connectivity.

In addition, some landscape types are characterised by peculiar drivers of change, which represent influential factors, for example when a prevalent and periodic disturbance abiotic factor act along a fixed trajectory. This is the case of riparian ecosystems, severely threatened in Europe, which have been nevertheless rarely the subject of researches aimed at assessing the significance of hydro-geomorphological factors to black locust spread (Akatov et al. 2016).

The existing research has focused on single regions, and it did not assess a form of diversity which has been recently proposed as a unifying concept, the ζ-diversity (Hui and McGeoch 2014). ζ-diversity makes possible to distinguish the role of specialists and generalists. This is an advantage, because β-diversity measures are usually calculated with pair-wise combinations or mediated over several sites, producing lack of independency

between observations, which hinder interpretability of the results and scaling of the relationships.

Moreover, a second advantage of ζ-diversity application is the possibility to observe turnover patterns along a distance between sites gradient thus allowing to interpret environmental variables effects on compositional turnover.

This study has been focused on a comparison of multiple land use patterns whose main features, natural and human, could represent a fast and conventional way to characterise them in terms of the expected differences of plant diversity between alien vs. native canopies. In this part of the thesis, the extent to which the differences of plant richness and composition between black locust and native canopy stands is retained among three well characterised land use patterns (rural, riparian, urban) was tested. The same was done with ζ-diversity, with the number of sites and with the distance between the sites under comparison.

We found that were not significant differences of plant species α-diversity in the understory among the three landscapes. On the contrary, the β-diversity calculated either with abundance or presence-absence, is markedly distinguishable among the three landscapes. Black locust stands are therefore more similar to the native stands within a single landscape, then with other black locust stands belonging to other landscapes.

We found also that, according to the patterns of ζ-diversity distance decay, in the rural landscape, compositional turnover is similar between black locust and native stands. On the contrary, in the riverine and in the urban landscape these patterns are different, respectively for generalists and for both specialists and generalists, i.e. at several ζ-orders. Moreover, the relative effects of environmental variables changes between types of stands.

This extends previous findings, confirming that landscapes with lower connectivity show higher differences between black locust and native stands. In addition, the patterns noted in our study were confirmed in the riverine landscape but with some peculiarities. Riparian native stands showed a stable composition at higher ζ-diversity orders, that is concerning generalists whereas in black locust stands we recorded steep patterns of species turnover. More in details, the trend of ζ values changes from similar values at low distances between sites to lower values at the maximum distance recorded compared to native stands. As a result, in the riverine landscape, species composition heterogeneity of black locust stands is strongly scale dependent.

This thesis therefore indicates that composition of black locust stands is more subjected to fine-scale disturbances. Given that different landscape use patterns involve distinct disturbance regimes, we found landscape-specific patterns of species turnover.

Hence, we could read this result by interpreting the higher compositional turnover in urban and riverine landscapes as deriving from the fact that black locust is relative more linked to disturbed contexts. Thus, more pronounced variations of disturbances may result in a less stable understory composition in black locust stands.

In any case, steeper patterns of compositional turnover in urban and riverine black locust stands seems to be driven by environmental gradients resulting in both higher and lower compositional homogeneity relative to native stands depending on distance between sites. This interpretation seems confirmed by the results of ζ-diversity decay observed in the landscape with higher connectivity. In fact, in the rural landscape, both native and black locust stands showed similar patterns of compositional turnover.

Most notably, this is the first study to our knowledge to investigate the ζ-diversity patterns in contrasted landscapes and with a matched sampling design. Our results provide evidence that the attribution of black locust vs. native stands to a specific landscape pattern may provide insights on the intensity of compositional turnover over spatial scales and over generalist vs. specialist plant species.

However, some limitations are worth noting. Although our results were supported statistically, the sample was not balanced among land use patterns and we did not evaluate the functional composition, but only the species composition. Moreover, we did not separate alien and native understory species richness.

Future work should therefore include follow-up work designed to evaluate whether the observed patterns are retained with functional composition and with native vs. alien understory species.

4.1.1. River geomorphic variables and black locust stands

Previous studies have documented that changes in natural disturbance regime affect the establishment of alien species. This is evident, for example, in rivers, especially when the effects of natural and human disturbance are coupled. For example, in gravel-bed rivers human-related degradation is discriminated by morphological and stand variability and an intermediate-disturbed river shows higher heterogeneity of woody species. Some alien species are associated to specific types of river landforms, like black locust, which is associated to river floodplains and islands in the Piave River, and only to floodplain in the Tagliamento River (Sitzia et al. 2016d). In general, researchers agree that water flow, frequency and magnitude of floods, and water availability, are the three main factors influencing rivers invasibility (Hood and Naiman 2000).

However, we still lack a study that compares black locust vs. native stands within the same rivers and with a matched sampling design. Here, we tested whether geomorphological variables were related to black locust vs. native stands, using sample pairs matched for land use pattern conditions, i.e. along the same gravel-bed river, the Piave.

We found that there is no significant difference in the mean of several geomorphological variables. However, differences in distance from thalweg between the two stand types resulted close to statistical significance. In fact, unlike native stands, we never found black locust stands at smaller distance from thalweg than 141 meters. Distance from the thalweg is a measure of watercourse proximity. As such, it is an indicator of flood frequency and water availability, in turn related to natural disturbance regime.

These findings extend those of Sitzia et al. (2016d), confirming that an intermediate disturbed river, like the Piave, may express unusual patterns in plant biodiversity, which do not conform to the standard transversal profiles that describe how plant composition varies from the floodplain to the river active channel. In general, black locust is not related to areas subject to relatively higher frequency of flooding, if compared to willow and poplar stands.

This study therefore indicates that the maintenance of natural river dynamics is a positive action towards avoiding further spread of black locust in intermediate-disturbed rivers. Contrary, a modest alteration of river dynamics may result in lower disturbed sites apparently more prone to invasion based on our results.

In accordance with our results, Oriolo et al. (2010) report that in the riparian contexts of Friuli Venezia Giulia (north-eastern Italy), black locust is one of the most common alien species but that its invasiveness is mainly evident in river terraces less exposed to river dynamics.

We stress that black locust is associated both to floodplain and islands in this river, while we sampled only the floodplain. Moreover, we did not measure distance from the thalweg along a historical sequence. It could be that black locust developed in times when the distance from the thalweg was closer than in native stands, and today is a relict. Future research should therefore also include the islands and a photointerpretation of historical aerial images and maps. In general, contrary to our expectations and to other riverine contexts (Poblador et al. 2019), the presence of black locust in the floodplain of Piave River was reduced. Hence, it was difficult to find pairs of native and black locust stands, according to our sampling design (close pair members and distant pairs). This could hinder any future research aiming to improve our achievements.

4.1.2. Biochemical soil nitrogen cycle in black locust vs. native stands

Research has shown that plant invasions have the potential to alter the soil nitrifying community that can in turn impact the soil nitrogen cycling (Hawkes et al. 2005). However, as in the case of black locust, specific focus has been given to soil bacteria communities in many cases without focusing on ammonia-oxidizing groups (Medina-Villar et al. 2016, Lazzaro et al. 2018) and completely overlooking the role of AOA. Moreover, these studies on black locust usually investigate general differences in composition and diversity compared to native tree species and forests.

The analysis conducted on AOA gene abundance is extremely relevant to understand changes in the soil nitrogen cycle as they mediate the first step in the nitrification process (Stevanato et al. 2016). In fact, compared to ammonia-oxidizing bacteria, AOA is commonly predominant in significance and abundance over a wide range of soil types (Leininger et al. 2006) indicating its important role in explaining underlying soil processes.

The observed higher abundance of AOA in black locust compared to native stands indicates an important effect of the alien tree invasion. This indicates a possible higher nitrification under the canopy of black locust. This species has already been linked to enhanced nitrification in nitrogen-limited soils in both its native (Montagnini et al. 1986) and alien range (Rice et al. 2004). However, the effect of black locust on nitrogen enriched ecosystems seems less straightforward as contrasting results in nitrogen availability have been observed (Poblador et al. 2019). From this perspective, given the wide range of soil conditions over which black locust was surveyed in our study, a high abundance of AOA is occurring regardless of whether soils are nitrogen limited or rich. Nitrification processes are therefore likely to be enhanced compared to the different native forest types. Nitrogen budgets after invasions can be altered due to the relationship between the presence of black locust and a higher biomass of AOA in the soil microbial community. Furthermore, a homogenization of nitrogen availability at the landscape scale (Poblador et al. 2019) could be a consequence of higher AOA.

This study enabled, for the first time, black locust to be linked with higher AOA gene abundance; hence, offering further microbiological explanation of the nitrification rates already reported in the literature. However, the lack of a deeper analysis considering the effect of landscape and other environmental variables is a main limitation of the study. Future analysis should investigate whether this effect is influenced by different landscapes (rural,

riverine and urban) and additional study efforts should aim to understand the overall contribution of AOA within the microbial community.

4.1.3. Chestnut vs. black locust woodlands in a rural area

In the rural landscape of the Euganean Hills, chestnut woodlands have a significant presence in the area. Even at national level, the coverage of these woodlands is not negligible. Indeed, short rotation coppice stands of chestnut cover 593,243 ha in the whole Italian territory (Tabacchi et al. 2007). Regularly coppiced chestnut stands are managed to be maintained as monospecific and even-aged populations in which the presence of other tree species may be limited. In fact, this kind of management is oriented towards a financial return of the owner. In recent decades, however, the market for chestnut wood has seen a collapse in demand, exacerbated by the pathologies that have affected this species. As a result, 24% of Italian chestnut coppices are abandoned, with important consequences for the structure and functionality of chestnut woodlands (Manetti et al. 2017). The silvicultural treatment of coppice forests is important to ensure the provision of forest functions and services. In neglected coppices, for example, there is an increase of susceptibility to pathogens resulting in the spread of chestnut blight (*Cryphonectria parasitica*) (Quatrini et al. 2017). Neglected coppice stands are more prone to fire due to high fuel loading (Manetti et al. 2017), as resulted in the Euganean Hills. In addition, sustainably managed coppice stands preserve water regulation function and maintain a better soil water availability, thus counteracting hydrogeological instability (Garfì et al. 2006). Furthermore, management can affect plant biodiversity. High forest stands are home to more plant species than coppice, however, within coppice stands, management variations result in differences in floral species richness (Mattioli et al. 2016). Coppice management therefore strongly influences the plant community of chestnut woodlands. This is influenced mainly by the extent of the cut, frequency and magnitude of the disturbance (Mattioli et al. 2016). Sound conservation forest management is therefore able to maintain high plant diversity while total abandonment can lead to a certain plant community homogenization, consequently a reduction of the variability in composition.

We found that heterogeneous management, involving the management of some woodlands and the abandonment of others, increases plant composition diversity within habitat type 9260 whereas this is not true for black locust woodlands. Scientific results such as those presented can provide effective management guidelines. In fact, the importance of maintaining a heterogeneous mosaic consisting of chestnut woodlands with different types of

management and treatment (Gondard et al. 2006) and the necessity to increase forest edges (Masutti and Battisti 2007) to ensure a certain diversity of species on a regional scale can be deduced from the results.

Moreover, considering the results and the aggressiveness of black locust, it is desirable to contain the expansion of black locust into sites of Community relevance for a sound conservation forest management. In Europe, many forest habitats in the continental biogeographical region are threatened by this invasive forest tree and habitat type "9260 *Castanea sativa* woodlands" is among them (Campagnaro et al. 2018a).

Conservation measures of Special Areas of Conservation (SACs) of Natura 2000 Network provide useful management guidelines in this regard. In the case of Veneto Region, for instance, conservation measures of SACs suggest a series of good practices including the conversion of neglected coppices, understory plantations with broad-leaved shade tolerant trees, but also the maintenance of buffer strips to protect habitats of Community interest from black locust colonization. Moreover, conservation measures suggest keeping black locust in the emergent canopy layer and let it age. In the case of coppice woodlands close to black locust, the maintenance of "no intervention" buffer strips is recommended.

When speaking of sound conservation management of forests, it is worthwhile pointing out the role of deadwood as one of the indicators of forest habitats conservation status (Cantarello and Newton 2008). Indeed, the role of decaying material in forest ecosystems is notoriously fundamental in determining nutrient availability and soil fertility. Deadwood plays a key role in the forest representing the substratum for the germination or development of many plant and animal organisms that populate the forest ecosystem, as well as a source of nutrition and shelter (Winter and Möller 2008). In this sense, among the Italian forests, chestnut woodlands contain the largest amount of deadwood with about 19 m^3 ha^{-1} in the north, 13.7 m^3 ha^{-1} in the centre and 9 m^3 ha^{-1} in the south of the country (data recorded for the category grouping chestnut and hornbeam woodlands) (Pignatti et al. 2009). In line with these values, we found that in Euganean Hills chestnut stands have a higher abundance of deadwood than black locust stands. Therefore, chestnut woodlands have a greater possibility to be home to species related to deadwood, thus highlighting the role of this forest type in the conservation of biodiversity. Deadwood and its different components are mentioned among the indicators of habitat quality suggested by ISPRA (Italian Superior Institute of Environmental Protection and Research) monitoring manuals for various species that are listed in the Habitat Directive annexes, such as *Cerambyx cerdo* (Stoch and Genovesi 2016). In addition, we found that total amount of deadwood is greater in the sites no longer

managed compared to those still coppiced and deadwood in chestnut coppices is relatively more than that observed in black locust stands. Positive implications seem to derive from this result; however, when preserving deadwood in chestnut woodlands forest planners must consider, in addition to the positive impact on biodiversity associated with it, all other implications arising therefrom. In the period from 2006 to 2011, indeed, forest fires in chestnut woodlands represented approximately 10 to 20% of the total number of forest fires in Italian forests (Barbati and Corona 2014). The accumulation of deadwood increases fire risk, which is already high in chestnut woodlands and well known in the Euganean Hills. In addition, the presence of deadwood, both standing and on the ground, has a negative impact on tourists' perception of the forest and may pose a danger to the safety of visitors in recreational and tourism-oriented forests (La Fauci and Mercurio 2008).

4.2. Urban land patterns and black locust effects in three cities

Urbanization is known to threaten biodiversity from direct loss of species and species habitats. Fostered by urban matrix disturbances, plant invasion is also taking part in the process of biodiversity impoverishment (McKinney 2006). Hence, urban ecosystems function is therefore transformed, and novel ecosystems are developed.

In urban woodlands, black locust dominance has been regarded as the main parameter for plant homogenization (Trentanovi et al. 2013). In addition, homogenization of native species has been linked to high proportions of built-up area, resulting in a possible reduction of species due to dispersal limitation in plots that are located in highly urbanized surroundings. However, in the complex matrix of cities, combinations of multiple factors can hinder the relationship between explanatory variables and plant richness (Rebele 1994).

Studies conducted in single cities are common, but synthesis among several cities are still lacking. Multiple contexts studies enable to compare different cities along latitudinal gradients to provide more robust insights into factors affecting plant composition in the growing urban environments.

In this research we tested the extent to which urban matrix properties can affect plant understory composition in native and black locust urban woodlands in three different European cities. We found that α-diversity shows significantly lower values in black locust stands only in Berlin, whereas this was not true for the other two cities (Padova and Roma). Different α-diversity analysed within all three cities samples was driven by black locust dominance and marginally by basal area which, as an index of stand density, is related to the

amount of light reaching the ground thus influencing the number of species that are able to grow in the understory.

Moreover, we did not record significant differences confronting average pairwise β-diversity among and between stand types. On the contrary, β-diversity calculated either with abundance or presence-absence, is markedly distinguishable among the three cities. Black locust stands are therefore more similar to the native stands within a single city than with other black locust stands in other cities. Hence, we found that understory composition of stands dominated by the invasive black locust tree can maintain some peculiarities of local floras. In other words, at the supranational scale and along the latitudinal gradient, the homogenizing effect of black locust dominance was not detectable.

In addition, we found that, according to patterns of ζ-diversity, compositional turnover was different between native and black locust stands in Berlin and Padova with city-specific peculiarities. The trends of ζ-values showed that in Berlin, native stands have more shared species between sites for all ζ-orders considered than black locust stands whereas this was not true for Padova and Roma. Furthermore, black locust stands of Berlin and Padova had a higher compositional turnover than native stands. The revealed patterns, detected thanks to the application of ζ-diversity, showed that, in black locust stands, understory composition changes are more pronounced by changes in scale. Contrary, in Roma no clear trends of ζ-values emerged from both stand types.

These results extended findings of the comparison among landscape types. Compositional turnover patterns are influenced by land use patterns and, in addition, this effect resulted more evident in black locust stands. Our interpretation is that lower connectivity matrices affect species composition and this effect can be modulated by plant invasions. However, we recorded contrasting results from different cities. Different result for Roma stands may be explained by the higher connectivity of its peri-urban matrix and lower magnitude of disturbances (Capotorti et al. 2013).

Hence, the results displayed that compositional turnover patterns can be differently influenced by environmental variables in different cities. Moreover, effect of environmental variables, i.e. of land urban patterns on plant biodiversity, differs depending on whether the stand is dominated by native or black locust tree.

This study provided an innovative and first application of ζ-diversity, observing patterns of compositional turnover on matched black locust and native urban woodlands. It indicates that, according to urban land use patterns, black locust understory composition can show higher species turnover which could be interpreted as a more pronounced response to

urban disturbances than native stands. In other words, since black locust woodlands are most often indicators of disturbed contexts, understory flora is strongly conditioned by the type of disturbance that occurred in a specific plot.

Our results provide evidence that the application of a matched sampling design on multiple cities can provide insights into the relative contribution of environmental variables thus disentangling the effect of urban matrix properties on compositional change accounting for both generalist and specialist plant species.

However, some limitations are inherent in the method. We applied not balanced samples and we only considered three cities. Moreover, we did not observe patterns of composition on native and alien plants separately. Future research should therefore try to widen the approach to other cities considering a number of areas as similar as possible.

4.3. Socio-economic and black locust distribution patterns in Italy

The importance of socio-economic factors on plant invasion is already known from the literature (Essl et al. 2011, Gallardo 2014). Indeed, income growth and globalization are recognized as important drivers of biological invasions, clearly associated with richness of alien floras in many parts of the world (Hulme 2009). Moreover, the role of anthropogenic factors has been found to be more relevant than climatic variables in explaining plant invasion risk.

Despite the number of studies describing these connections, very few have tried to understand the contribution of socio-economic drivers in the expansion of black locust (Radtke et al. 2013, Crosti et al. 2016). These contributions mainly provided insights into forest management implications on alien invasion in specific contexts, not always allowing generalizations to wider scales and general trends.

In this study we tested whether the spread of invasive black locust was relatively more associated to specific socio-economic contexts that may have fostered its expansion in the Italian territory. Using forest distribution maps from two different periods we were able to ascertain the current distribution of black locust and relative expansion to open spaces ('robinia afforestation') or previously uninvaded forests ('robinia replacement').

As a first result, we reconstructed a detailed distribution of black locust in Italy. We found that black locust is mainly present in northern Italy, particularly in the north-west. This is proved also by the fact that 7 out of the 10 municipalities with higher number of cells assigned to black locust spread (both 'robinia afforestation' and 'robinia replacement') are located in Piemonte. Moreover, we found that 'robinia afforestation' was relatively more

represented than 'robinia replacement' in high rurality contexts. Instead, moving toward middle situations along a rurality-urbanity gradient 'robinia replacement' showed relatively more importance. In addition, both 'robinia afforestation' and 'robinia replacement', were not associated to poorest municipalities. Contrary, forest expansion by native species occurred also in the poorest municipalities of the country.

These findings hence confirm that anthropogenic factors have significantly influenced the distribution of this invasive tree on a national scale. A relationship already claimed by Maráková et al. (2016).

We noted that black locust expansion on both forested and open space habitats may have been fostered by human activities related to high- and medium-income contexts in the country.

The origins of black locust plantations in Italian territories in which this tree is most common today are often due to initial economic interests of wood and honey production, and activities associated to local development like railway banks stabilisation. The subsequent historical circumstances have favoured escape and expansion from plantations: degradation of local forests due to over-exploitation of resources in time of war, instead, the abandonment of agricultural activities created many areas prone to invasion (IPLA 1996). It is therefore likely that the rarity of black locust woodlands in the poorest areas of the country is due to the lack of first introduction for economic reasons. In addition, direct intervention on post-war degraded forests with black locust plantations that took place in other regions of northern Italy as reported in Del Favero et al. (1998) could still be read as a process in line with the above mentioned interpretation of our research results.

In addition, the Community agricultural and forestry policies may have played a role in the expansion of black locust in Italy. These policies could result in fostering afforestation initiatives including also black locust plantations and in the land conversion that might promote black locust expansion. For instance, Council regulation (EEC) No 2080/92 and Council regulation (EEC) No 2078/92 have promoted respectively afforestation schemes with fast-growing species in agricultural lands and the conversion of arable land into extensive grassland through Community funding.

Most notably, this is one of the first studies to our knowledge to investigate the link of black locust invasion to socio-economic contexts on such a broad scale and applying complex and effective socio-economic indices.

5. Concluding remarks

The main achievements of each part of the thesis from original data, as presented in the previous sections, are summarized in this chapter.

First, we tested differences of plant richness and composition between invaded and non-invaded stands by black locust among rural, riparian and urban landscapes. Interestingly, we found that black locust stands are more similar to native stands within a single landscape then with other black locust stands belonging to other landscapes. Therefore, through a new scale of observation, we found that the homogenizing effects of a black locust canopy are less evident than expected.

In addition, by applying the innovative concept of ζ-diversity, we investigated the ζ-diversity patterns in contrasted landscape types and with a matched sampling design. We concluded that differences of plant compositional patterns between black locust and native canopy stands are landscape dependent. Hence, in more disturbed landscapes with lower connectivity, differences of plant compositional patterns between native and black locust stands are more evident, resulting in steeper compositional spatial patterns in invaded sites. Our results provide evidence that the attribution of black locust vs. native stands to a specific landscape pattern provide insights into the expected intensity of compositional turnover over spatial scales and over generalist vs. specialist plant species.

Aiming at deepening the role of urban matrix properties on plant composition patterns, we compared three European cities. We found that plant composition is markedly distinguishable among the three cities, showing that black locust stands are more similar to the native stands within a single city than with other black locust stands in other cities. In other words, as detected comparing three landscape types, at a supranational scale and along a latitudinal gradient, the homogenizing effect of black locust dominance was not detectable.

Analyzing plant compositional turnover through ζ-diversity, different patterns between native and black locust stands emerged in Berlin and Padova, with city-specific peculiarities. In black locust stands of Berlin and Padova, understory composition changes are evident varying the spatial scale of observation: we interpreted these results as mainly driven by land use patterns.

In general, spatial patterns of species composition are affected by lower connectivity matrices and this effect can be modulated by plant invasions such as in the case of black locust. This means that the compositional turnover in black locust stands might be higher

than in native stands, as more affected by fine-scale disturbances, but contrasts do exist between different urban mosaics and latitudes.

Another part of the thesis was focused on matched sites of black locust and chestnut woodlands in the rural landscape of Euganean hills. We found that higher diversity of plant composition in chestnut woodlands is achieved by heterogeneous silvicultural systems, combining intensive, extensive, and interruption of management. Chestnut woodlands have higher amount of deadwood than black locust stands, particularly when no longer coppiced. Hence, the maintenance of a heterogeneous land mosaic of chestnut woodlands managed with different intensity is one of the keys to promote a richer understory composition. Considering the aggressiveness of black locust on many habitats of Community relevance and the consequence of its spread, we stress the importance of containing further expansion of black locust into high conservation value habitats.

Another essential element to provide further insights into the consequences of black locust invasion has been represented by soil analysis. Although almost overlooked, we stressed the relevance of ammonia-oxidizing archaea in explaining changes in the soil nitrogen cycle. This thesis enabled, for the first time, black locust stands to be linked to a higher presence of ammonia-oxidizing archaea microorganisms, providing clues for the higher nitrification rates already observed in black locust stands and indicating its high potentiality to alter the biochemical equilibrium of soil with consequent changes of forest ecosystem.

With the aim to investigate whether black locust is related to specific and distinguishable geomorphological conditions, in an intermediate disturbed river, we found that black locust is not related to areas subject to relatively higher flooding frequency, if compared to native willow and poplar stands. This therefore indicates that the maintenance of natural river dynamics is a positive action not only towards enhancing conservation status of riverine habitats, but also to avoid further spread of black locust in intermediate-disturbed rivers. Contrary, a modest alteration of river dynamics may result in lower disturbed sites which could be more prone to invasion by black locust.

Finally, given the poor number of studies trying to explain the connections between black locust spread and economic drivers, we reconstructed a detailed distribution of black locust in Italy and we tested whether the spread of this invasive species was relatively more associated to specific socio-economic contexts. We noted that, contrary to forest expansion by native species, black locust expansion on both forested and open space habitats did not happen in the poorest municipalities of Italy, providing nation scale evidence of how the

characteristics of this administrative unit might explain black locust distribution. Hence, our results confirmed that anthropogenic factors have significantly influenced the distribution of black locust on the national scale of Italy. In addition, we pointed out that some Community agricultural policies might have favoured the expansion of black locust, especially in the Italian districts most eligible for European financing.

Future work should deal with functional composition, distinguishing native and alien understory species, applying a balanced sampling design, and deepening the connections between black locust canopy and soil microbiological community. Sampling units from rivers at various levels of disturbance should be also included, adopting a historical approach in assessing geomorphological features. In doing this, researchers should make more use of molecular biology techniques, how we did here. Regarding management, we advocate a landscape view which supports the diversification of silvicultural treatment frequency and intensity both in black locust and adjacent forest types. Further work should apply the concept presented in this thesis to regulatory, planning instruments, and technical guidelines. Black locust is an invasive, but iconic species, not only, we suggest it is a possible label for rich Italian regions.

Pursuing such a vast and articulated aim, we have perceived the difficulty of the task, we are certain that the efforts made, and the innovative methods used, have allowed us to increase the knowledge of this species that is as problematic as fascinating. We hope that this thesis, which faced the challenge to join ecologists, hydrologists and economists, could represent an inspiration for similar multidisciplinary studies.

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