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The invasive potential of non-native trees introduced in temperate forests of Western Europe: towards a forest invasion syndrome?

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The invasive potential of non-native trees introduced in temperate forests of Western Europe: towards a forest invasion syndrome?

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Abstract

Many exotic tree species have been introduced worldwide for ornamental or wood production purposes, and some have become invasive in the introduction area, representing a substantial threat to native biodiversity. Forestry is a major pathway of introduction of non-native trees (NNT), and this trend is increasing in Europe due to current afforestation programs promoting the use of NNTs to diversify and improve resilience of planted forests in the face of climate change. However, species selected for wood production are often fast-growing species massively planted on suitable sites, with silvicultural practices enhancing survival rates. These factors increase the probability of these species escaping from cultivation and invading natural habitats. We can therefore assume that an invasion debt exists in Europe regarding NNTs, concealed by the long lag-phase needed by trees to go through the introduction-invasion continuum.

Time since introduction and propagule pressure have been proven to increase the probability of naturalization of an NNT. Functional traits and dispersal capacities play a role in later stages of the invasion process. The process of invasion by NNTs has been extensively studied in the Southern hemisphere and with pioneer, light-demanding species such as pines, eucalyptus or acacias, yet there is a lack of understanding of the invasion process of NNTs in dense temperate forests. If these ecosystems have long been considered more resistant to invasions, there is an increasing number of records of shade-tolerant species invading native natural or semi-natural forests. It is therefore crucial to unveil the mechanisms underlying forest invasion by NNTs and to identify potentially invasive species before they become widely planted.

I used a network of eight old forest arboreta in Southern Belgium as sentinel sites to detect potentially invasive tree species. A systematic monitoring of the sites allowed me to gather data on the density, distance and size structure of the natural regeneration of NNTs. Abiotic characteristics of the habitat were also measured. Several NNTs displayed an abundant natural regeneration in the arboreta, which was further enhanced by planting intensity. Some of these species were already known to be invasive, such as *Quercus rubra*, *Prunus serotina* and *Robinia pseudoacacia*. Maple species were also found in dense regeneration patches, especially *Acer rufinerve*, which is already listed as invasive in Belgium. Most importantly, almost 20% of the frequently planted conifers displayed important regeneration and dispersal potential, and tolerated a wide range of environmental conditions, including shaded understorey, which could lead to the invasion of mature forests. *Tsuga heterophylla* was particularly prolific, and created dense, impenetrable stands. These maple and conifer species could be part of the invasion debt threatening European forests.

To further investigate the dispersal potential of exotic conifers, the realized dispersal of *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata* was quantified from isolated forest trials. The monitoring of recruitment curves of three of these conifer species

confirmed the high invasive potential of *Tsuga heterophylla* and *Abies grandis* if planted in favorable sites, especially under coniferous cover. However, *Thuja plicata* encountered more dispersal and regeneration limitations.

A strategy of fast resource acquisition through high relative growth rate (RGR) and specific leaf area (SLA) has been highlighted in numerous studies comparing native to invasive species, or non-invasive to invasive species. However, this hypothesis has almost always been tested on light-demanding species. The relationship between seedlings developmental traits and invasiveness was tested for the two groups of emerging invasive trees identified in the old arboreta, *i.e. Acer* and conifer species. To allow a finer analysis, invasiveness was quantified on continuous gradient instead of the usual non-invasive/invasive dichotomy. Global invasiveness was calculated based on proxies extracted from the GBIF Database (number of regions and countries invaded) and the Global Compendium of Weeds (number of citations and risk score). Local invasiveness combined values of regeneration densities and dispersal distances measured in the eight forest arboreta. For maples, invasiveness was positively correlated to growth rates in biomass and height, SLA and number of leaves. For conifers, more invasive species displayed faster height increment, presumably in a strategy of fast light acquisition. A strategy of fast resource acquisition is therefore a key component of the invasion process, even in shaded forest ecosystems.

The results of this PhD indicate that temperate forests are not immune to invasion by non-native trees, and that several tree species might still be in a lag-phase preceding invasion. Combining the results from the monitoring of forest arboreta and the growth experiments, a “forest invasion syndrome” emerges, combining shade-tolerance, high growth rate enhancing competitiveness in canopy gaps and long-distance dispersal ability. High planting intensity and enhanced habitat invasibility through frequent disturbance or silvicultural practices (*e.g.* abundant coniferous cover) may amplify this syndrome. This is consistent with recent studies indicating invasive tree species in forest adopt a “sit-and-wait” strategy, combining shade tolerance and high response to light after disturbances allowing them to outcompete native trees. Non-native trees, especially those alien to continental Europe, should not be promoted in afforestation program without a thorough risk assessment. Old forest trials and arboreta can act as sentinel sites and provide useful information for a wiser species selection and smarter management practices of temperate forests.

Résumé

De nombreuses espèces d’arbres exotiques ont été introduites dans le monde pour l’ornement ou la production de bois, et certaines sont devenues invasives dans l’aire d’introduction, représentant une menace pour la biodiversité. La silviculture est une voie d’entrée majeure d’arbres exotiques (NNT), et cette tendance se renforce en Europe au vu des programmes de plantation actuels visant à diversifier les forêts pour augmenter leur résilience face au changement climatique. Cependant, les espèces sélectionnées présentent généralement des hauts taux de croissance et sont massivement plantées sur des sites favorables, avec des pratiques sylvicoles qui augmentent les probabilités de survie. Ces facteurs augmentent les risques que ces espèces envahissent les habitats naturels adjacents. Nous pouvons présumer qu’une dette d’invasion existe en Europe en ce qui concerne les NNTs, dissimulée par le long temps de latence entre l’introduction d’espèces d’arbres exotiques et le moment où ils deviennent potentiellement invasifs.

Le temps depuis la première introduction ainsi que la pression de propagule augmentent la probabilité de naturalisation d’un arbre non indigène. Les traits fonctionnels et les capacités de dispersion jouent un rôle dans les stades ultérieurs du processus d'invasion. Celui-ci a été largement étudié dans l'hémisphère sud avec des espèces pionnières héliophiles telles que les pins, les eucalyptus ou les acacias. Cependant, on comprend encore mal le processus d'invasion des NNTs dans les forêts tempérées. Bien que ces écosystèmes aient longtemps été considérés comme plus résistants aux invasions, on observe de plus en plus d’espèces sciaphiles envahissant des forêts naturelles ou semi-naturelles. Il est donc crucial de comprendre les mécanismes sous-jacents à l'invasion forestière par les NNTs et d'identifier les espèces potentiellement invasives avant qu'elles ne soient largement utilisées dans les programmes sylvicoles.

J'ai utilisé un réseau de huit anciens arboreta forestiers dans le sud de la Belgique comme sites sentinelles pour détecter les espèces d'arbres présentant un potentiel invasif. Un échantillonnage systématique des sites m'a permis de recueillir des données sur la densité, la distance et la structure de taille de la régénération naturelle des NNTs. Les caractéristiques abiotiques de l'habitat ont également été mesurées. Plusieurs NNTs présentaient une régénération abondante dans les arboreta, renforcée par l'intensité de plantation. Certaines de ces espèces étaient déjà connues pour être invasives, comme *Quercus rubra*, *Prunus serotina* et *Robinia pseudoacacia*. Certains érables présentaient également de denses tapis de régénération, en particulier *Acer rufinerve*, déjà répertorié comme envahissant en Belgique. Plus important encore, près de 20% des conifères fréquemment plantés présentaient une régénération et une capacité de dispersion importantes, tout en tolérant un large éventail de conditions environnementales, y compris l’ombrage, ce qui pourrait conduire à l'invasion de forêts matures. *Tsuga heterophylla* était particulièrement prolifique et formait des peuplements denses et impénétrables. Ces espèces d'érables et de conifères pourraient faire partie de la dette d'invasion menaçant les forêts européennes.

Pour étudier plus en détail le potentiel de dispersion des conifères exotiques, la dispersion réalisée de Tsuga heterophylla, Abies grandis et Thuja plicata a été quantifiée à partir d'essais forestiers isolés. La caractérisation des courbes de recrutement de ces trois espèces de conifères a confirmé le fort potentiel invasif de Tsuga heterophylla et d'Abies grandis dans des sites favorables, notamment sous couvert résineux. Cependant, Thuja plicata rencontrait davantage de limitations en termes de dispersion et d’établissement.

Une stratégie d'acquisition rapide de ressources grâce à un taux de croissance élevé (RGR) et à une importante surface foliaire spécifique (SLA) a été mise en évidence dans de nombreuses études comparant des espèces indigènes à des espèces invasives, ou des espèces exotiques non invasives à des exotiques espèces invasives. Cependant, cette hypothèse a presque toujours été testée sur des espèces pionnières et héliophiles. Nous avons testé la relation entre traits fonctionnels de développement des plantules et invasivité pour les deux groupes d’espèces fréquemment rencontrées dans la régénération naturelle des arboreta, les érables et les conifères. Pour permettre une analyse plus fine, l'invasivité a été quantifiée sur un gradient continu au lieu de la dichotomie habituelle non-invasif/invasif. L'invasivité globale a été calculée sur base de données extraites de GBIF (nombre de régions et de pays envahis) et du Global Compendium of Weeds (nombre de citations et risk score). L'invasivité locale combine les valeurs de densités de régénération et de distances de dispersion mesurées dans les huit arboreta forestiers. Pour les érables, l'invasivité était positivement corrélée aux taux de croissance en biomasse et en hauteur, à la SLA et au nombre de feuilles. Pour les conifères, les espèces les plus invasives affichaient une augmentation plus rapide de la hauteur, probablement dans une stratégie de meilleure captation de la lumière. Une stratégie d'acquisition rapide de ressources est donc un élément clé du processus d'invasion, même dans les écosystèmes forestiers denses.

Les résultats de cette thèse indiquent que les forêts tempérées ne sont pas à l'abri d’invasions par des arbres exotiques et que plusieurs espèces pourraient encore être dans une phase de latence précédant l'invasion. En combinant les données obtenues en arboreta forestiers et les expériences de croissance de plantules, un "syndrome d'invasion en milieu forestier" émerge, combinant la tolérance à l'ombre, un taux de croissance élevé favorisant la compétitivité dans les trouées et une capacité de dispersion à longue distance. Une intensité de plantation élevée et une vulnérabilité accrue de l'habitat à cause de perturbations fréquentes ou de certaines pratiques sylvicoles (par exemple, un couvert principalement résineux) peuvent amplifier ce syndrome. Ces résultats sont en phase avec de récentes études indiquant que les arbres exotiques envahissants en forêt adopteraient une stratégie « sit-and-wait », combinant une bonne tolérance à l’ombre à une réponse rapide en cas de mise en lumière, leur permettant d’être plus compétitifs que les arbres natifs. Les arbres non indigènes, en particulier ceux d'origine non européenne, ne devraient pas figurer dans les programmes de reboisement sans une évaluation rigoureuse des risques. Les vieux essais forestiers et arboreta peuvent servir de sites sentinelles et fournir de précieuses informations pour une sélection plus avisée d’espèces de production et une gestion plus judicieuse des écosystèmes forestiers tempérés.

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List of acronyms

FER: Frontier Expansion Rate

GBIF: Global Biodiversity Information Facility

GCW: Global Compendium of Weeds

IAS: Invasive Alien Species

IUCN: International Union for Conservation of Nature

LDD: Long-Distance Dispersal

LMA: Leaf Mass per Area

NNT: Non-Native Tree

RD: Regeneration Density

RGR: Relative Growth Rate

RHGR: Relative Height Growth Rate

RLPR: Relative Leaf Production Rate

RNPR: Relative Needle Production Rate

SM: Seed Mass

SLA: Specific Leaf Area

SRGR: Shoot Relative Growth Rate

SSD: Stem Specific Density

WER: Wave Expansion Rate

WPLCP: Whole-Plant Light Compensation point

WRD: Weighted Regeneration Density

List of publications

Fanal A, Mahy G, Fayolle A, Monty A (2021) Arboreta reveal the invasive potential of several conifer species in the temperate forests of western Europe. NeoBiota 64: 23-42 64: 23–42.

Fanal A, Mahy G, Monty A (2022) Can we foresee future maple invasions? A comparative study of performance-related traits and invasiveness of eight Acer species. Plant Ecology 223: 1181–1192.

Fanal A., Porté A., Mahy G., Monty A. (2023) Fast height growth is key to non-native conifers invasiveness in temperate forests. Submitted to Biological Invasion, major revision.

Fanal A., Mahy G., Monty A. Recruitment curves of three non-native conifers in temperate forests: implications for invasions. In prep.

1

General introduction

1. The basics of biological invasions

Over the centuries, humans have intentionally or unintentionally transported plants, animals, and fungi to new locations. Some of these non-native species were able to reproduce and spread into the natural habitats of the introduction area, sometimes inflicting great damages to the native biodiversity or to human activities. These species are called invasive species and are one of the five main drivers of species loss worldwide (IPBES 2019).

The cost of impacts and management of invasive species has increased exponentially over the years. Diagne et al. (2021) estimated that biological invasions in the world cost a minimum of 1.288 trillion US dollars between 1970 and 2017, mostly in damage costs (reduced crop yield, damages inflicted to infrastructures, reduction of ecosystem services values…). In Europe more specifically, a recent study estimated the total cost of invasive species around 116.6 billion € between 1960 and 2020 (Haubrock et al. 2021). However, not all types of damages are easily quantifiable, notably negative impacts on native biodiversity, human well-being or other regulating and cultural ecosystem services.

A difficulty often encountered by researchers and managers is the diversity of definitions existing for an invasive species. The International Union for Conservation of Nature (IUCN) defines invasive alien species (IAS) as "*animals, plants or other organisms that are introduced into places outside their natural range, negatively impacting native biodiversity, ecosystem services or human well-being*". The European Commission uses a similar definition: "*Invasive alien species (IAS) are animals and plants that are introduced accidentally or deliberately into a natural environment where they are not normally found, with serious negative consequences for their new environment*" (European Commission 2023). These two widely used definitions include the notion of "impact" on natural habitats or human activities and well-being. However, this impact is sometimes difficult to evaluate, especially in the early stages of invasions, and the interpretation can be subjective – what about species having both positive and negative impacts? For example, black locust (*Robinia pseudoacacia*), a tree originating from Northern America and invasive in Europe, is an economically important tree used for wood, biomass and honey production, in addition to being planted for erosion control or ornamental purposes. However, it is also a highly detrimental species in areas of great ecological value such as dry grasslands (Vítková et al. 2017). Non-native species can also have a negative impact on the introduced environment without being widespread. In their recent "EICAT" classification system for alien taxa, the IUCN states that "the requirement that an invasive alien taxon causes threat or harm is common in policy usage, but less so in scientific usage where "invasive" usually simply implies that the taxon has spread widely and rapidly from the point of establishment" (IUCN 2020) and refers to the definitions of Richardson et al. (2011). In their proposed unified framework for biological invasions, Blackburn et al. (2011) therefore excluded the potential economic or environmental impacts of invasive species. To be invasive, a non-native species must have self-sustaining populations in the wild, with “individuals dispersing, surviving and reproducing a significant distance from the original point of introduction” (Blackburn et al. 2011). Richardson et al. (2000) suggested the threshold of 100 m from introduced populations in less than 50 years to quantify the spread of invasive plants reproducing by seeds.

As illustrated in the unified framework of Blackburn et al. (2011), non-native species must cross several barriers to become invasive (Fig. 1). The first one is of course the geographical barrier, *i.e.* the species is, intentionally or not, introduced by humans out of its native range. The species is “introduced” or “casual” if it survives in its introduced area. If the species can reproduce and maintain a self-sustaining population without human intervention, the species becomes “naturalized”. It is considered “invasive” if it further spreads into natural habitats.

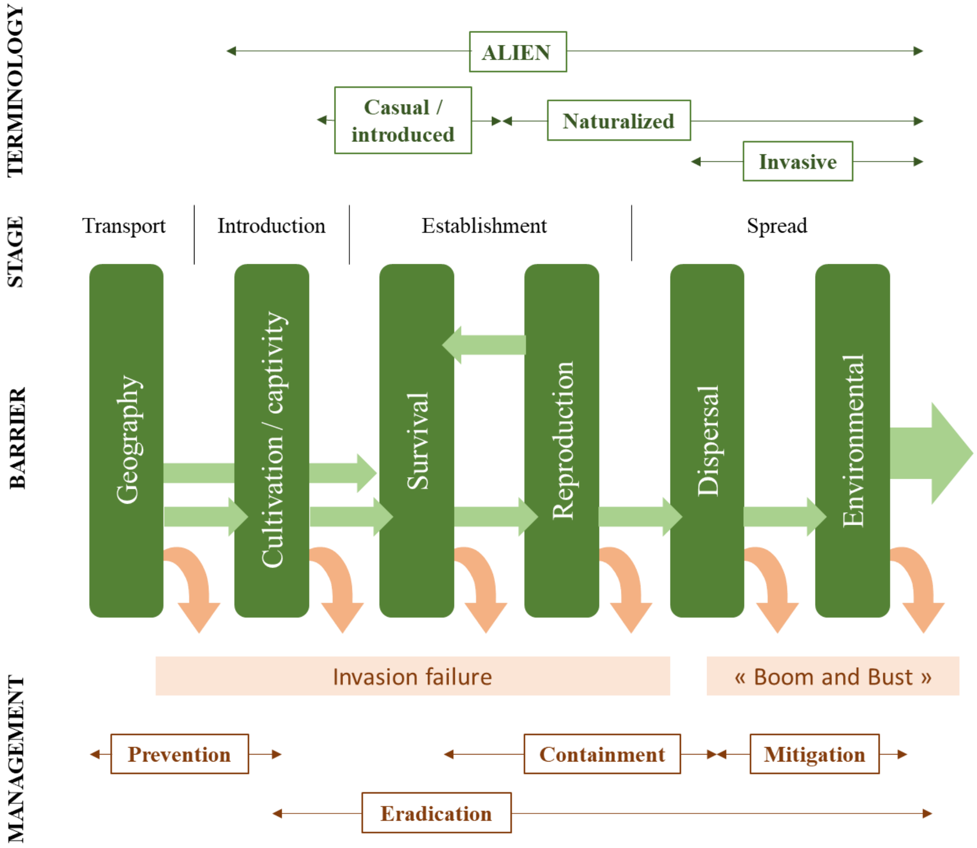


Figure 1-1: A unified framework for biological invasions, adapted from Blackburn et al. (2011).

As it will only be question of plants in this thesis, we will use the definitions proposed by Richardson et al. (2000) in Table 1 throughout the document. These definitions were constructed in order to harmonize the terminology used to describe the status of alien plants (Jarvis 1979, Williamson 1996, Crawley 1997). They are widely used in studies concerning invasive tree species (Foxcroft et al. 2004, Richardson and Rejmánek 2011, Wilson et al. 2014, Nygaard and Øyen 2017, Bindewald 2021), notably for they provide approximate spread rates thresholds for invasive plants. If these rates might appear subjective, they have the merit to provide a common basis for studies investigating invasive behaviors of plant species, and must be considered as an order of magnitude.

Table 1-1: Definitions of casual alien, naturalized and invasive plants recommended by Richardson et al. (2000).

Casual alien plants	Alien plants that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence.
Naturalized plants	Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, seminatural or human-made ecosystems.
Invasive plants	Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: > 100 m; < 50 years for taxa spreading by seeds and other propagules; > 6 m/3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area.

The exact number of invasive plant species in the world is not known, but it increases exponentially over time, even in areas that have been extensively studied. In a meta-analysis performed on existing scientific publications by Laginhas et al. (2023), it appears that the current literature only documents about 64% of the estimated global number of invasive plant species, with 3008 species reported so far. In Europe, several plants figure amongst the ten most cost-contributing genera: ragweeds (*Ambrosia artemisiifolia* and *Ambrosia polystachya*) and water-primroses (*Ludwigia grandiflora*, *Ludwigia peploides* and *Ludwigia repens*) (Haubrock et al. 2021).

The DAISIE project identified four tree species in the list of ”100 of the Most Invasive Alien Species in Europe”: *Ailanthus altissima*, *Prunus serotina*, *Robinia pseudoacacia* and *Acacia dealbata* (DAISIE 2008).More recently, a list of “worst alien species” in Europe based on 12 categories of ecological and economic impacts was proposed by Nentwig et al. (2018).It comprises 54 plants, including seven trees: *Robinia pseudoacacia*, *Acacia dealbata*, *Acacia longifolia*, *Elaeagnus angustifolia*, *Eucalyptus camaldulensis*, *Prunus serotina* and *Eucalyptus globulus*. Based on the definition of an invasive plant species by Richardson et al. (2000), Rejmánek and Richardson (2013) identified 71 invasive exotic trees in Europe, mainly from the *Pinaceae*, *Fabaceae* and *Rosaceae* families. van Wilgen and Richardson (2014) reported that over 430 non-native trees are invasive worldwide.

Trees often have the capacity of modifying the abiotic and biotic conditions of the ecosystem, acting as “ecosystem engineers”. Invasions by non-native trees (NNTs) can therefore deeply modify the ecosystem, notably in terms of biomass production, litter decomposition or carbon sequestration (Lamarque et al. 2011, Pyšek 2016). Woody species usually become problematic when they form dense stands in natural habitats. If invasions by light-demanding, pioneer tree species in disturbed habitats are well studied (*Robinia pseudoacacia*, *Buddleja davidii*, *Ailanthus altissima*, etc.), shade-tolerant species may also display an invasive behavior once introduced in closed forests (*Prunus serotina*, *Acer platanoides*, etc.) (Webb et al. 2000, Hernandez et al. 2016). The amount of literature produced on invasive or introduced NNT species has consistently increased over the last 20 years, yet there is still a lack of understanding of the ecology and evolution of invasive trees (Krumm and Vítková 2016).

Management actions against invasive NNTs are often taken too late, when the species is already widespread into natural habitats with prohibitive management costs (Rejmánek and Pitcairn 2002, van Wilgen and Richardson 2014). With early detection and rapid response programs, an eradication of the problematic species is feasible within the first stage of invasion (Fig. 1-2).

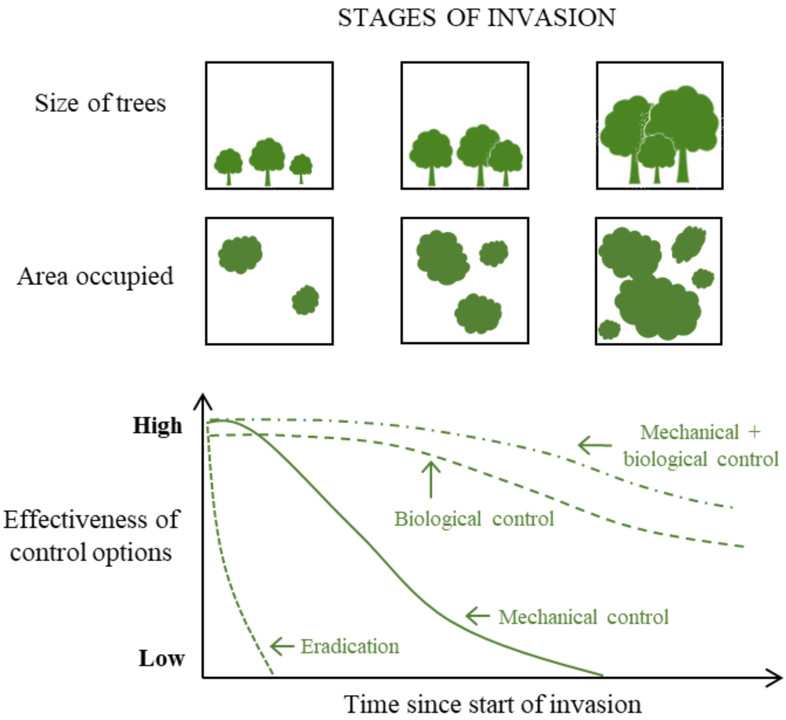


Fig. 1-2 The stages of invasion by trees, and the corresponding effectiveness of different types and combinations of control options. Eradication is only an option in the early phases of invasion, when tree populations are localized. The combination of biological and mechanical control techniques has proven to be the most effective control combination in some cases where it was tested on a large area. Adapted from van Wilgen and Richardson (2014).

2. How trees become invasive

A wide variety of factors influence the invasion success of NNTs at different phases of the invasion process. On the one hand, intrinsic characteristics of a species determine its **invasiveness**, *i.e.* the probability that it becomes a successful invader. On the other hand, characteristics of the receiving environment (disturbance regime, species richness, etc.) determine its inherent vulnerability to invasions, which is called the habitat **invasibility** (Richardson et al. 2010). Invasiveness and invasibility are strongly inter-dependent – no species is invasive everywhere, and no habitat is invasible by every exotic species (Heger 2016). Furthermore, socio-cultural factors strongly influence the invasion outcome all along the process. The most prominent example is the effect of the **propagule pressure**, which encompasses quantity, quality, composition and rate of supply of NNTs and is highly dependent on human interventions (rate of introductions and plantings, diversification of origins, total area planted…). The more a tree species is planted, the most likely it is to become naturalized and invasive (Lockwood et al. 2005, Křivánek et al. 2006, Pyšek 2016) (Fig. 1-3). Time since introduction and propagule pressure mainly play a role in the first phases of the invasion process (Blackburn et al. 2011).

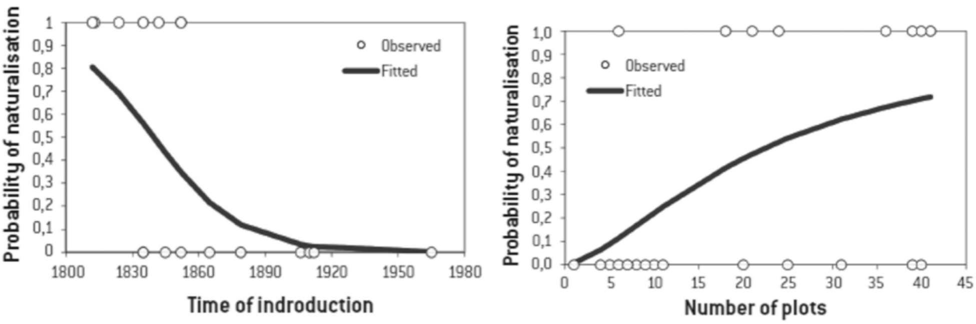


Figure 1-3: Probability of naturalization of an introduced tree species in Czech Republic based on the planting effort and time since first introduction. Figure from Pyšek (2016), taken from Křivánek et al. (2006).

2.1. Species invasiveness

Dispersal ability is a crucial element in the invasiveness of a plant species. Whether the propagules are dispersed by animals, wind or other vectors, the capacity to reach new suitable sites at far distance is key to invasiveness (Herron et al. 2007, Münzbergová et al. 2010). Plant species will encounter several dispersal and establishment limitations in their dispersal process (Amm et al. 2012, Gallien et al. 2015) (Figure 1-4). First, dispersal limitations, comprising limitations in seed production and dispersal distance. It has been demonstrated that conifer species producing a large number of seeds with short intervals between large seed crops are more prone to rapid spread in the environment (Richardson and Rejmánek 2004). Dispersal by animals also considerably increases the chances of long-distance dispersal (Clark et al. 2005, Sagnard et al. 2007).

After dispersal, the germination and recruitment of seedlings are critical in the abundance and spatial structure of natural regeneration and population dynamics (Amm et al. 2012). Realized dispersal is the combination of seed dispersal and establishment of seedlings (Bullock et al. 2006). The distribution of surviving seedlings can be impacted by various factors such as the spatial distribution of suitable micro-habitats, post-dispersal predation, pests and intra- or inter-specific competition (Amm et al. 2012). In this way, the Janzen-Connell hypothesis states that survival rates of seeds and seedlings located closer to parent trees are lower due to the presence of specialist natural enemies such as herbivores and pathogens (Janzen 1970, Connell 1971). This effect has been broadened by Howe and Smallwood (1982), and rephrased as the “escape hypothesis”, which suggests that effect of intra-specific competition and herbivory are stronger near the parent trees where the density of seeds is the highest, leading to survival rates increasing with distance from parent trees.

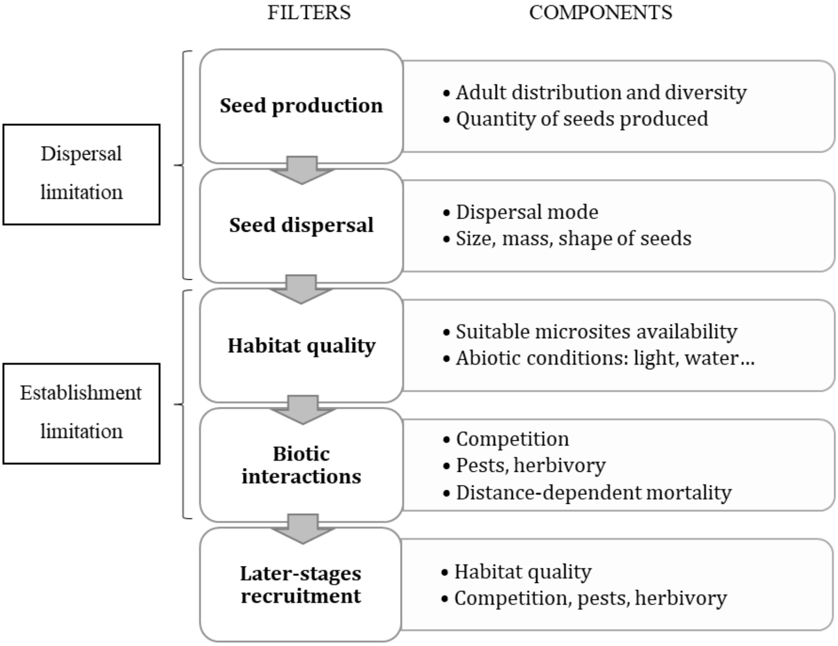


Figure 1-4: Dispersal and establishment limitations met by exotic tree species once introduced in a new area.

Species do not expand in an area on a continuous front, but rather according to combined effect of both local and long distance dispersal events (Pysek and Hulme 2005). The phenomenon is called “stratified dispersal” and is observed in the spread of many organisms. Isolated populations form ahead of the invasion front and then expand as isolated colonies that ultimately coalesce with each other and with the main invasion front (Liebhold et al. 2020). The existence of long-range dispersal helps elevate the rates of range expansion above levels that would occur through simple diffusive dispersal (Fig. 1-5).

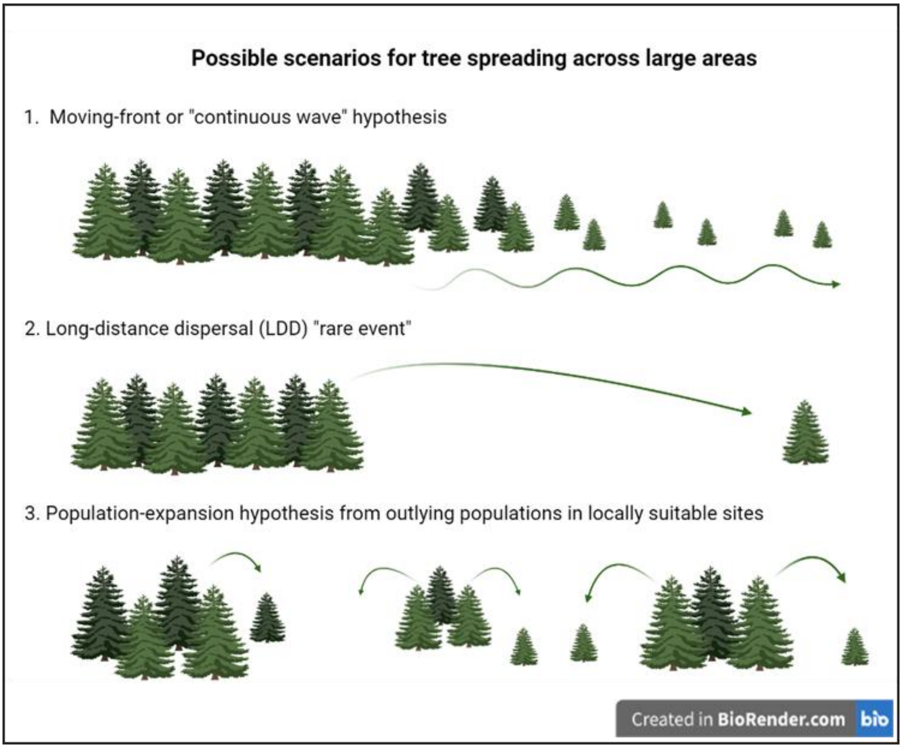


Figure 1-5: possible scenarios for the rapid spread of trees in an interglacial stage. Scenarios 2 and 3 are likely the most important, with populations expanding from outlying populations in locally favorable sites. The changing geographical distribution of trees along the glacial-interglacial cycles can inform modern ecologists about forests dynamics, including the dispersal process of NNTs over large areas. Adapted from Birks and Tinner (2016).

To complete the invasion process, invasive tree species possess a combination of functional traits that allow them to invade a given ecosystem and outcompete native species (Moravcová et al. 2015). A few simple traits allow to describe a fast-slow plant economics spectrum and help understand and explain ecological strategies of plants and functioning of ecosystems (Reich 2014). Using three key traits (SLA, height and seed mass), Divíšek et al. (2018) found that invasive plant species occupy the edge of the trait space shared with native species in a given habitat. Invasive NNTs tend to display an acquisitive strategy, with traits that allow rapid growth, especially in resource-rich environments (Leishman et al. 2007, Grotkopp et al. 2010, Gallagher et al. 2014, Mathakutha et al. 2019, Shouman et al. 2020). Using Grime's adaptative strategies (ruderals, competitors and stress tolerant plants – CSR), Guo et al. (2022) provided evidence that naturalized species with a C strategy had higher probability of becoming invasive than ruderal or stress tolerant species (Fig. 1-6). Studies have highlighted that invasive trees present a more important specific leaf area (SLA), relative growth rate (RGR), germination rate, height at maturity or height increment rate compared to non-invasive NNTs (van Kleunen et al. 2010a, Lamarque et al. 2011, Hodgins et al. 2018, Kutlvašr et al. 2019). This fast growth strategy has been demonstrated specifically for pine species (Richardson et al. 1994, Grotkopp et al. 2002), maples (Porté et al. 2011, Shouman et al. 2020) and acacias (Gallagher et al. 2011). In a meta-analysis from Lamarque et al. (2011), the relative growth rate appeared to be the most efficient predictor of trees invasiveness. In 2019, Dyderski and Jagodziński suggested that outcompeting native species may be achieved either by a general investment in foliage (biomass allocation to leaves and higher SLA), or by the tree's overall growth rate.

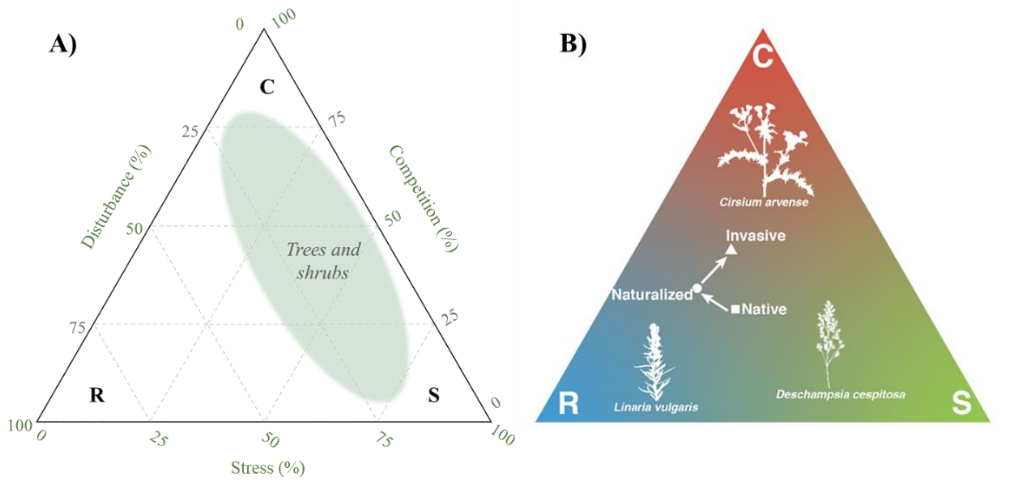


Figure 1-6: A) Grime's model describing the three CRS strategies (competitors C, ruderals R and stress tolerant S) and their equilibria according to the relative importance of disturbance, stress and competition. Woody plants tend to be found along the C – S axis (Grime 1977) B) Native, naturalized and invasive species within the CRS triangle based on a sampling of the flora of Czech Republic. Illustration from Kun Guo (Guo et al. 2022).

The methodology to choose for traits comparison depends on the specific question addressed. Many studies investigating the role of traits in the invasion process compared native and invasive species, in order to identify which traits enhance the competitivity of invasive species in a given area (Pyšek et al. 2009a, Godoy et al. 2011, Funk 2013, Wang et al. 2018, Dyderski and Jagodziński 2019a, Mazzolari et al. 2020, Kumar and Garkoti 2021). Fewer studies compared invasive vs. non-invasive exotic species to investigate which traits distinguish successful invaders from the other introduced non-native species. van Kleunen et al. (2010a) attested that values of growth traits of invasive species are not significantly different from those of native species being invasive elsewhere. This is why, in order to understand why some NNTs are inherently more prone to become invasive, it is important to consider the invasiveness of species at a global scale and to differentiate between invasive and less-invasive or naturalized non-invasive species (Divíšek et al. 2018). van Kleunen et al. (2010b) developed a framework of the diverse comparison types that can be used to test the relationship between traits and invasiveness (Fig. 1-7). Comparing alien trees with similar introduction history but differing in invasiveness is the most direct approach to test key traits determining the global potential of invasion success.

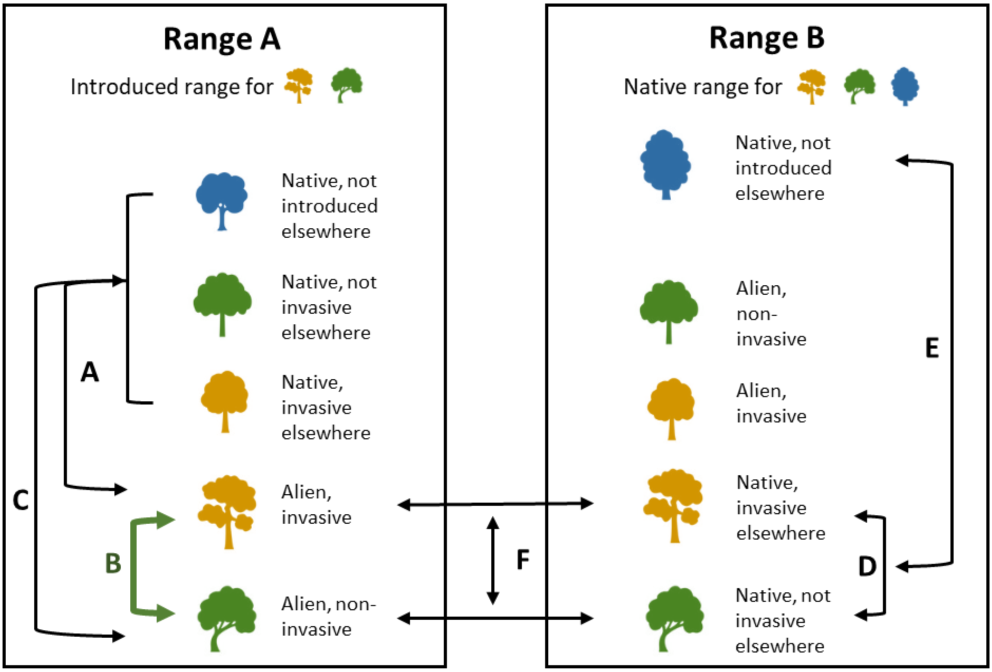


Figure 1-7: Schematic diagram of the major types of traits comparisons used to assess determinants of invasiveness, adapted from van Kleunen et al. (2010b). In the introduced range (range A), we can compare invasive alien to native **(A)** and non-invasive alien **(B)** species, and we can compare non-invasive alien to native species **(C)**. Native species can be subdivided for comparison between species not introduced elsewhere, not invasive elsewhere and invasive elsewhere in the world. In the native range (range B), we can compare native species that have become invasive elsewhere to native species not invasive elsewhere **(D)**, and native species introduced vs. not introduces elsewhere **(E)**. For species that have been introduced elsewhere, we can do intraspecific comparisons between the introduced and native ranges as well as intraspecific comparisons between the invasive and non-invasive species **(F)**.

2.2. Habitat invasibility

The habitat invasibility can be defined as "the properties of a community, habitat or ecosystem that determine its inherent vulnerability to invasion" (Lonsdale 1999). For Hui et al. (2016), the invasibility of an ecosystem is defined as the width of opportunity niche available for potential invasions. In wetlands for example, invasive species richness was higher in habitats with an intermediate disturbance level and a high nutrients level, and decreased in habitats with lower nutrients levels and light availability (Liccari et al. 2020). At a local scale, richness in native species as well as dispersal capacities of native species in the meta-population level increase resistance to biological invasions (Howeth 2017). The empty niche hypothesis also states that, in ecosystems where the community of native species does not have a complete use of resources, exotic species can exploit vacant niches and become invasive (Elton 1958, Hierro et al. 2005). This empty niche could be the result of various factors, such as a low species richness or the extinction of native species creating an ecological opportunity (MacArthur 1970).

Lonsdale (1999) discusses the challenges in comparing invasibility between regions, as there are many variables influencing exotic richness beyond invasibility, such as immigration rates and characteristics of the invading species. Using data from 184 sites worldwide, he found that nature reserves had fewer exotic species than sites outside reserves, and island sites had more exotic species than mainland sites. However, site area and habitat diversity also influenced the number of exotic species, and there was considerable variation within biomes. He concludes that many patterns observed in invasion ecology could be explained by differences in species and ecosystem properties or propagule pressure, making it difficult to draw conclusions about invasibility of ecosystems.

Forests (especially natural or semi-natural forests) have long been considered more resistant to biological invasions, because of the low disturbance regime, continuous cover of dominant tree species and low resource availability (Martin et al. 2009, Wagner et al. 2017). However, an increasing number of invasions by shade-tolerant trees are reported. In Belgium, the best known-case is *Prunus serotina* invading the shady understorey of deciduous forests. In a study conducted in Germany, Bindewald et al. (2021b) demonstrated that, in forest ecosystems with sufficient light reaching the undergrowth and native species with lesser competitivity, *Pseudotsuga menziesii* and *Quercus rubra* might spread and change the species composition in absence of management. The type of silviculture applied (large clearcuts *vs.* continuous cover and natural regeneration, monospecific *vs.* mixed-species stands) can also significantly impact the vulnerability of forest ecosystems to invasions (Jagodziński et al. 2015, Liebhold et al. 2017).

2.3. In a nutshell

In brief, a species escaping from cultivation is not primarily related to its biological and ecological traits, but rather to high levels of propagule pressure from large-scale plantations. However, biological traits do play a role in later stages of invasion and define the **invasive potential** of a species (Fig. 1-7). In the end, all factors and their interactions (specie straits × habitat characteristics × introduction events) as well as the potential negative impacts determine the **invasion risk** of a species in a particular area (see Box 1), and their importance depends on the stage of invasion (Pyšek et al. 2009b, 2020, Pyšek 2016, Divíšek et al. 2018).

Box 1: About the risk

What does an « invasion risk » mean? The definitions of risk vary amongst publications in the field of biological invasions. According to Fletcher et al. (2016), invasion risk is “a combination of the likelihood of the species being introduced (e.g. the presence of an introduction pathway) and the suitability of the environment in the new region (e.g. climate suitability for the species)”. However, an exotic species introduced in a favorable environment might only become naturalized without invading natural habitats. Allen and Bradley (2016) use the notion of risk in a multi-species perspective, using exotic species richness and invasion debt in a geographical area. The invasion risk of NNTs is sometimes assessed using spread and establishment success of young trees (Potter et al. 2022, Wyse et al. 2022).

Taking a step back from the field of invasion biology, we can see that discussions about the meaning of risk have been ongoing for decades in varying fields of research. For the consultant in health research ethics Lowrence William (1976), “risk is a measure of the probability and severity of adverse effects”. For Yacov Haimes (2009), professor of systems engineering, consequences for each risk scenario are “functions of the threat […], the vulnerability and resilience of the system, and the time of the event”. Information on threats encompass the probability of the threat, its specificity, and the probability of its consequences.

Therefore, based on these definitions of risks and the MAFIA framework illustrated in Fig. 1-8 (Pyšek et al. 2020), I will throughout this thesis discuss the invasion risk of NNT in forest ecosystems as being function of:

- The intrinsic invasive potential of an exotic species, *i.e.* its potential to establish and spread in natural habitats out of its native range;
- The climatic and environmental adequation in the receiving area;
- The invasibility of the receiving ecosystem (empty niches, low species richness, high disturbance regime…)
- Anthropogenic factors enhancing invasion success, such as introduction effort and forestry practices;
- Potential negative impacts of the NNT on the ecosystem functioning and ecosystem services.

Invasions of tree species are therefore highly context-dependent. Some characteristics may increase the potential of a species to become invasive in a specific ecosystem, but the same characteristics may lower its invasiveness in other situations (grassland *vs*. dense forest for example) (Heger 2016). In a Mediterranean ecosystem, increased biomass allocation in roots is an asset to survive summer droughts (Erskine-Ogden et al. 2016) while resistance to low temperatures is advantageous in temperate central European forests (Pyšek et al. 2009b). Giorgis et al. (2016) highlighted how patterns of habitat invasibility are not equal when considering the type of growth form:

in a mountainous ecosystem, both shrublands and outcrop soils were resistant to invasion by woody species, but not by grasses and forbs, while grasslands and native woodlands were resistant to alien grasses, but not to woody and forbs invasions.

Pyšek et al. (2020) proposed a unified Macroecological Framework for Invasive Aliens (MAFIA) explaining the invasion process with three classes of factors: alien species traits, location characteristics and introduction events. This framework highlights the context dependence and possible bias in the assessment of invasion factors. Figure 1-8 represents this framework, as well as the factors that will be more specifically addressed in this thesis.

Globalization and economic growth are recognized as drivers of biological invasions (Taylor and Irwin 2004, Hulme 2009, Diagne et al. 2021). However, the majority of the most problematic plant species in Europe today were introduced several decades ago (Essl et al. 2011b). Given the time lag between introduction and the phases of naturalization and invasion, many future invasive species have already been introduced but have not yet reached their full invasive potential (Rouget et al. 2016). For trees, this lag phase can be particularly long, and was estimated to last 170 years in average in a German study (Kowarik 1995). Due to the increase in plant species introductions during the second half of the 20th century, there is little doubt that an "invasion debt" exists today in Europe (Essl et al. 2011a).

As a result of this lag phase, the flora of a region may contain species that are not yet naturalized or invasive, but could become so in the future, especially if climate change alters their potential distribution area. In a study conducted in 2017 by Dullinger et al., it was found that the risk of naturalization of exotic species from botanical gardens would increase if the climate warms, as well as the risk of negative impacts from these species. In particular, the Atlantic coast from France to Germany is a hotspot for naturalization risk.

Furthermore, climate change represents a real challenge for foresters in the years to come. Indeed, it is expected that the distribution, composition, and functioning of forests will be impacted, especially since the migration capacity of trees is limited (Himpens et al. 2017). Among the expected effects of climate change that could impact woody species, we can mention an increase in temperature, longer heat waves, summer water deficits, or more frequent storms (Campioli et al. 2009, Heger 2016, Dullinger et al. 2017, Himpens et al. 2017).

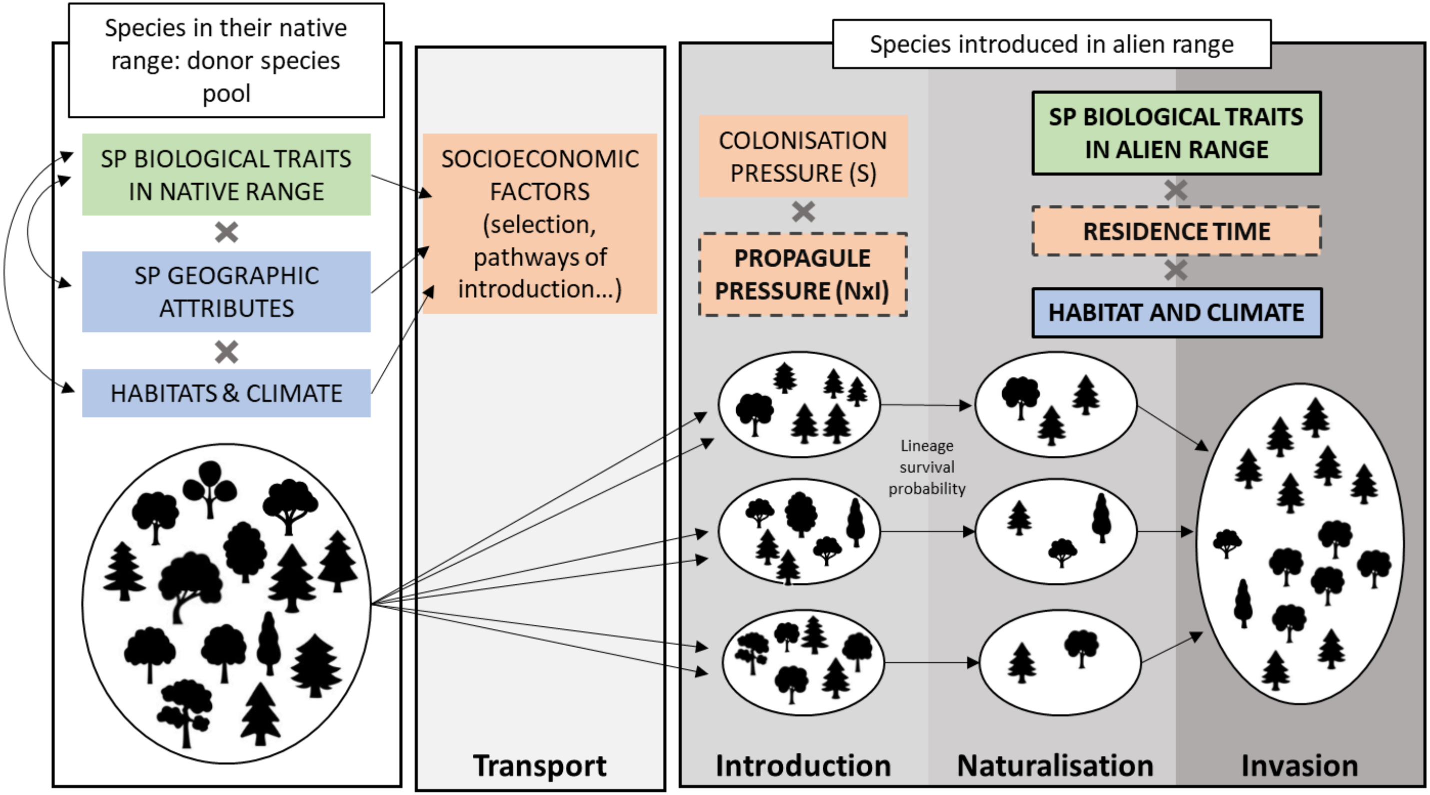


Figure 187: The Macroecological Framework for Invasive Aliens (MAFIA) proposed by Pysek et al. (2020). The colors represent the three classes of factors influencing the invasion success: event-related factors in orange, alien species traits in green and habitat characteristics in blue. **S** is the number of species introduced, **N** the number of individuals introduced per introduction event, and **I** the number of introduction events. In bold are the factors that will be investigated in the following chapters, dotted boxes are factors of which influence will be taken into account.

3. History of introduction of non-native trees in Europe and the role of silviculture

Introduction and assisted migration of exotic tree species for human needs dates back to the Mesolithic, primarily with species acting as food sources such as hazel or sweet chestnut (Nyssen et al. 2016). In the 16th and 17th century, a growing interest for species originating from the European colonies led to the introduction of exotic trees such as the black locust *(Robinia pseudoacacia)* or the white cedar *(Thuja occidentalis)* in botanical gardens and parks (Fig. 1-9). Major afforestation programs were set in the second half of the 18th century, as timber and fuel wood were needed for the industry. This reforestation of wastelands catalyzed the use of NNTs. In Belgium, it was mainly marked by the use of *Picea abies*, *Pinus nigra* and *Pinus sylvestris*, species that were naturally present in neighbor countries such as France and Germany. Later, large planting of non-European species such as *Pseudotsuga menziesii* and *Quercus rubra* started, even if they still represent a minority of the production tree species.

In 2019, at least 150 NNT species were grown in European forests and trials. In total, NNTs are found in an area of approximately 8.54 million ha, or 4% of the European forest area. The five most abundant species, *Robinia pseudoacacia, Eucalyptus globulus*, *Picea sitchensis*, *Pseudotsuga menziesii, and Pinus contorta,* make up for 77% of this area. Most of NNTs in Europe originate from North America (47%) and Asia (30%) (Brus et al. 2019). In Southern Belgium, 41.5 % of the forest area was planted with conifers in 2021, mainly *Picea abies*. *Pseudotsuga menziesii* is the non-European species with the largest planted area, representing 4.8 % of the productive forest (23 000 ha). *Larix* sp., *Pinus* sp. and *Quercus rubra* are also cultivated but in a very small proportion (< 5 %).

In recent years, numerous European projects have emerged to determine the best strategies to mitigate the effects of climate change on forest ecosystems. For example, the NNEXT (Non-Native Tree Species for European Forests - Experiences, Risks and Opportunities), REINFFORCE (REsource INFrastructures for monitoring, adapting and protecting European Atlantic FORests under Changing climate), ECHOES (Expected Climate Change and Options for European Silviculture), and FUTUREforest projects (Campioli et al. 2009, Orazio et al. 2013, Hasenauer et al. 2017). One strategy for enhancing forest resilience in face of climate change is the diversification of tree origins and species, both native and exotic. In this regard, the REINFFORCE project involves the establishment of 36 arboreta in several European countries, containing a mixture of 35 species, both native and exotic. In Belgium, the “Trees for future” project chose the same approach by implementing 25 to 30 forest arboreta to test several native or exotic species with varying provenances (Dassonville et al. 2021).

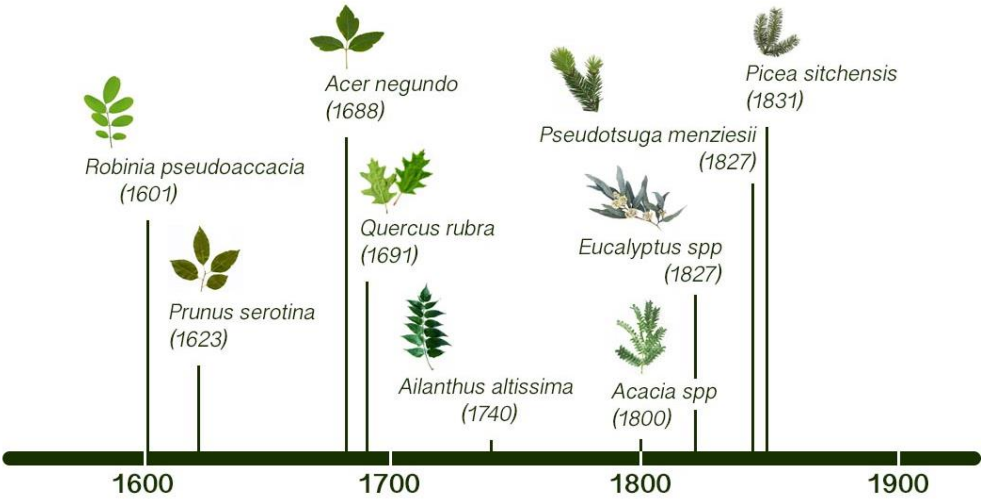


Figure 1-9: timeline of the introduction of some major non-native trees in Europe, from Krumm and Vítková (2016).

While exotic species may have good potential in terms of wood production, there are concerns regarding their invasive potential in natural environments. In Europe, a quarter of invasive tree species have been introduced for forestry, making it the second most important introduction pathway (Richardson and Rejmánek 2011). In the Czech Republic, one-third of trees introduced for forestry become naturalized, and one-quarter become invasive (Křivánek et al. 2006).

Silviculture is indeed a major entry point for invasive tree species. *Pinus* species for example have been widely introduced worldwide for timber production, and many species have become invasive in the neighboring natural habitats (Grotkopp et al. 2002, Nuñez et al. 2017, Calviño-Cancela and van Etten 2018, Wyse and Hulme 2021). Essl et al. (2010) observed that conifer species introduced for commercial forestry were more likely to escape cultivation and become invasive than species introduced for other purposes. This is probably due to the high introduction effort on suitable sites (matching edaphic and climatic conditions), which creates a massive propagule pressure (Mack 2005, Křivánek et al. 2006, Essl et al. 2010, Pyšek 2016). Species selected for production usually present high growth rates, which has been linked to a higher invasive potential (Richardson and Rejmánek 2004). Plantations of exotic species are protected from environmental stochasticity and regularly produce seeds that disperse outside the planting area. Some of these seeds eventually form new populations that will spread (Mack, 2005).

Many of these species have high commercial value, which creates conflicts of interest in natural resource management (Richardson and Rejmánek 2011). We can cite *Robinia pseudoacacia*, *Quercus rubra* or even *Pseudotsuga menziesii*, classified as invasive in the "German–Austrian Black List Information System" (Stiers et al. 2014, Krumm and Vítková 2016). While many exotic species have marginal impacts on native ecosystems, their invasive potential must be considered when implementing new forestry strategies (Richardson and Blanchard 2011, Brundu and Richardson 2017). The most cost-effective approach is indeed to replace potentially invasive species with native or safer exotic species (Richardson and Rejmánek 2011). Preventing the introduction of new invasive exotic species is also defined as a priority by the European Union (EU Regulation No 1143/2014).

Forest trials and arboreta are not new, and have been established in Europe since the surge of importation of exotic species in the end of the 19th century. At that time, the Belgian Forest Department also set up a network of 23 forest arboreta between 1890 and 1914 throughout the country to monitor the growth and wood production potential of native and exotic species. Exotic species mainly originated from Asia and the west coast of North America (Nyssen et al. 2016). The arboreta were implemented in order to cover the diversity of climates and soil types of the most forested areas of the country. However, every arboretum differed in its species selection, and most of the time, the geographical origin of the plants remains unknown. With the recent policy of forest diversification, a new interest in these arboreta emerged and inventories were performed in 2016 to study the production potential of exotic species in the light of climate change (Lhoir and Scholzen 2017). In several of these arboreta, the natural regeneration has been mostly untouched for the last two decades. These sites therefore offer the opportunity to monitor the regeneration and dispersal dynamic of non-native species. They are also likely to act as entry sites for new invasions (Richardson and Rejmánek 2004, Brundu and Richardson 2016).

4. Existing knowledge gaps in tree invasion processes

The vast amount of literature produced on trees invasiveness has been growing for the past two decades (Fig. 1-10). However, there is still a lack of long-term empirical data regarding the ecology and evolution of invasive tree species (Krumm and Vítková 2016).

Forest ecosystems have long been considered to be more resistant to biological invasions than open or highly disturbed habitats, except maybe for floodplain forests which are more subject to frequent disturbances (Lapin et al. 2019). The research effort in this type of ecosystem is therefore lower, many studies about determinants of tree invasiveness focusing on pioneer, light-demanding species. Yet we have seen that several shade-tolerant tree species have already invaded millions of hectares of forest, such as *Prunus serotina*, *Fraxinus pennsylvanica* and *Quercus rubra* in Europe (Drescher and Prots 2016, Dyderski and Jagodziński 2018), or *Acer platanoides* and *Prunus avium* in North America (Lamarque et al. 2015, Potter et al. 2022). Research is still needed on the determinants of invasiveness in various habitats (van Kleunen et al. 2010a) and various positions on the naturalization-invasion continuum (Pyšek et al. 2015a).

Silviculture is one of the main paths of entry of invasive species. Invasions by NNTs introduced for wood production are mainly studied in the Southern hemisphere, where impressive cases of invasions have been observed for decades following the massive introduction of pines, acacias or eucalyptus species (Richardson et al. 1994, Carrillo-Gavilán and Vilà 2010, Simberloff et al. 2010, Gallagher et al. 2011, Nuñez et al. 2017). However, monitorings of the spread of NNTs in European forests are still insufficient (Carrillo-Gavilán and Vilà 2010, Brundu and Richardson 2016).

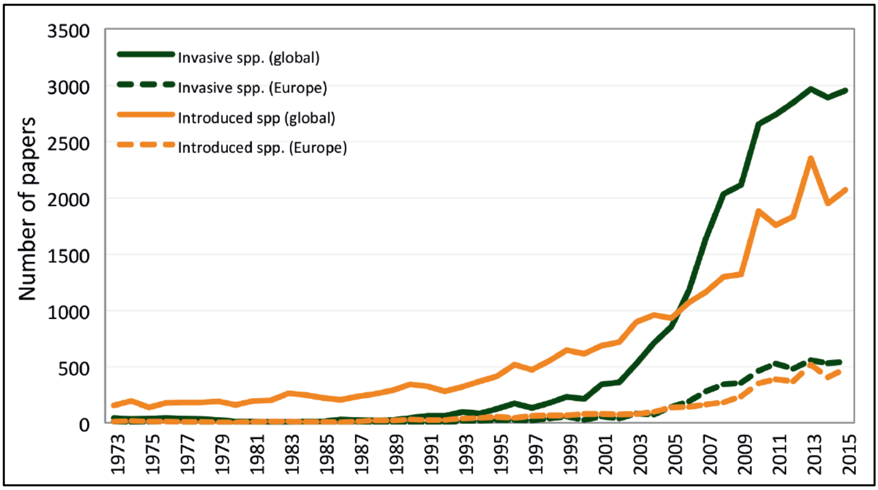


Figure 1-10: number of scientific papers on introduced and invasive tree species published since 1973 on both European and global levels, in Krumm and Vítková (2016). The research was conducted with the CAB Abstracts database, resulting in 30 537 scientific papers.

Due to their size and longevity, the study of trees generally does not conform to conventional methods used for plants with shorter life cycles (Harper 1977). Forest trials are therefore valuable assets for shedding light on different aspects of the invasion process. In particular, botanical gardens and arboreta can play a crucial role in evaluating the invasive potential of certain species (Richardson and Rejmánek 2011). Many programs of species diversification in forest plantings emerged in the last decade to enhance forest resilience in face of climate change. Non-native species frequently figure amongst the species recommended for planting, yet with little concern to the potential invasion risk. Given the substantial invasion debt weighing on Europe, it is essential to identify new invasive tree species before they spread into natural habitats or are heavily planted in afforestation programs.

5. Research strategy

Throughout this thesis, I try to better understand the mechanisms of tree invasions in European temperate forests and to improve assessments of the invasive potential of non-native trees. In this way, I focus on a selection of factors influencing the naturalization and invasiveness of non-native trees, namely propagule pressure, residence time, functional traits (mainly growth traits) and invasibility of the habitat, as illustrated in the theorical framework in Figure 1-7. These factors will mainly be studied at a local scale, except for traits of species that will also be analyzed in relation to invasiveness at a global scale. Figure 1-11 presents the research questions developed in the coming chapters and the global articulation of the thesis.

Firstly, I used old forest arboreta as sentinel sites to detect new invasions (Carrillo-Gavilán and Vilà 2010). I selected eight public arboreta in Southern Belgium and monitored the regeneration of all non-native trees in and around these sites. These arboreta were more than a century old and were rich in species exotic from Western temperate Europe: 69 % of planted species were non-native conifers and 12 % were non-native broadleaves. The protocol will be detailed in chapter 2 and 5, as well as the results that lead me to study specifically conifers on one hand, and maple species on the other hand. The locations of the arboreta and the other study sites used in this thesis are detailed on the map in Figure 1-12. Species composition and orthophotos of the selected arboreta are also available in Appendix 1 and 2.

In **Chapter 2,** I focus on gymnosperms and describe the monitoring of the 8 selected arboreta to identify conifer species displaying an invasive behavior. Indeed, an abundant regeneration of exotic conifers was observed while few information on the invasive potential of exotic conifers is available in Belgium (and overall in Europe). Moreover, conifer species' composition across the arboreta was rather similar, which allowed for environmental analyses. A systematic sampling was performed to quantify the natural regeneration of non-native species as well as environmental data. With information on the density, distance to parent trees and size structure of the natural regeneration, I was able to assess the invasiveness of non-native conifers in Belgian forests. I also tested the influence of planting intensity and time on the density of regeneration, as well as the influence of environmental characteristics to make the association with the habitat invasibility. These results were published in the "NeoBiota" journal in 2021 and provide useful information to stakeholders in the sectors of forestry and conservation.

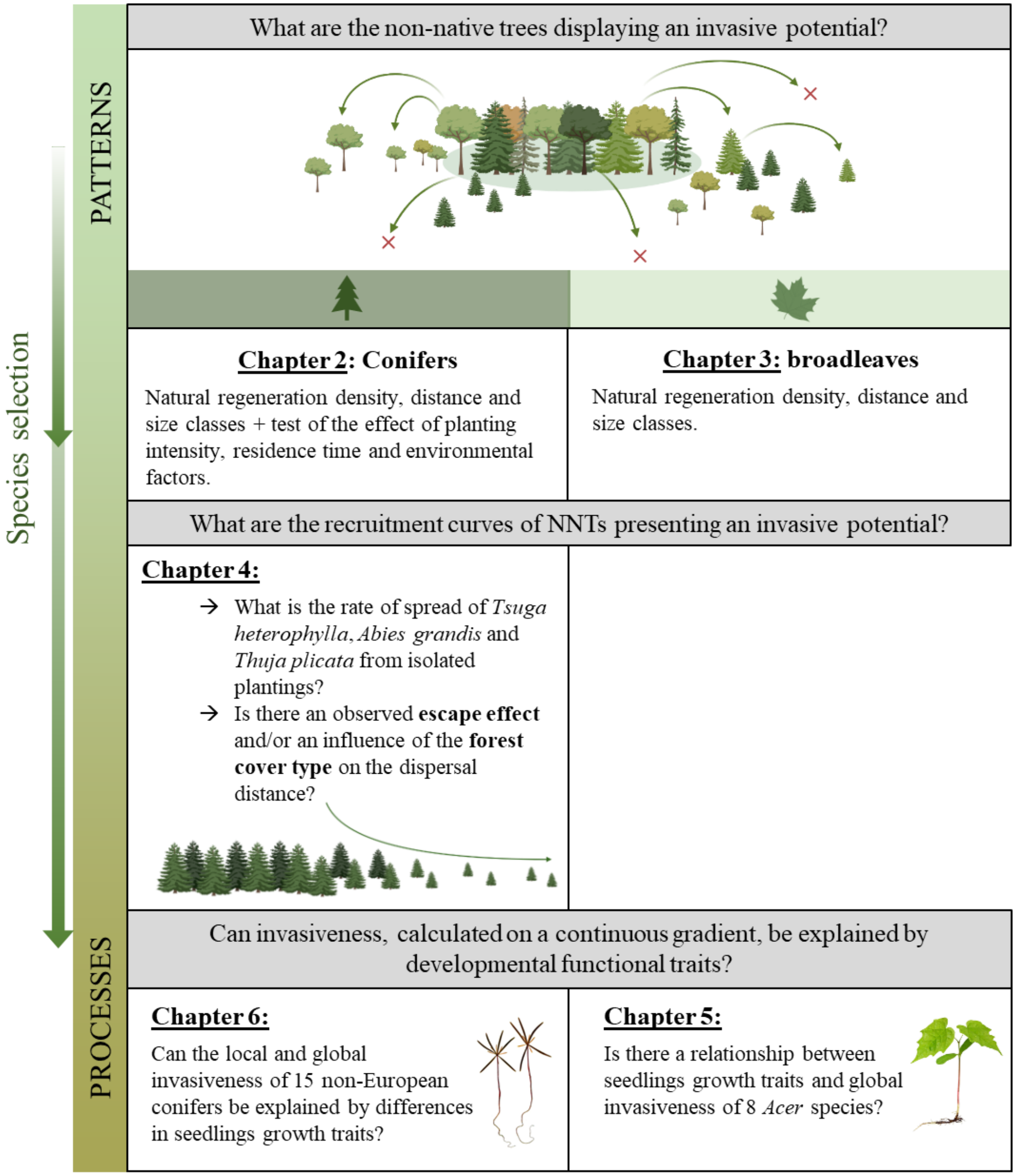
During the field work, both coniferous and broadleaved trees were identified. In **Chapter 3**, I shortly present the observed regeneration of non-native deciduous tree species in the same eight public arboreta. Density, distance to parent trees and size classes are also analyzed. However, given the heterogeneity of broadleaved species composition in the arboreta, testing the environmental conditions was not relevant and therefore not performed. This study identifies several *Acer* species displaying important natural regeneration.

In **Chapter 4**, I further assess the spread rate of three conifers identified in Chapter 2 as having an invasive potential. Indeed, dispersal distance was already studied in Chapter 2, but the study design did not allow the detection of long-distance dispersal events. Isolated planting sites were selected in Southern Belgium and the regeneration was exhaustively described on 750-m long circle sectors around the sites. This comprehensive data allowed me to describe the shape of the recruitment curves of the three conifer species and to test for an escape effect. The rate of spread was quantified as well as the influence of the forest cover type. Implications for the invasion risk in temperate forests are also discussed.

Based on the hypothesis that functional traits play a role in the transition from "naturalized" to "invasive", I tested the relation between growth traits and invasiveness in **Chapter 5** to try and understand why some maple species displayed a higher invasive potential than others. To this end, an innovative method was developed to quantify the global invasiveness of tree species. Seedlings of eight *Acer* species were grown and several performance traits measured to test the relationship with global invasiveness. This study contributes evidence that growth traits can help predict the invasive potential of species, even in dense forest ecosystems. Intrinsic invasive potential is a crucial component of the assessment of the invasion risk of a species in a given ecosystem. It was published in 2022 in "Plant Ecology".

In **Chapter 6**, the relationship between growth traits and global invasiveness was tested for 15 conifers. Global invasiveness was calculated with the same method used in Chapter 5. Local invasiveness was also calculated with the regeneration data from Chapter 2. The research question is "Can the local and global invasiveness of 15 non-European conifer species be explained by differences in growth traits at the seedling stage?". A paper presenting the results has been submitted in the journal "Biological Invasions" on April 28, 2023.

Finally, I will discuss the results of these studies and integrate them in the global framework of the invasion process. I will develop how the results can be useful in risk assessment and in choosing the right species for afforestation programs. The relevance of using non-native tree species in order to enhance the resilience of European temperate forests will also be addressed.



What are the non-native trees displaying an invasive potential?

Chapter 2: Conifers

Natural regeneration density, distance and size classes + test of the effect of planting intensity, residence time and environmental factors.

Chapter 3: broadleaves

Natural regeneration density, distance and size classes.

What are the recruitment curves of NNTs presenting an invasive potential?

Chapter 4:

- → What is the rate of spread of *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata* from isolated plantings?
- → Is there an observed **escape effect** and/or an influence of the **forest cover type** on the dispersal distance?

Can invasiveness, calculated on a continuous gradient, be explained by developmental functional traits?

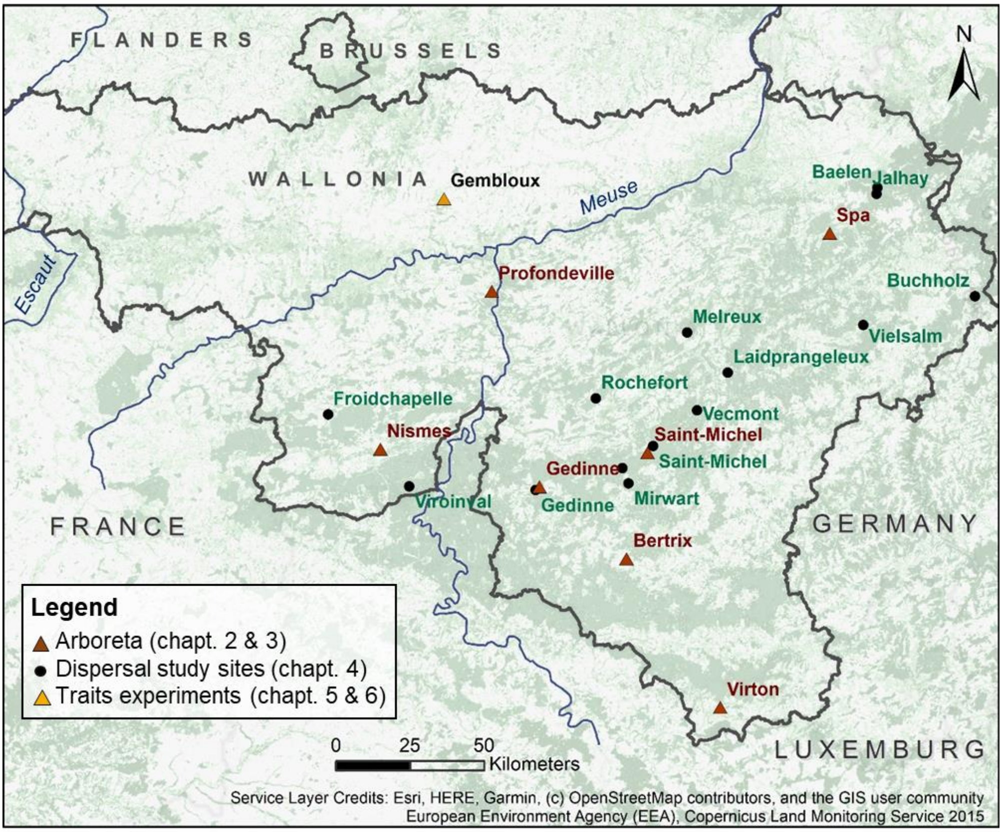
Chapter 6:

Can the local and global invasiveness of 15 non-European conifers be explained by differences in seedlings growth traits?

Chapter 5:

Is there a relationship between seedlings growth traits and global invasiveness of 8 *Acer* species?

Figure 1-11: Research strategy of the thesis and research questions raised in each chapter.



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European Environment Agency (EEA), Copernicus Land Monitoring Service 2015

Figure 1-12: Location of the sites used in this thesis. Brown triangles are the eight old forest arboreta used for chapters 2 and 3. Black dots are the isolated forest trials used to describe the recruitment curves of *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata* (chapter 4). The orange triangle is the location of the lab and field where the growth experiments were performed (Gembloux Agro-Bio Tech – chapters 5 and 6).

2

Invasiveness of conifers assessed in old forest arboreta

Arboreta reveal the invasive potential of several conifer species in the temperate forests of western Europe

FANAL Aurore, MAHY Grégory, FAYOLLE Adeline, MONTY Arnaud

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1. Abstract

Identifying emerging invasive species is a priority to implement early preventive and control actions. In terms of number of invasive tree species, forestry represents the second largest pathway of introduction, with an invasive debt likely existing for alien conifers in Europe. In the early 1900s, a network of arboreta was established in southern Belgium to assess the wood production potential of prospective conifer and broadleaved species. Here, we use eight arboreta as natural experiments to identify alien conifers presenting invasive behavior. Through systematic sampling, we quantified the natural regeneration of alien conifers and recorded local environmental variables. For each species, regeneration density, dispersal distances, and age structure were analyzed. Generalized mixed effects models were fitted to test the effect of planted area and tree-stand type on regeneration. The environmental space occupied by regenerating alien conifers was evaluated using principal component analysis. Out of 31 planted alien species, 15 (48%) were identified in natural regeneration, of which eight (26%) exhibited important regeneration density and dispersal distances. The most invasive species were Tsuga heterophylla and Abies grandis, confirming earlier field observations. Both large planted areas and areas planted with alien conifer species increased the density of regeneration. Species that had the highest regeneration density tolerated a wide range of environmental conditions, including shaded understorey, which could lead to the invasion of mature, undisturbed forests. This study showed that 17% of the studied alien conifers are potentially invasive because they show important regeneration, long-distance dispersal, and, of importance, have already produced offspring that have matured and are capable of creating new satellite populations. In conclusion, our results provide a guideline for future planting operations, recommending extreme caution when planting these species in the temperate forests of Western Europe.

2. Introduction

Early identification of emerging invasive species remains one of the most challenging issues in invasion science. Following numerous introductions worldwide for ornamental or production purposes, many tree species have since been recognized as invasive (Dodet and Collet 2012, Richardson et al. 2014). Rejmánek (2014) identified 76 tree species exhibiting invasive behavior in Europe. Alien woody species have the capacity to modify the structure of invaded ecosystems substantially and cause extensive ecological and economical damage (Lamarque et al. 2011, Pyšek 2016). In addition, management actions are often taken too late, when the species are already widespread and when the management costs of mitigation are prohibitive (Rejmánek and Pitcairn 2002, van Wilgen and Richardson 2014).

Most problematic tree species in Europe were introduced decades or centuries ago (Nyssen et al., 2016) and actively spread by human. In parallel, some dispersed outside their cultivation areas and spread *via* small satellite populations over kilometers (Mack 2005, Pysek and Richardson 2012). Delays between the installation of these satellite populations and their capacity to reproduce create an important lag phase between the introduction of a species in a new area and its invasion of natural habitats (Wangen and Webster 2006). In Germany, this lag phase has been estimated to last 170 years on average for trees (Kowarik 1995). Future invasive species might, therefore, already have been introduced but might not have completed the naturalization–invasion continuum, yet. This time-delayed invasion is referred to as the invasion debt (Rouget et al. 2016). Because introduction events increased during the second half of the 20th century, an invasion debt, without doubt, exists in Europe for trees (Essl et al. 2011a) and must be evaluated to anticipate new invasions (Richardson and Rejmánek 2011).

When the number of introduction events increases, so does the probability of naturalization (Heger 2016). Along with the propagule pressure, several functional traits can help predict the invasiveness of plant species such as an important SLA, growth rate, height, germination rate and fitness (van Kleunen et al. 2010a, Lamarque et al. 2011, Kutlvašr et al. 2019). For conifers specifically, Richardson and Rejmánek (2004) identified a small seed mass, short juvenile period and short intervals between large crops as traits associated with invasiveness.

The forestry sector has been introducing alien tree species for centuries in Europe for timber production, including many conifers from Asia and north America (Krumm and Vítková 2016, Gil-Moreno 2018). Species selected for forest plantations often originate from regions with a similar climate and present high growth rates, two factors contributing to enhanced invasiveness (Richardson and Rejmánek 2004). Introduced species are also grown in large-scale plantations using cultivation techniques that enhance survival rates, which lowers the probability of local extinctions and creates a massive propagule pressure, increasing the probability of them escaping from cultivation (Mack 2005, Křivánek et al. 2006, Pyšek et al. 2014). For example, in the Czech Republic, 25% of tree species introduced for forestry have become invasive (Pyšek 2016). Most invasive trees in Europe are light-demanding and have better invasion success in disturbed habitats (Richardson and Rejmánek 2004, Meloni et al. 2016). However, shade-tolerant species also exhibit invasive behavior once introduced to mature forests with low disturbance. For instance, *Prunus serotina* invaded the undergrowth of forests in western Europe (Hernandez et al. 2016).

Conifers in particular have been introduced to many areas and were widely planted for timber production, providing substantial opportunity for invasion (Richardson and Rejmánek 2004, Broncano et al. 2005). Globally, 36 species of conifers are already considered invasive (Richardson and Rejmánek 2004) with alien conifers used in commercial forestry having a significantly higher probability of escaping cultivation compared to species not used for timber production (Essl et al 2010). Conifers are still not often perceived as problematic in Europe because their invasions have been primarily documented in the southern hemisphere so far. Yet, studies indicate that alien conifers are showing invasive behaviors in Europe, too (Carrillo-Gavilán and Vilà 2010, Essl et al. 2010). If the planting of alien species in European forests continues, which is likely to happen with the dieback of several native species, it is necessary to distinguish high risk species from those that are unlikely to become invasive (Dodet and Collet 2012, Heger 2016).

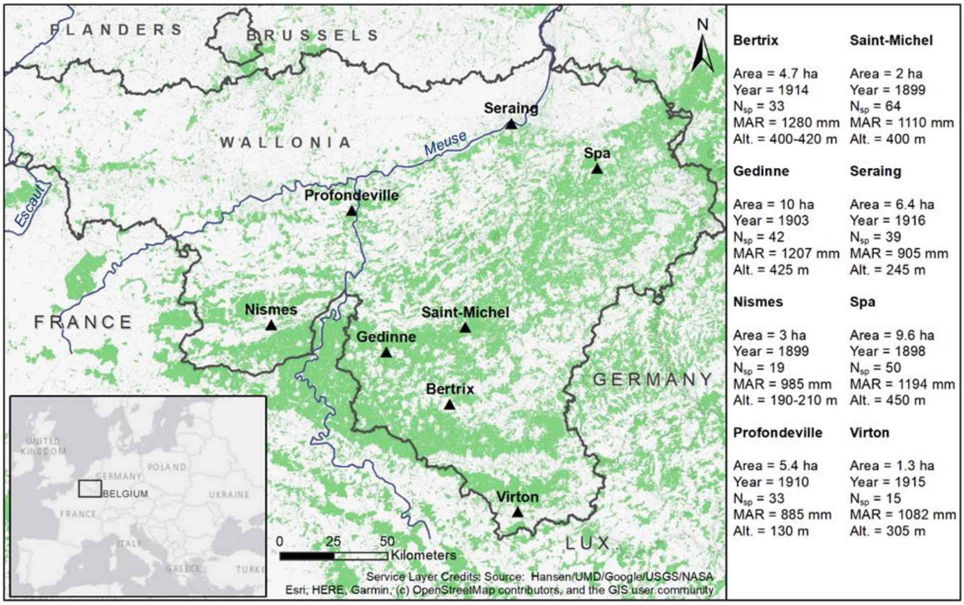
Forest trials and arboreta offer the opportunity to monitor the regeneration dynamic of exotic species, acting as sentinel sites of which careful observations could facilitate the detection of new invasions (Carrillo-Gavilán and Vilà 2010). These areas are also likely to act as sources of propagules and sites of entry for new invasions (Richardson and Rejmánek 2004, Brundu and Richardson 2016). During the 19th century, the Belgian Forest Department started to diversify forests plantations with exotic species. A network of 23 forest arboreta was set up between 1890 and 1914 throughout the country to monitor the growth and wood production potential of both native and alien species, especially ones from Japan and the west coast of North America (Nyssen et al. 2016). The arboreta were implemented in various ecological regions to cover the diversity of climates and soil types of the country. Every arboretum differed in its setup and list of species. Unfortunately, the geographical origin of the seeds remains unknown. Recently, a new interest in these arboreta emerged and new inventories were performed in 2016 to study the production potential of exotic species in the light of climate change (Lhoir and Scholzen 2017). In several of these arboreta, no management actions of the understory were implemented over the last 15 years except for clearing the pathways. The natural regeneration is therefore mostly untouched.

In this study, we aimed to identify alien conifer species presenting invasive potential. To do so, we systematically quantified the natural regeneration of alien species in and around eight selected arboreta. Richardson et al. (2000) defined invasive plant species as species producing reproductive offspring in very large numbers and at considerable distances from parent plants. By combining information on tree density, realized dispersal, and the size structure of the natural regeneration of alien conifers, we assessed their invasive potential. Specifically, we evaluated i) the density of natural regeneration and the realized dispersal distances from nearest parent trees; ii) whether a diverse size structure exists in the natural regeneration of species that regenerated; and iii) the influence of tree-stand type and environmental conditions on the regeneration density of species of highest concern. The correlation between the regeneration density and traits linked to invasiveness in previous studies was also assessed.

3. Material and Method

3.1. *Study area*

The study area covered the Walloon Region in Southern Belgium (49.5966 °N to 50.5705 °N latitude, 4.5469 °E to 5.8852 °E longitude). Eight arboreta, further referred to as “sites”, were selected (Fig. 2-1) based on three criteria: i) at least 15 planted alien conifer species, ii) no management actions in the understory that would have influenced the natural regeneration for the last 15 years, and iii) information being available on plantation dates.



Service Layer Credits: Source: Hansen/UMD/Google/USGS/NASA
Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Bertrix
Area = 4.7 ha
Year = 1914
N_{sp} = 33
MAR = 1280 mm
Alt. = 400-420 m

Saint-Michel
Area = 2 ha
Year = 1899
N_{sp} = 64
MAR = 1110 mm
Alt. = 400 m

Gedinne
Area = 10 ha
Year = 1903
N_{sp} = 42
MAR = 1207 mm
Alt. = 425 m

Seraing
Area = 6.4 ha
Year = 1916
N_{sp} = 39
MAR = 905 mm
Alt. = 245 m

Nismes
Area = 3 ha
Year = 1899
N_{sp} = 19
MAR = 985 mm
Alt. = 190-210 m

Spa
Area = 9.6 ha
Year = 1898
N_{sp} = 50
MAR = 1194 mm
Alt. = 450 m

Profondeville
Area = 5.4 ha
Year = 1910
N_{sp} = 33
MAR = 885 mm
Alt. = 130 m

Virton
Area = 1.3 ha
Year = 1915
N_{sp} = 15
MAR = 1082 mm
Alt. = 305 m

Figure 2-1: Location and description of the arboreta used in this study (triangle symbols) on a background map of tree cover in 2000 (Hansen et al. 2013). For each arboretum, the following characteristics were obtained: Year = year of first plantings, N_{sp} = number of alien conifer species planted in the arboretum, MAR = Mean Annual Rainfall between 1981 and 2010 obtained from the Royal Meteorological Institute of Belgium (RMI, n.d.), and Alt. = Altitude (m).

In this study species were considered alien when they did not naturally occur in continental Europe. Sixty-nine percent of the total planted area within the arboreta was occupied by alien conifers. Only 8% percent was planted with European conifers (mainly *Picea abies* and *Abies alba*). The remaining area was planted with native and alien broadleaves. All the arboreta consist of forest ecosystems, even though a few small clearings with solitary individuals could be found. Thus, the planted area varied greatly across species, from 6 m^2 to 9.1 ha.

3.2. Sampling procedures

Field sampling was conducted from April to July 2018. Sampling was systematic and covered the entire arboreta and a 100-m buffer, representing a total of 129.5 ha. For each arboretum, a 30 × 30 m grid was applied and a plot was installed at each intersection, generating 1565 plots. Sampling plots consisted of circles of 2-m radius. Plots situated on roads, ponds, private land, and recent forest plantings were excluded along with sites with insecure access, such as rocky scree. In total, 1109 plots were sampled in forested areas (from 71 to 244 plots per arboretum). In each plot, all individuals of alien conifer species (from young seedlings to adult trees) were recorded and their height measured from the ground to the tip of the main stem. They were then assigned to the following size classes: class 0 for seedlings between 0 and 0.3 m high, class 1 for saplings between 0.3 m and 1.3 m high (height of measurable diameter at breast height, DBH), class 3 for trees higher than 1.3 m but with DBH smaller than 5 cm, class 4 for trees with DBH between 5 and 9.9 cm, and so on for every 5-cm increment in DBH.

Identifying seedlings was sometimes challenging and 1878 fir seedlings (including 850 in only one plot) were excluded from further analyses, as it was not possible to determine species with certainty due to their stage of development (probably *A. grandis* or *A. alba*). The regeneration data for *Abies* species was therefore underestimated.

We measured environmental variables that influence the settlement of species (Dyderski and Jagodziński 2018). The thickness of litter (mm) was measured with a ruler at four different places in the plot and the mean was calculated (ranging from 0 to 100 mm, median = 20 mm, mean = 24.14 mm). The pH was measured with a pH-kit on the field in the center of the plot with a precision of 0.5 units (range: 4 to 6.5, median = 4.0, mean = 4.3). Canopy openness was assessed with a spherical convex densiometer in four cardinal directions (Forestry Supplier spherical crown densiometer, Convex – Model A), and ranged from 0.2 to 90.2 % (median = 7.2 %, mean = 11.1 %). Soil drainage was attributed from the plot geographical coordinates based on the Digital Soil Map of Wallonia (Bah et al. 2007, Service Public de Wallonie 2019). Soils ranged from being excessively well-drained (1) to poorly drained (5). Soil drainage classes are defined according to soil morphological attributes, more precisely the depth of appearance of gleyic color pattern reflecting the presence of stagnant water (Bah et al. 2007). Most soils were excessively well-drained (median = 1, mean = 1.89). Out of the 1109 prospected plots, the tree-stand type was defined: 545 plots were under coniferous stands, 557 plots were under broadleaved species (mainly *Fagus sylvatica* in the buffer zones), and seven plots were in open areas (clear-cuts).

3.3. Statistical procedures

A generalized linear mixed effect model (GLMM) with Poisson family was used to determine whether there was a significant influence of several variables on the regeneration ability of alien species regenerating in at least two sites. The lme4 package was used (Bates et al. 2015). The fixed variables were the species, the area of plantation, the time since plantation, the distance to the nearest parent trees, and the tree-stand type (broadleaves, open areas, European conifers or exotic conifers). The exact number of planted trees per species was unknown. We therefore used the area of plantation as a proxy for the propagule pressure, as the density of plantation was similar for the coniferous species. The site and the plot nested within the site were included as random effects. Zero-inflation was tested and not detected. A significant *p* value threshold was set at 0.05. An ANOVA with the “car” package was performed on the regression result (Fox and Weisberg 2019).

The two first key determinants of invasiveness that we analyzed were the density of regeneration and dispersal distances from the closest parent trees. Regeneration Density (RD) was calculated for every species as the mean number of individuals per ha. For the capacity of regeneration of different species to be comparable, we calculated the Weighted Regeneration Density (WRD) which represented the density of regenerating individuals per ha for 1 ha planted of the same species. The WRD was calculated by dividing the regeneration density (RD) in each plot by the planted area of species in the corresponding arboretum. Because WRD is the density of individuals (indiv.ha^{-1}) divided by an area (ha), the unit is $\text{indiv.ha}^{-1}.\text{ha}_{\text{planted}}{}^{-1}$. For each species in each plot, the realized dispersal distance (DD) was measured as the distance to the nearest planted parent trees with ArcMap v. 10.5.1 (ESRI 2019). For species with at least 10 individuals found in the regeneration, boxplots and density plots of the distribution of dispersal distances were constructed. As long-distance dispersal events are of major importance in the invasion process, the 95th percentile of distribution of distances was represented to characterize the tail (Higgins and Richardson 1999, Monty et al. 2013). A “summary plot” (Fig. 2B) combining the WRD and 95th percentile of dispersal distances was built to characterize the behaviors of species visually regarding these two aspects of invasiveness. The plots and analyses were performed using R software (R Core Team 2022).

Richardson et al. (2000) delineated a threshold of 100 m in 50 years as a rule of thumb for the dispersal of an alien plant defined as invasive (Richardson and Rejmánek 2004, Nygaard and Øyen 2017). To compare dispersal observed in the arboreta with the threshold provided in this definition, dispersal distances over 50 years (DD50) were also calculated. Dispersal distances (DD) for every individual were divided by the time since planting minus the age of maturity of the species, and were then multiplied by 50 (Eq. 1). Data on the age of maturity were compiled from Kattge et al. (2011), Petit et al. (2017), and Forestry Commission Scotland (2015).

$$DD50 = \frac{DD \times 50}{time\ since\ planting - age\ of\ maturity} \qquad \text{(Eq. 1)}$$

Because an invasive species must be capable of producing mature offspring, the size structure of natural regeneration was also observed. A table on size structure was constructed for the 10 species with at least 10 measured individuals to examine the viability of the natural regeneration.

We investigated whether the most invasive species occupy a wide range of environmental conditions. We selected species presenting a combination of important regeneration density (WRD > 100 indiv.ha^{-1}.ha$_{\text{planted}}^{-1}$), high dispersal distance (Perc. 95 > 50 m), and a developed size structure with older individuals (DBH > 10 cm). To detect environmental gradients through the measured plots, we performed a principal component analysis (PCA) on the environmental matrix containing all plots and the four quantitative environmental variables using the ade4 package (Dray and Dufour 2007). The plots in which the selected species were regenerating were projected in the environmental space made by the first two Principal Components. Density lines for each species on the two axes of the PCA were drawn, allowing us to delineate the environmental space occupied by each species. This method is widely used to estimate niche overlap of species (Broennimann et al. 2012).

Finally, data was gathered for two traits associated with invasiveness, namely the seed mass and the maximal height of the species, both linked to the capacity to disperse at long distances (Richardson and Rejmánek 2004, Kutlvašr et al. 2019). Data was compiled from Greene and Johnson (1993), Kattge et al. (2011) and Johnson and More (2014). As a Shapiro-Wilk test rejected the normality of our variables, we performed a non-parametric Kendall correlation test on these two variables related to the Weighted Regeneration Density of all species planted in at least half of the arboreta.

4. Results

In total, 1109 plots were surveyed and 4148 individuals recorded, from small seedlings to mature trees over 60 cm of DBH. Due to the size of the sampling plots, we never found more than one non-planted tree with a DBH > 20 cm in one plot. These individuals belonged to 31 alien conifer species planted between 1898 and 1916 in eight arboreta across the Walloon Region (Table 2-1). For 15 of the planted species, no regeneration was detected, while six species had less than 10 individuals recorded across all sites. In contrast, some species presented abundant regeneration. The most frequent individuals encountered were *Tsuga heterophylla* and *Abies grandis*. The planted area, time since planting and distance to the nearest parent trees significantly affected the density of regeneration (Table 2-2). We further use the Weighted Regeneration Density (WRD) for between-species comparison.

Species	Native distribution	Planted area	N sites planted	N sites found	N plots	N indiv.	Mean RD	Mean WRD	Median DD	Perc. 95 DD	Max DD	Perc. 95 DD 50	Max DD50
Tsuga heterophylla	North America	2.1	8	6	136	1729	1240.7	2794.0	3.8	124.3	298.0	84.3	201.3
Abies grandis	North America	1.803	8	6	103	915	656.6	1493.8	0.0	67.4	330.1	39.5	177.5
Abies nordmanniana	Caucasus	0.581	6	2	4	145	126.2	688.3	5.8	5.8	5.8	4.03	4.0
Thuja plicata	North America	1.567	8	4	39	284	203.8	637.8	11.2	90.3	213.8	54.9	127.2
Pinus strobus	North America	0.325	6	2	9	12	10.7	357.8	23.9	124.2	162.2	73	95.4
Chamaecyparis lawsoniana	North America	2.088	8	5	46	150	107.6	279.4	28.7	126.7	187.7	77.3	120.3
Pseudotsuga menziesii	North America	9.011	8	6	177	627	449.9	248.8	12.8	87.0	243.3	40.4	95.0
Chamaecyparis obtusa	Japan	0.08	5	1	2	4	4.7	243.8	7.0	7.0	7.0	4.5	4.5
Larix kaempferi	Japan	3.247	8	3	39	224	160.7	136.6	18.1	74.3	132.3	49.5	88.2
Abies cilicica	Middle-East	0.09	4	1	1	3	4.2	117.0	2.9	2.9	2.9	*2.3*	2.3
Chamaecyparis pisifera	Japan	0.236	6	1	1	6	4.6	116.3	0.8	0.8	0.8	0.5	0.5
Picea sitchensis	North America	0.789	4	2	9	33	37.1	104.2	4.2	36.5	136.7	33.8	126.5
Abies homolepis	Japan	0.336	6	2	2	4	3.3	84.8	0.0	15.9	18.7	15.9	25.2
Abies veitchii	Japan	0.578	5	3	7	10	9.3	76.6	6.6	145.4	166.0	125	133.9
Abies procera	North America	0.352	5	1	1	1	0.9	20.7	0.0	0.0	0.0	0	0.0
Picea orientalis	Caucasus	0.294	7	1	1	1	0.8	8.5	5.7	5.7	5.7	4.4	4.4
Abies concolor	North America	0.294	5	0	0	0	0	0	-	-	-	-	-
Abies numidica	North Africa	0.122	4	0	0	0	0	0	-	-	-	-	-
Cedrus libani	Middle-East	0.049	4	0	0	0	0	0	-	-	-	-	-
Cryptomeria japonica	Japan	0.265	8	0	0	0	0	0	-	-	-	-	-
Metasequoia glyptostroboides	Asia	0.281	6	0	0	0	0	0	-	-	-	-	-
Picea engelmannii	North America	0.236	4	0	0	0	0	0	-	-	-	-	-
Picea glauca	North America	0.14	4	0	0	0	0	0	-	-	-	-	-
Picea jezoensis	Asia	0.107	5	0	0	0	0	0	-	-	-	-	-
Picea koyamae	Japan	0.234	6	0	0	0	0	0	-	-	-	-	-
Picea rubens	North America	0.143	4	0	0	0	0	0	-	-	-	-	-
Picea torano	Japan	0.115	4	0	0	0	0	0	-	-	-	-	-
Pinus ponderosa	North America	0.141	4	0	0	0	0	0	-	-	-	-	-
Sequoiadendron giganteum	North America	0.244	7	0	0	0	0	0	-	-	-	-	-
Tsuga canadensis	North America	0.238	5	0	0	0	0	0	-	-	-	-	-
Xanthocyparis nootkatensis	North America	0.045	4	0	0	0	0	0	-	-	-	-	-

Table 2-1: List of species planted in at least four of the eight selected arboreta. **N sites planted** = number of arboreta where species were planted. **Native distribution** of species is also given. **Planted area** = total planted area of species in all sites. **N sites found** and **N plots** are the number of sites (arboreta) and plots (1109 plots in total) where the natural regeneration of species occurred. **N indiv.** = number of trees recorded in natural regeneration. For each plot, the regeneration density (**RD**) in indiv.ha-1 and weighted density of regeneration (**WRD**) in indiv.ha-1.haplanted-1 were calculated, and the mean is given in the table. The median, maximum, and 95th percentiles of dispersal distance distributions are given (**Median DD**, **Max DD** and **Perc. 95 DD**). The maximum dispersal distance over 50 years (**Max DR50**) and the 95th percentile (**Perc. 95 DR50**) were calculated.

Tsuga heterophylla was the most represented alien conifer in natural regeneration with a WRD of 2794.0 indiv.ha^{-1}.ha$_{planted}^{-1}$. This species was followed by *Abies grandis* (WRD = 1493.8 indiv.ha^{-1}.ha$_{planted}^{-1}$), *Abies nordmanniana* (688.3 indiv.ha^{-1}.ha$_{planted}^{-1}$) and *Thuja plicata* (637.8 indiv.ha^{-1}.ha$_{planted}^{-1}$).

Table 2-2: Results of the generalized linear mixed effect model on the count of regeneration. Estimates, standard errors, Z values and p values are given for fixed effects.

Variable		Estimate	Std. Error	Z value	p value
Species	*Abies grandis*	*(base)*			
	Abies homolepis	-3.17E+00	4.63E-01	-6.85	< 0.001
	Abies nordmanniana	-5.55E-01	1.17E-01	-4.744	< 0.001
	Abies veitchii	-2.28E+00	3.20E-01	-7.121	< 0.001
	Chamaecyparis lawsoniana	-9.86E-01	1.09E-01	-9.078	< 0.001
	Larix kaempferi	-6.29E-01	1.12E-01	-5.61	< 0.001
	Picea sitchensis	-9.07E-01	1.85E-01	-4.9	< 0.001
	Pinus strobus	-2.79E+00	2.82E-01	-9.902	< 0.001
	Pseudotsuga menziesii	-2.40E+00	1.10E-01	-21.872	< 0.001
	Thuja plicata	-2.74E-01	9.48E-02	-2.894	0.00381
	Tsuga heterophylla	1.84E+00	8.61E-02	21.336	< 0.001
Canopy type	Broadleaves	*(base)*			
	European conifers	1.28E+00	8.64E-02	14.862	< 0.001
	Exotic conifers	1.46E+00	7.58E-02	19.259	< 0.001
	Open areas	3.61E+00	1.73E-01	20.869	< 0.001
Time since plantation		5.24E-02	3.15E-03	16.638	< 0.001
Surface planted		5.56E-05	3.24E-06	17.179	< 0.001
Distance from plantation		-2.16E-02	5.69E-04	-37.956	< 0.001

Ten species had at least 10 individuals recorded in the natural regeneration. They tended to be found close to parent trees (Fig. 2-2). However, the seedlings of nine species were sometimes detected at >100 m distance from possible parent trees. Four species had a 95th percentile for dispersal distance distribution exceeding 100 m. Only *Abies nordmanniana* displayed very low dispersal distances, with all recorded individuals occurring within 6 m of planted parent trees. The maximal DD exceeded 200 m for *Tsuga heterophylla*, *Pseudotsuga menziesii*, and *Thuja plicata*, and even 300 m for *Abies grandis*.

For the same 10 species with 10 recorded individuals, size structure was used to investigate the survival of the regeneration. Ninety-three percent of recorded trees in natural regeneration were <1.3 m high. All individuals of *P. sitchensis* and *P. strobus* were seedlings <0.3 m high (Table 2-3). However, older trees with a DBH >20 cm were detected for *C. lawsoniana*, *P. menziesii, T. plicata, L. kaempferi,* and *T. heterophylla*.

Though conifers and broadleaved stands were almost equally represented in the plot data, alien conifers mainly regenerated under coniferous stands. Specifically, 69% of individuals were found under exotic conifers, 18 % under European conifers, 7% in clear-cut areas, and only 6% under broadleaved species. Open areas and exotic coniferous stands significantly increased the regeneration count of alien conifers (Table 2-2).

Table 2-3: Size class distribution of percentages for species with more than 10 recorded individuals. The two first classes are composed of individuals smaller than 1.3 m, for which DBH could not be calculated. The other classes were based on DBH intervals (cm). Classes were aggregated to improve readability.

		Height (m)		DBH (cm) | H > 1.3 m					
Species	*N*	0 - 0.3	0 - 1.3	< 5	5-10	10-20	20-30	30-50	> 60
A. grandis	939	53.2	34.6	11.4	0.5	0.2	0	0	0
A. nordmanniana	145	98.6	1.4	0	0	0	0	0	0
A. veitchii	10	30	40	30	0	0	0	0	0
C. lawsoniana	163	39.3	30.7	20.2	8.0	1.2	0	0	0.6
L. kaempferi	227	52.4	31.7	14.5	0	0.4	0.9	0	0
P. menziesii	623	64.5	23.6	7.7	1.9	1.3	0.6	0	0.3
P. sitchensis	15	100	0	0	0	0	0	0	0
P. strobus	9	100	0	0	0	0	0	0	0
T. heterophylla	1732	80.1	9.2	9.5	0.8	0.2	0.1	0.1	0
T. plicata	287	49.1	38.3	10.8	0.7	0.3	0	0.7	0

From the principal component analysis (Fig. 2-3), two environmental gradients were identified and were regulated by soil pH (first Principal Component, PC1) and canopy openness (PC2). Wet soil tended to be more acidic. Litter was thicker on acidic plots with low light availability. Along these gradients, we projected the presence of six species showing a combination of important WRD (>100 indiv.ha^{-1}.$ha_{planted}{}^{-1}$), high dispersal distance (perc. 95 > 50 m), and developed size structure (individuals >10 cm DBH): *Tsuga heterophylla*, *Abies grandis*, *Thuja plicata*, *Chamaecyparis lawsoniana, Larix kaempferi,* and *Pseudotsuga menziesii.* We found that these species occupied a wide range of environmental conditions of the arboreta, including areas with low canopy openness. Ecological niches and optimums of presence were rather similar for the six species. *Abies grandis* also occurred on dry and basic soils.

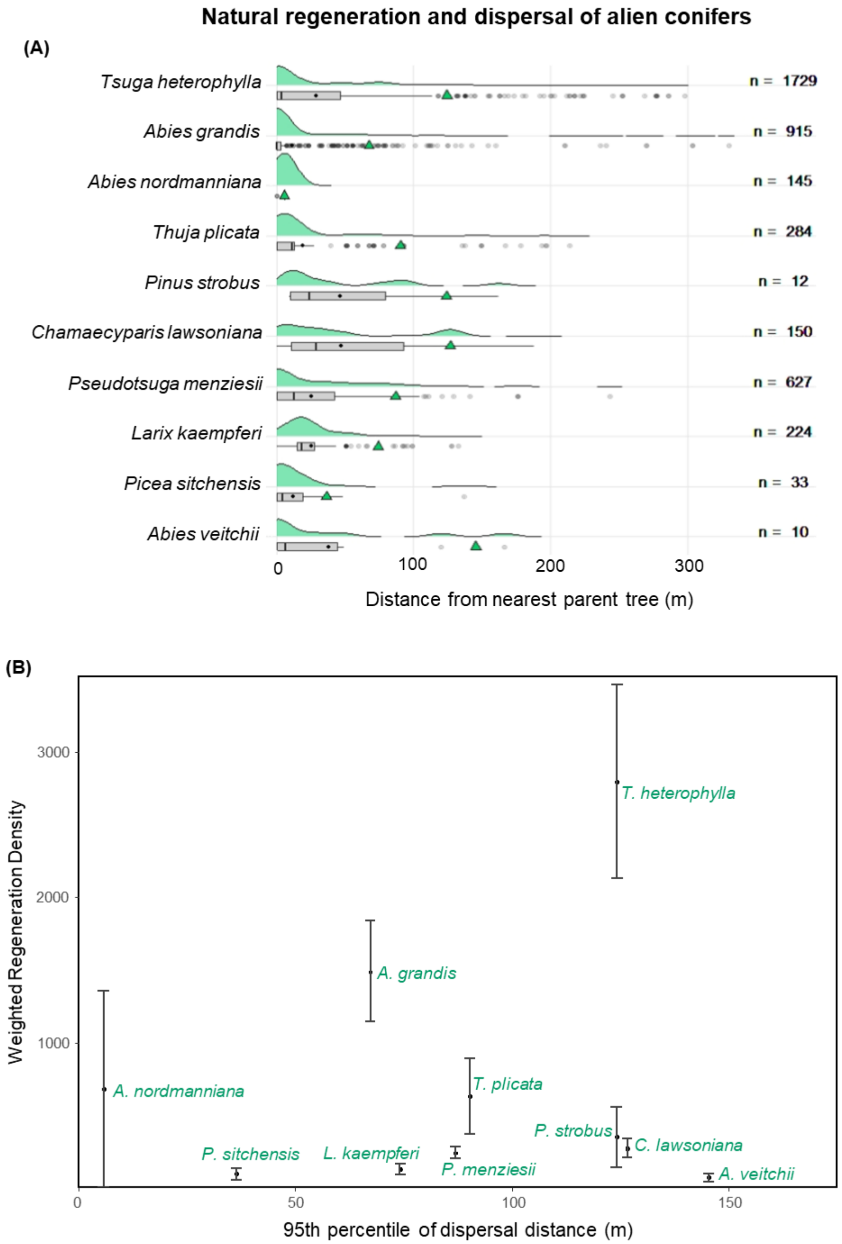


Figure 2-2: Regeneration density and dispersal of alien conifers. **A** Boxplots and density plots of dispersal distances for species of which at least 10 individuals were recorded. Species are ordered in descending order using WRD. The total number of individuals per species (n) is indicated on the right. The mean (point) and median (vertical bar) are indicated. The 95th percentile was also represented with a green triangle. **B** Comparison of species based on mean WRD ± standard error (indiv.ha^{-1}.ha$_{planted}^{-1}$) and 95th percentile of dispersal distances (m).

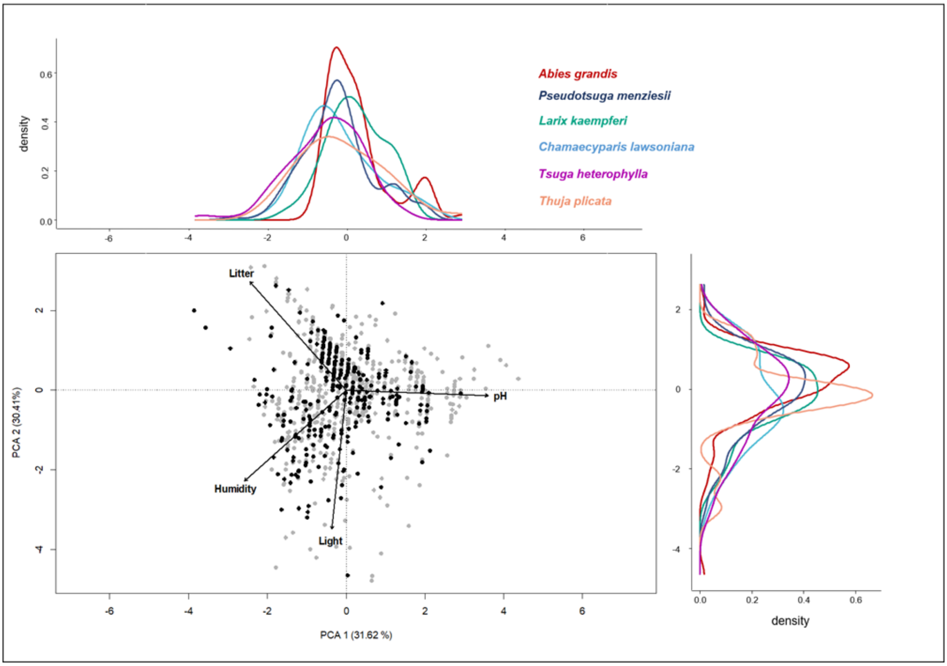


Figure 2-3: Regeneration of six conifers in the environmental space made by the two first axes of the PCA. The circle of correlation of four environmental variables was projected on the graph: pH, litter thickness, canopy openness (referred to as “Light”), and soil drainage class (referred to as “Humidity”). The percentage of explained variance for each Principal Component is indicated. Dots represent all plots of the eight arboreta. Black dots are those in which at least one of the six species is regenerating. Density lines are drawn for each species along the two axes of the PCA.

Kendall’s correlation highlighted a significant positive relationship between the height of species and their WRD (tau=0.459, z=3.096, p value = 0.002). On the other hand, the correlation was not significant for the seed mass (tau = -0.064, z=-0.411, p value = 0.681).

5. Discussion

This study demonstrated that alien conifers naturally regenerated in each arboretum that was visited, sometimes in dense patches. Of the 31 alien species considered, 16 were detected regenerating. Eleven species (35%) had a Weighted Regeneration Density of more than 100 indiv.ha^{-1}.ha$_{\text{planted}}^{-1}$. The planted area and the time since plantation both had a positive significant effect on the count of regeneration, confirming the important influence of the propagule pressure on the regeneration of alien species (Lockwood et al. 2009, Pyšek et al. 2009b).

Most species primarily regenerated close to parent trees. Long dispersal events of over 100 m were detected for nine species. For the prolific species *Tsuga heterophylla,* five percent of regeneration occurred past 124 m, and some even reached 300 m one century after planting. Thus, long-distance dispersal events are frequent for this species. The 95th percentile of dispersal distance also exceeded 100 m for *P. strobus*, *C. lawsoniana,* and *Abies veitchii*. However, the prospected area was limited, with even longer distances from the closest parent trees being possible. Our estimates of long-dispersal distances can therefore be considered conservative. Given the importance of long-distance dispersal events in the invasion process, more exhaustive inventories of the dispersal potential of these species along transects are required until no individual is found for a given distance lapse (Higgins and Richardson 1999).

The weighted regeneration density and the dispersal distance are useful tools for monitoring the invasive behavior of alien conifers. However, as invasive species must maintain viable populations, the age structure of natural regeneration must be incorporated (Wilson et al. 2014). For *A. nordmanniana*, the high number of individuals was attributed to a single large germination event resulting in hundreds of seedlings of less than one-year-old being detected in one plot; 142 out of the 145 individuals recorded were young seedlings beneath a parent tree, indicating that most regeneration is not viable. *Pinus strobus* and *P. sitchensis* seedlings were recorded at further distances, but only seedlings smaller than 0.3 m were found. In comparison, *T. heterophylla, P. menziesii, A. grandis, C. lawsonianna, L. kaempferi,* and *T. plicata* also tended to exhibit large germination events beneath parent trees but older trees were also recorded (see Table 2-3), including mature ones. Thus, these species likely have the capacity to create new satellite populations.

The question of whether some species cross the benchmark of 100 m dispersal distance over 50 years was evaluated in this study. Richardson et al (2000) stated that, for a species to be invasive, there must be “clear evidence that it regenerated naturally and recruited seedlings more than 100 m from parent plants”. This distance is associated with a time-lapse of 50 years since introduction, and reproductive offspring must be found beyond 100 m. These events involve the tail of the dispersal curve, as only a small number of long-distance dispersal events producing reproductive offspring is necessary to create a new population at a far distance. Individuals of *A. grandis, T. heterophylla, T. plicata, C. lawsonianna, P. sitchensis,* and *A. veitchii* occurred over a DD50 of 100 m. If no mature individuals were measured, individuals taller than 1.3 m were recorded for *A. grandis* and *T. heterophylla* over the specified distance. It means they survived the most vulnerable seedling and sapling stages, and could potentially grow to sexual maturity.

Six species exhibited high invasive potential based on the three studied factors: *T. heterophylla, A. grandis, T. plicata, C. lawsoniana, L. kaempferi,* and *P. menziesii*. They were selected for the environmental analysis. Once projected on the PCA, these six species occupied a large proportion of the environmental space encountered at the surveyed sites, and displayed generalist behavior across common environmental conditions. Of note, *T. heterophylla* preferentially regenerated on acidic soils, supporting existing knowledge on the ecological preferences of this species (Rooney et al. 2000). In comparison, *A. grandis* tolerated drier soils, which might be beneficial under climate change as water stress is likely to become more frequent in the near future (Campioli et al. 2009). Although we could not statistically test the influence of microsites, we noted frequent regeneration of conifers on stumps and fallen logs. Efimenko and Aleinikov (2019) recently observed that the presence of elevated microsites such as tree stumps or mounds are required for a successful survival and growth of coniferous undergrowth of tall-herb spruce-fir boreal forests.

An important regeneration was recorded in open areas resulting from clear cuts. Interestingly, these six species also exhibited shade tolerance during regeneration with many individuals occurring in plots with low canopy openness, allowing them to spread in closed forest ecosystems. Martin and Marks (2006) demonstrated that invasions of undisturbed forests by shade-tolerant alien species frequently occur but require a longer time span than invasions in disturbed habitats, resulting in their invasiveness often being underestimated. The combination of a generalist behavior across soil types and shade-tolerance could allow these alien conifers to invade mature, undisturbed forests. This phenomenon is likely to be facilitated by areas planted with conifers. Consequently, because of the capacity of conifers to transform habitat, increasing the proportion of coniferous stands in wood production forests might accelerate the invasion rate of alien conifers (Jagodziński et al. 2015). In 2011, 48 % of the southern Belgium forest was planted with conifers (Lecomte 2017). *Pseudotsuga menziesii* represented 6 % of the surface inventoried by the Belgian permanent forest inventory in 2011, far more than the other species highlighted in our study, and its proportion has increased by 52% since 2001. *Larix* sp., *A. grandis*, *T. plicata*, *T. heterophylla* and *C. lawsoniana* together represent a marginal section inventoried surface in 2011, and it is difficult to know the real extent of these species in public and private forests (Bauwens 2020). However, trials with alien species are becoming more frequent (Richardson et al. 2014), and exotic conifers are more and more considered as replacement species to compensate for the die-back of native productive species. For example, *C. lawsoniana* and *T. plicata* are selected for the REINFFORCE arboreta network, aiming to collect data on the growth of alien species in view of the diversification of European Atlantic temperate forests in light of climate change (Orazio et al. 2013).

Our sampling covered a large diversity of environmental conditions met in southern Belgium forests, from calcareous to acidic soils, from forests dominated by native broadleaves to spruce plantations. These species can potentially invade a large proportion of forest lands, especially productive lands planted with conifers and managed with clear-cut regimes. However, this study did not cover the full diversity of temperate forests in Western Europe, with wider gradients potentially generating greater differences in the environmental space occupied by each species.

These six highlighted species also exhibit invasive behavior in other European countries (Rejmánek and Richardson 2003, Richardson and Rejmánek 2004, Broncano et al. 2005, Orellana and Raffaele 2010, Forestry Commission Scotland 2015). In western Norway, *T. heterophylla* is considered to be a very invasive conifer due to its high potential for spreading into neighboring stands and clear cuts (Oyen

2001). Plantations of *T. heterophylla* generate intense shade with few plants being able to live beneath them (Harmer et al. 2011). Galoux (1951) demonstrated the high regeneration capacity of *T. heterophylla* in Belgian arboreta, mentioning dense regeneration patches that occur beneath seed-bearers and in the neighboring plantations. The same author also stressed the abundant seed production and regeneration potential of *C. lawsonianna*, *P. menziesii,* and *A. grandis*. As the report was written in the middle of the 20th century, we know that the natural regeneration of these species has been ongoing for at least 70 years in the arboreta.

A small seed mass and an important maximal height have been linked to a better invasion success of plants in previous studies (Richardson and Rejmánek 2004, van Kleunen et al. 2010a, Kutlvašr et al. 2019). Both traits are linked with the capacity of species to spread at long distances. We did find a positive correlation between the maximal height and the Weighted Regeneration Density, but not with the seed mass. Dawson et al. (2011) surveyed exotic plants escaping from a tropical botanical garden. They concluded that propagule pressure was of greater significance than the functional traits in the establishment of alien plants in natural habitats. In a study conducted in North America, Pyšek et al. (2015) concluded that the importance of biological traits is highly dependent on the invasion stage, and often over-estimated. Further investigation on the role of functional traits on the invasiveness should be led in the local conditions of the Belgian arboreta, including the relative growth rate and specific leaf area, to test whether similar conclusions can be drawn.

The species exhibiting an important invasive potential in our study could be part of the invasion debt *sensu* Rouget et al (2016) in Belgian forests. The important lag phase might be misleading concerning the potential impact of alien conifers, especially *T. heterophylla*. Twenty percent of the studied species exhibited invasive tendencies and they will certainly continue to expand in the future, especially if planting effort increases. In comparison, we did not detect any regeneration for half of the studied species. If foresters want to diversify forest plantations, they should avoid introducing species with high invasiveness and prefer native species or low-risk alien species (Brundu et al. 2020).

We identified species that were likely to become invasive based on small forest trials. The effect of mass plantings was not addressed. However, we demonstrated that the size of planted areas positively impacts regeneration density. Previous studies showed that propagule pressure has the potential to overwhelm ecological resistance of ecosystems to invasions (Von Holle and Simberloff 2005). Even species considered to be dispersal-limited but with strong potential for wood production might cross a propagule pressure threshold and become invasive in the future due to high planting intensity (Richardson et al. 2004, Jagodziński et al. 2018).

Ennos et al. (2018) demonstrated that using non-native species for wood production and the diversification of forests presents great ecological and economic risks, potentially to the detriment of native tree species and associated biodiversity. Based on experience in countries with longer histories of using alien conifers, along with objectives to prevent further ecological damage, risk analyses of introduced alien conifers must be performed by monitoring old forest trials and arboreta (Richardson and Rejmánek 2004).

6. Conclusion

Given the observed natural regeneration and dispersal of alien conifers in the old forest arboreta of southern Belgium, we recommend exercising caution when planting them in western temperate Europe. Half of the studied species regenerated, with almost 20% of these exhibiting an invasive behavior. Species showing the highest risk of being invasive were *T. heterophylla* and *A. grandis*, and to a lesser extent *C. lawsonianna*, *T. plicata*, *L. kaempferi*, and *P. menziesii*. Species with more limited dispersal capacities or a lesser proportion of mature trees, such as *A. nordmanniana*, *P. strobus*, *P. sitchensis*, and *A. veitchii*, could become of concern if planted at large scales. The results show that forest arboreta act as entry points for invasive species, especially now that more forestry trials are being set up to compensate for the die-off of native productive species. Thorough monitoring of alien conifers introduced for wood production is therefore needed to take early action for control and avoidance of larger introductions.

3

The invasive potential of exotic deciduous trees assessed in Belgian arboreta

1. Introduction

As trees often act as ecosystem engineers modifying biotic and abiotic conditions of their habitat, tree invasion can be particularly impacting on native biodiversity (Pyšek 2016). Seventy-six tree species have already been identified as invasive by Rejmánek in 2014, but there can be a long lag phase between the introduction of an exotic tree species and the moment it becomes invasive. Therefore, an invasion debt exists in Europe regarding invasive trees (Essl et al. 2011b).

Many tree species were introduced in Western Europe in the 19th century for ornamental or sylvicultural purposes (Nyssen et al. 2016). Several deciduous trees are already considered invasive in Belgium, such as *Prunus serotina*, *Acer negundo* and *Robinia pseudoacacia*. The two latter are mainly invasive in open, disturbed habitats (Vítková et al. 2017, Sikorska et al. 2019). However, invasions of trees also occur in closed forests, as seen with *Prunus serotina*, a cherry tree introduced for wood production that quickly invaded forest understories and turned out to be economically useless (Vanhellemont et al. 2009). Shade-tolerant exotic species are often underestimated as invaders because of a longer lag-phase and low surveillance, and might reveal to be particularly at risk of becoming invasive (Martin et al. 2009).

Richardson et al. (2000) defined an invasive plant species as a naturalized species producing a large number of reproductive offspring, often at far distance from the parent plants. A benchmark of dispersal is set at > 100 m in 50 years for invasive plant species dispersed by seeds. By measuring the natural regeneration from mature plantings, it is therefore possible to assess the invasiveness of introduced exotic trees (Fanal et al. 2021). In Wallonia, Southern Belgium, trial plantings were set in public forests in late 1800s and early 1900s to test species for wood production, both native and exotic, broadleaved and coniferous. These trials are now over a century old and represent a great opportunity to study the natural regeneration and dispersal of exotic trees.

In this study, we used old public arboreta as natural experiments to assess the potential invasiveness of exotic deciduous tree species in Western Europe forests. To this end, we quantified the natural regeneration in terms of abundance and distance to parent trees.

2. Material and Method

The sampling method is the same as in Chapter 2 (Fanal et al. 2021). We selected 8 public arboreta with low management over the last 15 years and similar species compositions.

Field sampling was conducted from April to July 2018. Sampling was systematic and covered the entire arboreta and a 100-m buffer, representing 129.5 ha in total. For each arboretum, a 30×30 m grid was applied and a plot of 2-m radius was installed at each intersection. In total, 1109 plots were sampled in forested areas (from 71 to 244 plots per arboretum). We considered as exotic species non-native from Western continental Europe for consistency with Fanal et al. (2021).

In each plot, all individuals of tree species (from seedlings to mature trees) were identified and their height measured from the ground to the tip of the main stem. We considered as “individuals” single stems originating from seeds or non-visible vegetative reproduction. Resprouts from the base of mature trees were not counted. Individuals were then assigned to the following size classes: class 0 for seedlings between 0 and 0.3 m high, class 1 for saplings between 0.3 m and 1.3 m high (height of measurable diameter at breast height, DBH), class 3 for trees higher than 1.3 m but with DBH smaller than 5 cm, class 4 for trees with DBH between 5 and 9.9 cm, and so on for every 5 cm increment in DBH.

The distance of trees resulting from natural regeneration to the closest potential parent trees was measured with the ArcGIS program (ESRI 2019). Density of regeneration according to the distance was plotted with the “ggplot2” and “ggridges” packages (Wickham 2016) for species with more than 30 measured recruited individuals. The percentage of stems in each size class was also calculated.

Regeneration Density (RD) was calculated within each arboretum by dividing the number of stems by the total area of plots (ha) surveyed in the arboretum. The mean RD across arboreta was then calculated for each species. The area of planted exotic trees in the arboreta varied greatly between species, leading to very heterogeneous propagule pressures. Therefore, the density of regeneration was also divided by the planted area (ha) of the species for each arboretum, which resulted in the Weighted Regeneration Density (WRD). The Mean WRD across all arboreta was also calculated for each species.

3. Results

Exotic deciduous trees represented 12 % of the surface planted in the arboreta. 76 % of trees originating from natural regeneration were European, mainly *Quercus petraea*, *Fagus sylvatica* and *Acer pseudoplatanus* for broadleaves, and *Picea abies* for conifers. Exotic broadleaves represented 9% of measured the natural regeneration. Six percent of the individuals counted were species recognized as invasive in Belgium: *Quercus rubra*, *Prunus serotina*, *Robinia pseudoacacia* and *Acer rufinerve*.

Figure 3-1 presents the mean regeneration density of deciduous species per hectare. Maple species represent half the species for which more than 30 stems were measured. Figure 3-2 represents the mean weighted density of regeneration of the same species. WRD of *Cornus nuttallii* peaks at 455 940 estimated trees per ha. However, the species was planted only in one arboretum, and the observed regeneration was a dense regeneration patch under the parent trees. These parent trees were planted only on a small area of 20 m², resulting in a disproportionate WRD (Table 3-1). All the species were planted on less than one ha, thus WRD is always greater than RD.

Table 3-1: Eleven exotic species for which more than 30 stems were measured. N sites = number of arboreta where the species was planted, planted surface = total planted area across all sites (ha), N plots = number of plots in which the species was found, N stems = number of measured stems, Mean RD = mean regeneration density across sites (stems.ha^{-1}), WRD = mean weighted regeneration density (stems.ha^{-1}.ha$_{planted}$$^{-1}$).

Species	**N sites**	**Planted surface**	**N plots**	**N stems**	**Mean RD**	**Mean WRD**
Acer rufinerve	1	0.039	10	223	1258.6	31943.3
Quercus rubra	8	0.806	66	1342	1146.7	13274.4
Cornus nuttallii	1	0.002	2	86	866.3	455940.2
Acer palmatum	1	0.011	6	126	699.8	65404.7
Prunus serotina	3	0.164	131	444	583.3	31345.7
Acer lobelii	2	0.065	11	124	427.6	20361.1
Zelkova serrata	2	0.021	3	38	382.8	23058.9
Acer japonicum	1	0.029	3	41	231.4	8090.8
Robinia pseudoacacia	3	0.315	17	85	159.9	513.5
Acer saccharinum	3	0.066	8	62	138.9	6311.7
Acer rubrum	7	0.396	18	129	109.3	4649.3

Most of the regeneration was found close to the parent trees, with mean distances under 50m from the closest planting, with the exception of *Prunus serotina* with a mean dispersal value of 72 meters. *Quercus rubra* and *Prunus serotina* present flatter density lines, with important dispersal far from parent trees and stems found around 300 meters (Figure 3-3). All species were found further than 100 meters, except for *Cornus nuttallii*, *Acer palmatum* and *Zelkova serrata*.

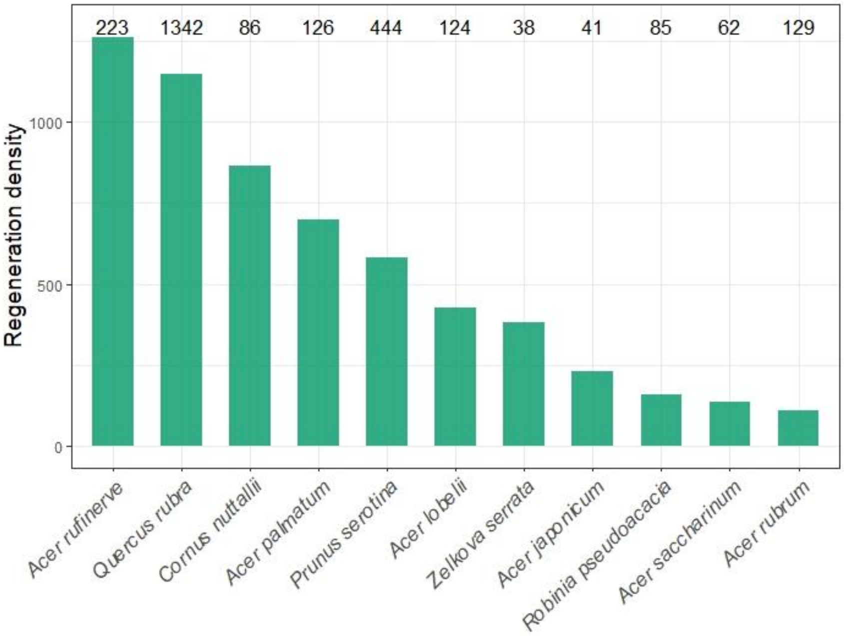


Figure 3-1: Mean regeneration density for the 30 deciduous species with more than 30 measured recruited trees (stems.ha^{-1}).

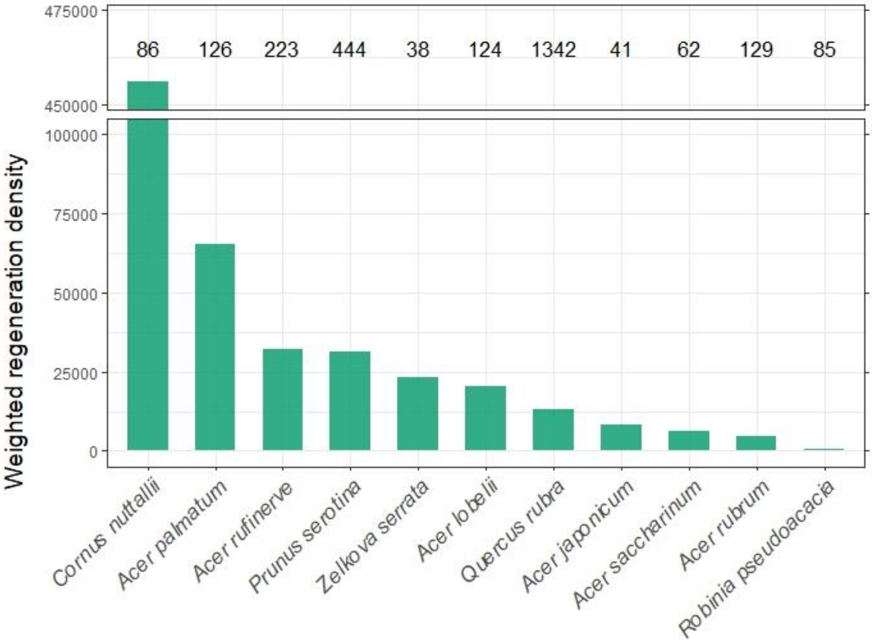


Figure 3-2: Mean weighted regeneration density for the 30 deciduous species with more than 30 measured recruited trees (stems.ha^{-1}.ha$_{planted}^{-1}$).

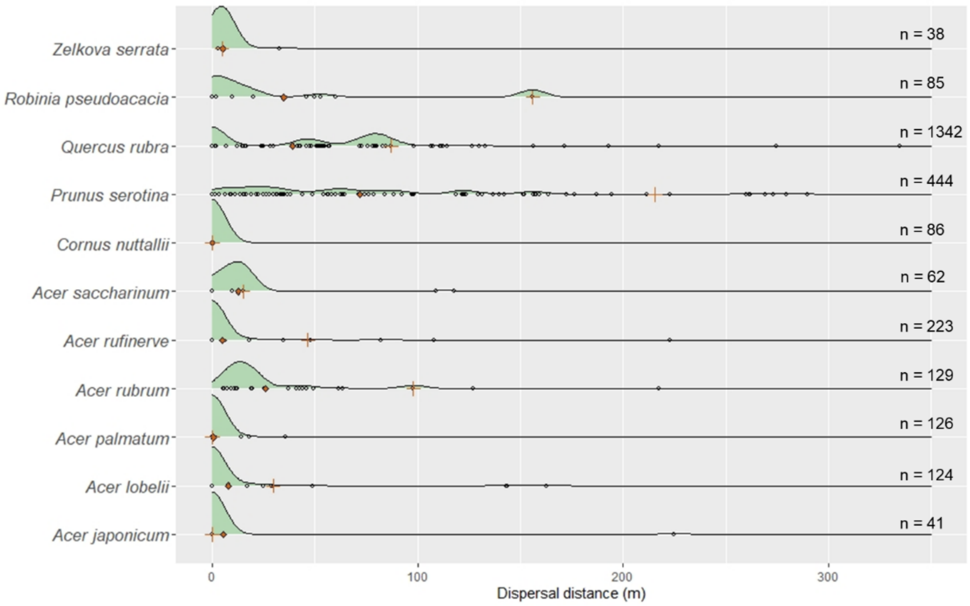


Figure 3-3: Density lines of the distance of exotic trees from the closest potential parent. An orange point represents the mean distance, an orange cross represents the 95th percentile. n = number of counted individuals.

The majority of the measured trees were seedlings under 0.3 m high, except for *Robinia pseudoacacia* and *Cornus nuttallii* for which most of the regeneration was made of saplings between 0.3 and 1.5 m high. Except for *Acer rubrum*, all species had young trees over 1.5 m in the sampled regeneration. Trees with DBH over 15 cm were found for *Acer saccharinum*, *Acer rufinerve*, *Prunus serotina* and *Quercus rubra* (Figure 3-4).

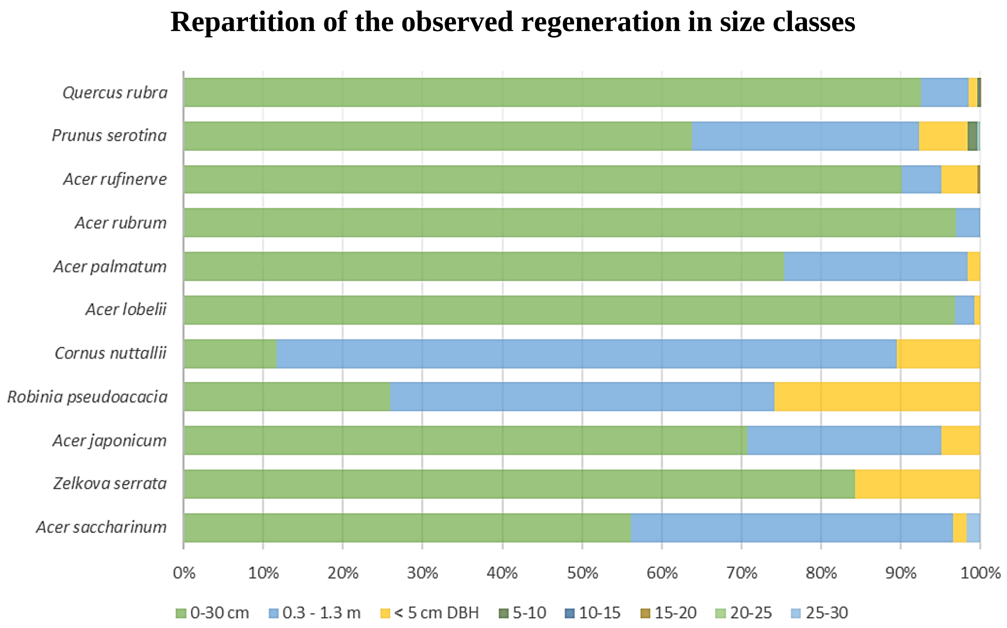


Figure 3-4: Repartition of the regeneration into the size classes. First class is for seedlings less than 0.3 m high, second class is for saplings between 0.3 and 1.5 m, class 3 is for young trees over 1.5 m but less than 5 cm of DBH, next classes are 5 cm increments in DBH.

4. Discussion

Monitoring old arboreta allowed us to identify some exotic deciduous species presenting abundant regeneration and important dispersal distances from parent trees. In the results, we focused on the species for which we found more than 30 recruited trees in the plots. Four of these species are known invasive trees: *Acer rufinerve*, *Quercus rubra*, *Robinia pseudoacacia* and *Prunus serotina*. In addition of Acer rufinerve, five other *Acer* species also figure in our “top eleven” of regenerating species: *Acer rubrum*, *Acer japonicum*, *Acer palmatum*, *Acer saccharinum* and *Acer lobelii*.

Considering the regeneration density, *Acer rufinerve* and *Quercus rubra* are the two most common exotic species in the regeneration. Both are shade tolerant species capable of growing under the forest cover. *Robinia pseudoacacia*, a prolific exotic tree, only occupies the 9th position; most of our plots were situated under a dense canopy, while this pioneer species is light-demanding at the seedling stage and was found in plots situated in small forest clearings. Under Belgian latitudes, this species also predominantly displays vegetative regeneration. Seeds germination rates are indeed low, especially in cold regions with frequent spring frost events (Vítková et al. 2017, Bouteiller et al. 2018).

In our similar study on the regeneration of exotic conifers in the same 8 arboreta (Fanal et al. 2021), we ranked the species based on their weighted regeneration density to take into account the varying propagule pressure amongst species. We executed the same procedure with deciduous species. However, caution is needed when interpreting the results. Some of the species were planted in only one arboretum and on a really small surface. If a dense patch of seedlings is measured under the parent trees, the calculated WRD becomes unreasonably excessive. This is the case for *Cornus nuttallii*, planted on 20 m² in the arboretum of Virton, of which 86 small seedlings were found in two plots near the parent trees and WRD culminates above 450 000 trees/ha.ha$_{\text{planted}}$. When judging the invasive behavior of a species, one must take into account that the weighted regeneration density must be viewed with a critical eye. The occurrence of the species, i.e. the number of plots in which it was found, can also give some insight on the invasive potential. Likewise, part of the regeneration needs to reach maturity for the species to become invasive. If most of the sampled trees were seedlings and saplings under 1.5 m high, taller trees were found for *Acer saccharinum*, *Acer rufinerve*, *Prunus serotina* and *Quercus rubra*, indicating their potential to reach maturity and in turn produce offspring.

Another critical component of invasiveness is dispersal. *Zelkova serrata*, *Cornus nuttallii*, *Acer palmatum* and *Acer japonicum* were only found close to the parent trees. Their potential to disperse and colonize areas at far distances is therefore limited. Rare long dispersal events were found for *Acer rubrum*, *Acer saccharinum*, *Acer rufinerve*, *Acer lobelii* and *Acer japonicum*, with 1 to 5 stems found past 100 meters and at maximum 250 meters. On the contrary, many saplings of *Robinia pseudoacacia*, *Quercus rubra* and *Prunus serotina* were found at greater distance, well above 100 meters, confirming their invasiveness. The capacity of these species to disperse at further distance is likely due to their dispersal mode: zoochory allows faster colonization rates than anemochory (Dyderski and Jagodziński 2019b, Masaki et al. 2019). For example, seeds of *Quercus rubra* are frequently carried over 1500 m away from parent trees by jays, which increases the rate of LDD events compared to win-dispersed species which relies more on extreme wind speeds or turbulences (Bullock and Clarke 2000, Myczko et al. 2014). Rare LDD events can also happen *via* human-mediated dispersal through walking shoes or forestry machines (Pickering and Mount 2010). A human walker can easily unknowingly disperse seeds over 5 km (Wichmann et al. 2008). Species planted along forest walking paths and logging trails would more likely benefit from this type of dispersal.

The genus *Acer* is the most prolific genus in term of regeneration in our public arboreta. This is particularly the case in the arboretum of Seraing, where several ornamental maple species were planted as the site is regularly visited by local dwellers. As their potential for wood production is low, except for *Acer rubrum*, most of these species were not planted in the other arboreta. Several maple species are already known to be invasive worldwide, such as *Acer negundo*, *Acer rufinerve*, *Acer pseudoplatanus* or *Acer platanoides*, and it seems that the *Acer* genus is a substantial source of potentially invasive species and must therefore be watched carefully.

In our similar study on exotic conifer species, environmental variables were also studied to understand the abiotic conditions and types of forest cover enhancing the regeneration of exotic species. These analyses were facilitated by the fact that most of the studied conifers were planted in almost all the arboreta, which is not the case with our studied deciduous species. Indeed, some species were only planted in one or two sites. This situation complicates the analysis of suitable habitats as well as the determination of their invasive behavior.

5. Conclusion

Our study confirms the invasive behavior of already well-known invasive deciduous trees, and provides more evidence that invasions of trees also occurs in forest ecosystems with low disturbance. Abundant regeneration of *Acer* species was found, the genus being the most prolific in the exotic regeneration found in our arboreta. *Zelkova serrata* and *Cornus nuttallii* only regenerated under their own cover and present low risk of dispersing in the nearby environment. However, given the high densities of seedlings observed and their recruitment to the sapling stage, these species must be watched carefully in the future in case the propagule pressure would increase.

4

Recruitment curves of three non-native conifers in temperate forests.

Recruitment curves of three non-native conifers in temperate forests: implications for invasions.

Fanal Aurore, Mahy Grégory, Monty Arnaud

6. Abstract

Few conifers are considered invasive in Europe, yet several recent studies indicate that several coniferous species used for forestry display an invasive behavior with abundant regeneration and spread into surrounding natural habitats. Three species have been identified as being particularly at risk in old forest arboreta in Southern Belgium, but data is lacking regarding their dispersal ability. In this study, we characterize the recruitment curves of *Tsuga heterophylla* (Raf.) Sarg., *Abies grandis* (Douglas ex D.Don) Lindl. and *Thuja plicata* Donn ex D.Don. Four to six isolated plantations were monitored and realized dispersal (*i.e.* seedlings and recruited regeneration) was exhaustively recorded and measured over 750 meters in three different directions. We calculated the wave expansion rate and frontier expansion rate for each planting site, and fitted dispersal kernels for each site and species. Regeneration was classified in three size categories (seedlings, saplings and trees taller than 1.5 m), and the recruitment distances were analyzed for each size class. The effect of the forest type cover (deciduous, coniferous, open or mixed) on the density of regeneration was also investigated with regression models. The recruitment curves varied greatly across sites, showing heterogeneous habitat suitability and uneven post-germination processes. Considering the frontier expansion rate, the three conifers cross the threshold rate of invasiveness in at least three sites per species. Forest cover type had a significant effect on the regeneration density, which is favored by coniferous covers as well as open areas for *Tsuga heterophylla*. An escape effect is also noticed as mean and maximal distances of saplings and taller trees were greater than those of seedlings. Our study indicates that *Tsuga heterophylla* displays the higher risk of rapid spread into adjacent natural habitats, followed by *Abies grandis*. *Thuja plicata* faces more important establishment and recruitment limitations. We argue that on-site monitoring of dispersal and recruitment of exotic tree species is crucial to predict the risk of invasion into natural habitats, including forest ecosystems.

7. Introduction

Silviculture is one of the main paths of introduction of invasive tree species (Pyšek 2016). Essl et al. (2010) demonstrated that conifers introduced for wood production had higher chances of escaping cultivation than conifers introduced for other purposes. Invasions by conifer species are mainly documented in the Southern hemisphere, for example with *Pinus* species in New Zealand and South Africa, or *Cryptomeria japonica* in the Réunion Island (Richardson and Rejmánek 2004, Richardson et al. 2004, Edwards et al. 2021). In Europe, few cases of invasion by conifers are reported. It may be because of a more recent history of introduction, as well as a phylogenetic proximity of introduced species with native conifers (Carrillo-Gavilán and Vilà 2010). However, some conifer species are known to have an invasive behavior in temperate forests of Europe. For example, *Picea sitchensis* is considered invasive in Norway, reports of dense regeneration of *Tsuga heterophylla* exist in Scotland and studies recommended not to plant *Pseudotsuga menziesii* close to sensitive natural habitats in Germany (Forestry Commission Scotland 2015, Nygaard and Øyen 2017, Bindewald et al. 2021a).

Dispersal is a critical component of the invasion process. An invasive tree species must be capable of creating new populations far from the planted parent trees. Dispersal curves are built to model the dispersal over the distance from a seed source. They correspond either to the predicted density of seeds as a function of distance, or to probability density function, also called dispersal kernels, representing the distribution of post-dispersal locations at different distances from the parent trees (Nathan et al. 2012). Several standardized dispersal kernels are described in the literature, which perform relatively well according to the studied growth form or dispersal mode (Bullock et al. 2017). Wald, 2DT, Lognormal and mixed models are often preferred for wind-dispersed species (Bullock and Clarke 2000, Greene et al. 2004, Martin and Canham 2010, Norghauer et al. 2011, Loebach and Anderson 2018, Wyse and Hulme 2021). However, the preliminary choice of a function is quite subjective, and the best approach is to fit several functions and assess their relevance with a best-fit approach and examination of the credibility of the tail prediction (Bullock et al. 2006).

Some functional traits have also been related to dispersal capacities, such as the propagule size and mass and its terminal velocity, plant height, and number of seeds produced (Caplat et al. 2012, Moravcová et al. 2015, Johnson et al. 2019). In 2014, Tamme et al. demonstrated that decent predictions of maximum dispersal distances can be achieved using a combination of simple traits, such as dispersal syndrome, growth form, seed mass, seed release height and terminal velocity.

Most seeds dispersed by wind fall near the seed source – those that fall within the canopy rarely exceed a distance of a few tree heights from the parent trees. However, seeds at the top that can encounter updrafts and rise above the canopy are good candidates for Long-Distance Dispersal events (LDD) if the wind is favorable in terms of speed and turbulence (Bullock and Clarke 2000, Horn et al. 2001).

If the study of seeds dispersal if crucial to understand the capacity of a species to reach long distances, the germination and recruitment of seedlings also play a critical role in the abundance and spatial structure of the natural regeneration and in populations dynamics (Amm et al. 2012, Beckman et al. 2020) (Fig. 4-1). Realized dispersal is the combination of seed dispersal and establishment of seedlings (Bullock et al. 2006). The distribution of surviving seedlings can be impacted by the spatial distribution of suitable micro-habitats in the surroundings, post-dispersal predation, intra- or inter-specific competition as well as the mortality rate of the seedlings (Amm et al. 2012), hence the shape of the recruitment curve can be quite different from the shape of the seed shadow. This vulnerability to predators is often believed to be more important close to the parent trees, this distance-dependent process being called the Janzen-Connell effect (Janzen 1970, Connell 1971). Recruitment of seedlings should therefore be more important far from parent trees – this effect has been rephrased more simply as the “escape hypothesis” by Howe and Smallwood (1982). However, Hubbell (1980) argues that recruitment near adult trees is more important due to the much higher seed densities. Martin et al. (2010) clearly identified a density-dependent effect for recruitment curves of both native and exotic species in closed temperate forests of Connecticut, the mean dispersal distance of seedlings being further from parent trees than the mean dispersal distance of seeds. The escape hypothesis was also validated in a study on *Pinus halepensis* in Israel, where Nathan et al. (2000) found that the probability of seedlings’ survival increased with the distance from plantation.

Replacing seed traps by seedlings counts on large areas and analyzing the recruitment curves allows to better understand the spatial distribution of the offspring and bring post-germination processes to light (Amm et al. 2012). In late successional forests, these post-germination events and microsites availability are even more important that the seed dispersal limitations for the spread of a species (Sagnard et al. 2007).

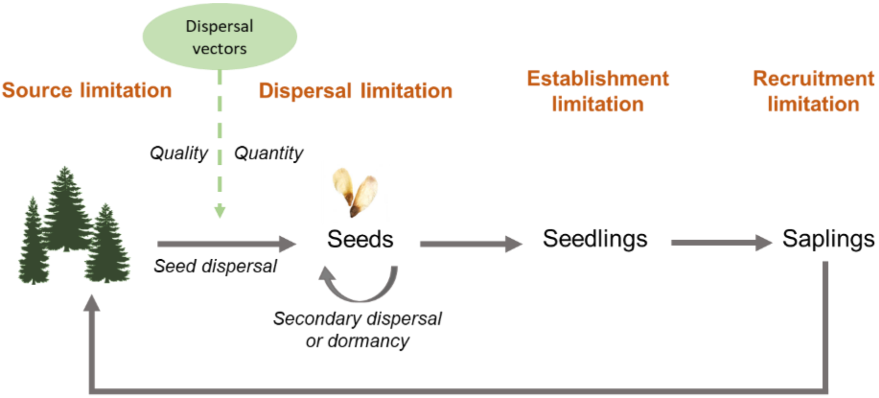


Figure 4-1: Consequences of seed dispersal for plant recruitment, adapted from Beckman et al. (2020).

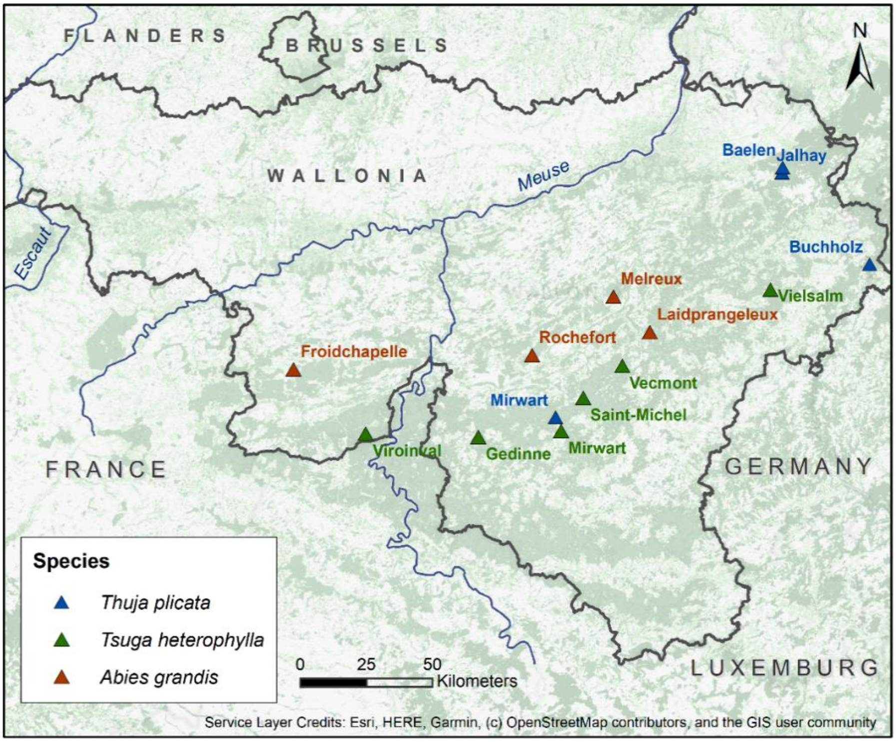
Richardson et al. (2000) suggested the threshold of 100 meters in 50 years for seed-dispersed plants to be considered invasive. As an application of this definition, Nygaard and Øyen (2017) described the dispersal of established regeneration *Picea sitchensis* around plantings in Norway with two indicators: the Wave Expansion Rate (WER), which is the median distance divided by the parent stand age minus their maturity age, and the Frontier Expansion Rate (FER) is the maximum dispersal distance divided by the parent stand age minus their maturity age. These indicators allow to discuss invasiveness with empirical and objective quantitative data.

In a study performed in old forest arboreta of Southern Belgium, Fanal et al. (2021) identified several conifer species displaying an important natural regeneration density and trespassing this threshold of dispersal over 100 meters from plantings in 50 years. However, the measurement of the dispersal was restricted to a 100 m buffer around the arboreta, leading to truncated dispersal curves. In this study, we selected the three wind-dispersed species presenting the highest invasive potential in Fanal et al. (2021) based on the combination of their regeneration density, dispersal distance and size structure*: Tsuga heterophylla*, *Abies grandis* and *Thuja plicata*. These three species were planted in forest trials in Southern Belgium during the last century, but to a very limited extent.

The aim of this study is to (1) describe the fitted recruitment curves of the three non-native conifers in several isolated planting sites and test a potential escape effect, (2) characterize the realized dispersal with quantitative indicators to assess the invasiveness of the three species, and (3) test whether the type of forest around the plantings impacts the dispersal distances and regeneration densities.

8. Material and method

Four to six sites per species were selected in Southern Belgium. These sites are isolated, monospecific and even-aged small stands (less than 1 hectare), at least 2 km away from plantings of the same species or related species that could be confounded at the seedling stage, and are at least 50 years old. Dates of planting ranged from 1919 to 1970. The elevation of the sites ranges from 197 to 634 meters above sea level. The exact location of these sites is given in Table 1 and Fig. 4-2. Surroundings of plantings varied according to the location but mainly consisted in forest areas, from native beech forests to intensively planted spruce stands, sometimes with the presence of open clearcuts or grasslands.



Service Layer Credits: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 4-2: Location of the study sites for each species in Wallonia, Belgium. Background on the map is the tree cover in 2000 (Hansen et al. 2013).

Fieldworks took place from 2018 to 2022. At each site, three directions were randomly chosen. A circle sector of 10° and 750 meters long was delimited for each direction, starting 20 meters inside of the planting to describe the regeneration under the parent trees as well (Fig. 4-3). This methods ensures a constant sampling effort along increasing distance (Bullock and Clarke 2000). For each 10-meters interval, the number of individuals originating from the natural regeneration was counted and assigned to one of the three size classes: 0 to 0.3 m (A), 0.3 to 1.5 m (B) and more than 1.5 m (C). The type of forest cover (deciduous, coniferous, mixed or open) was also noted for each 10-m interval.

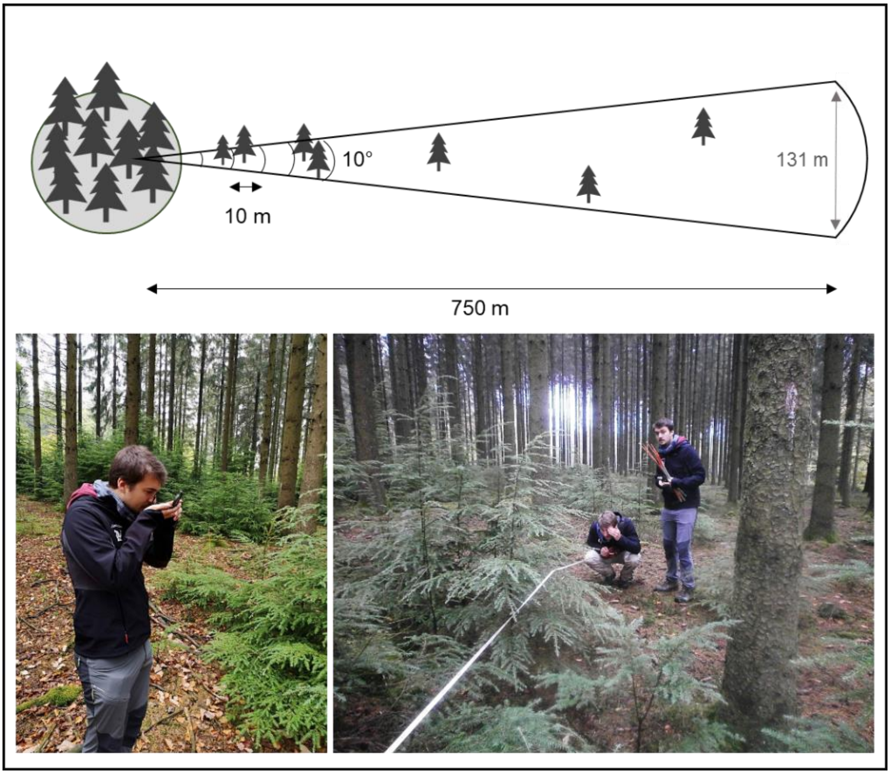


Figure 4-3: Delimitation of a 10° circle sector starting 20 meters inside the planting. The 10-m sections were delimited with stakes and the direction was held with the help of a compass.

For each site, histograms of the logarithm of the density in relation to the distance to the planting are plotted. They also include the regeneration density values in the 20 meters inside the plantings. For the rest of the analyses, only seedlings outside plantings will be considered.

Descriptive statistics are retrieved for each site: the mean, median, maximum and 95th percentile of dispersal distance and the maximum regeneration density. An Anova on rank-transformed maximal value of dispersal was performed on the maximum dispersal values in each sector with the species and sites as grouping variables to test whether the maximum dispersal distances differ significantly between species. The Wave Expansion Rate (WER) and the Frontier Expansion Rate (FER) were calculated following the method described in Nygaard and Øyen (2017). Age of first fecundity of the three species was retrieved from Petit et al. (2017): 25 years for *Tsuga heterophylla* and *Abies grandis*, and 20 years for *Thuja plicata*. Descriptive statistics on dispersal distances and number of seedlings per size class were also retrieved.

The “dispfit” package was used to model the probability density functions for each species. The “dispfit” package fits and compares several parameterized functions usually used in dispersal studies to describe dispersal curves and predict dispersal distances (Proença-Ferreira et al. 2023). For each site as well as the combination of all sites per species, the best function was selected based on AIC. The parameters value, mean, skewness and kurtosis were extracted with the “dispfit” package. The predicted values were plotted with the “ggplot2” package (Wickham 2016). All analyses were performed in R Studio (R Core Team 2022).

To test the influence of the forest cover type on the density of regeneration, zero-inflated Gamma regressions were fitted on the dispersal distances for each species with the “glmmTMB” package (Brooks et al. 2017). Forest cover type and distance were set as fixed effects, site as random effect and the logarithm of density as response variable. The distance was also used as covariate for the zero-inflated part of the model. Significance threshold was set at P=0.05. The predicted values for each cover type were plotted with the “ggeffects” package (Lüdecke 2018). The effect of time since planting on the maximum regeneration density and on the mean and maximum dispersal distances was finally tested with the “lmerTest” package (Kuznetsova et al. 2017), with the interaction of age and species as fixed effect and site as random effect.

9. Results

In total, 11077 *Tsuga heterophylla*, 26435 *Abies grandis* and 1070 *Thuja plicata* were counted across all sites (seedlings, saplings or even mature trees originating from natural regeneration). If we remove the first 20 meters inside the plantings, the numbers drop to 4889, 18347 and 378 respectively. Therefore, 35 to 69 % of the counted regeneration was situated under the planting. However, 92 to 93 % of this under-parent’s regeneration was under 0.3 m high. The raw dispersal data, expressed as the natural logarithm of the density of regeneration according to the distance from plantings, is shown for the three species in Figures 4-4A, 4-5A and 4-6A.

When we consider the regeneration outside plantings (after distance 0), the number of individuals ranged from 55 to 3593 for *Tsuga heterophylla*, 6 to 33 for *Thuja plicata* and 213 to 12485 for *Abies grandis* (Table 4-1). Maximum regeneration densities reached 5.27 trees/m² for *Tsuga heterophylla*, 3.02 trees/m² for *Thuja plicata* and 55.2 trees/m² for *Abies grandis*. The mean dispersal distance across all sites was 68.4 m for *Tsuga heterophylla*, 30.1 m for *Thuja plicata* and 23.25 m for *Abies grandis*. Median distance observed was 50 m for *Tsuga heterophylla*, 22.5 m for *Thuja plicata* and 15 m for *Abies grandis*. WER ranged from 0.14 to 6.21 m/year for *Tsuga heterophylla*, from 0.11 to 1.22 m/year for *Thuja plicata* and from 0.17 to 1 m/year for *Abies grandis*, while FER varied from 0.38 to 17.12 m/year for *Tsuga heterophylla*, from 1.49 to 6.02 m/year for *Thuja plicata* and from 2.93 to 10.14 m/year for *Abies grandis*. The maximum density of regeneration also varied greatly between sites, from 0.55 to 5.27 trees/m² for *Tsuga heterophylla*, 0.07 to 3.02 trees/m² for *Thuja plicata* and 1.26 to 55.2 trees/m² for *Abies grandis*.

Time since planting varied from 50 to 101 years. However, we did not find any significant effect of time since planting on the maximum regeneration density, nor on the mean and maximum dispersal distances.

The probability density functions show right-skewed, leptokurtic recruitment curves, with parameters varying greatly between sites (Table 4-2). Particularly, the curve of Mirwart presents a remarkably flat shape and fat tail and differs greatly from all the other recruitment curves of *Tsuga heterophylla* (Figure 4-5). In most cases, most of the seeds fall in the first 100 meters of the seed source. Among all the tested functions, the Wald function was the most often selected, followed by the 2Dt function.

Dispersal parameters also varied according to the considered size class. Looking at Table 4-4, mean and median distances are often higher for trees above 0.3 m (B) and 1.5 m (C) than for seedlings under 0.3 m (A). If we consider the 95th percentile of distance, saplings and well-established trees are found further from plantings than seedlings: 201.9 (B) and 195.3 m (C) against 93 m for seedlings of *T. heterophylla*, 85.9 (B) and 82.7 m (C) against 55 m for seedlings of *A. grandis* and 89.3 (B) and 71.5 m (C) against 48.3 m for seedlings of *T. plicata*.

Tsuga heterophylla

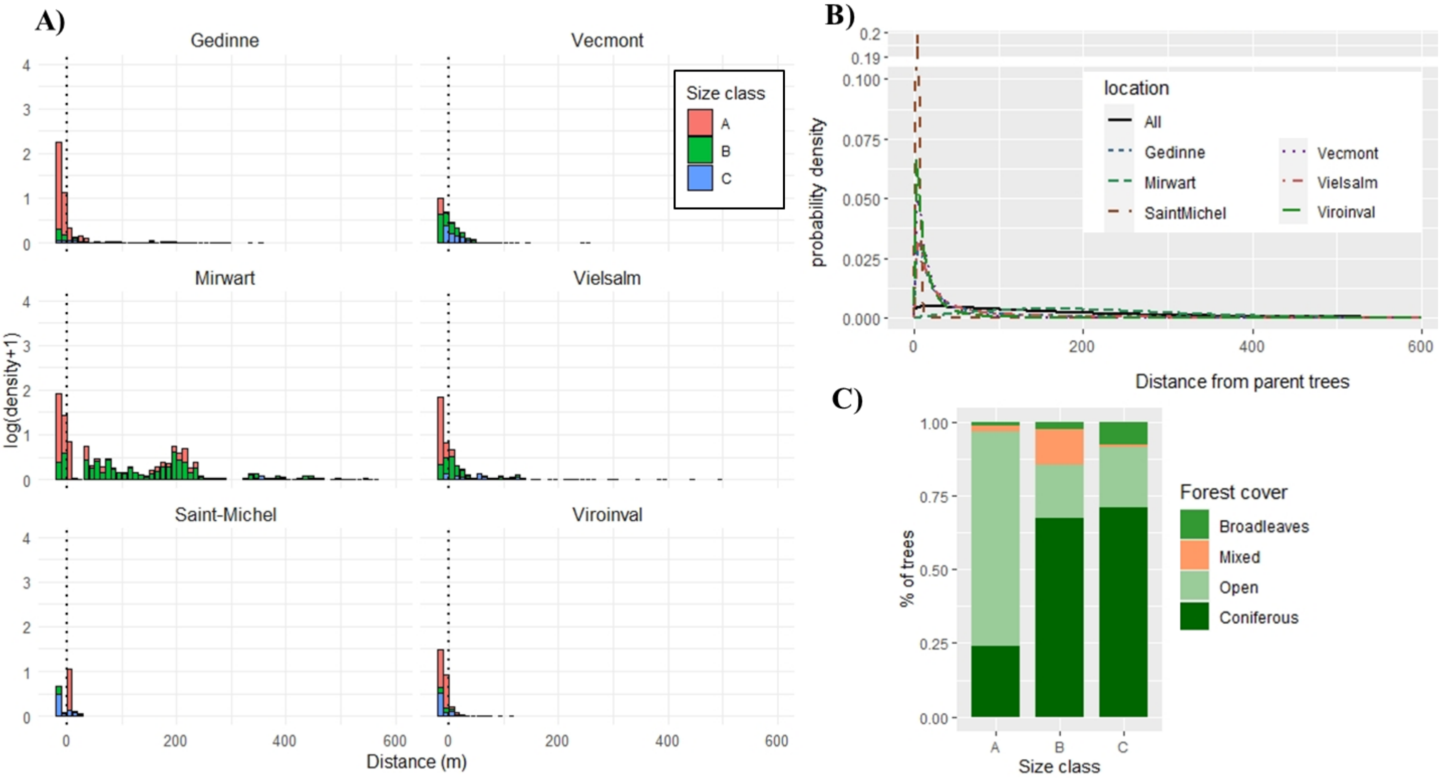


Figure 4-4: **A)** Raw data of dispersal of *Tsuga heterophylla* per site. Y axis is the mean of the log of regeneration densities between 3 sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the size classes: A for seedlings < 0.3 m, B for saplings between 0.3 and 1.5 m, C for young trees > 1.5 m. **B)** Comparison of predicted values of dispersal (probability density functions) for each site and for the combination of all sites. Best model, based on AIC, is used each time. **C)** Proportion of trees found under each forest cover type.

Abies grandis

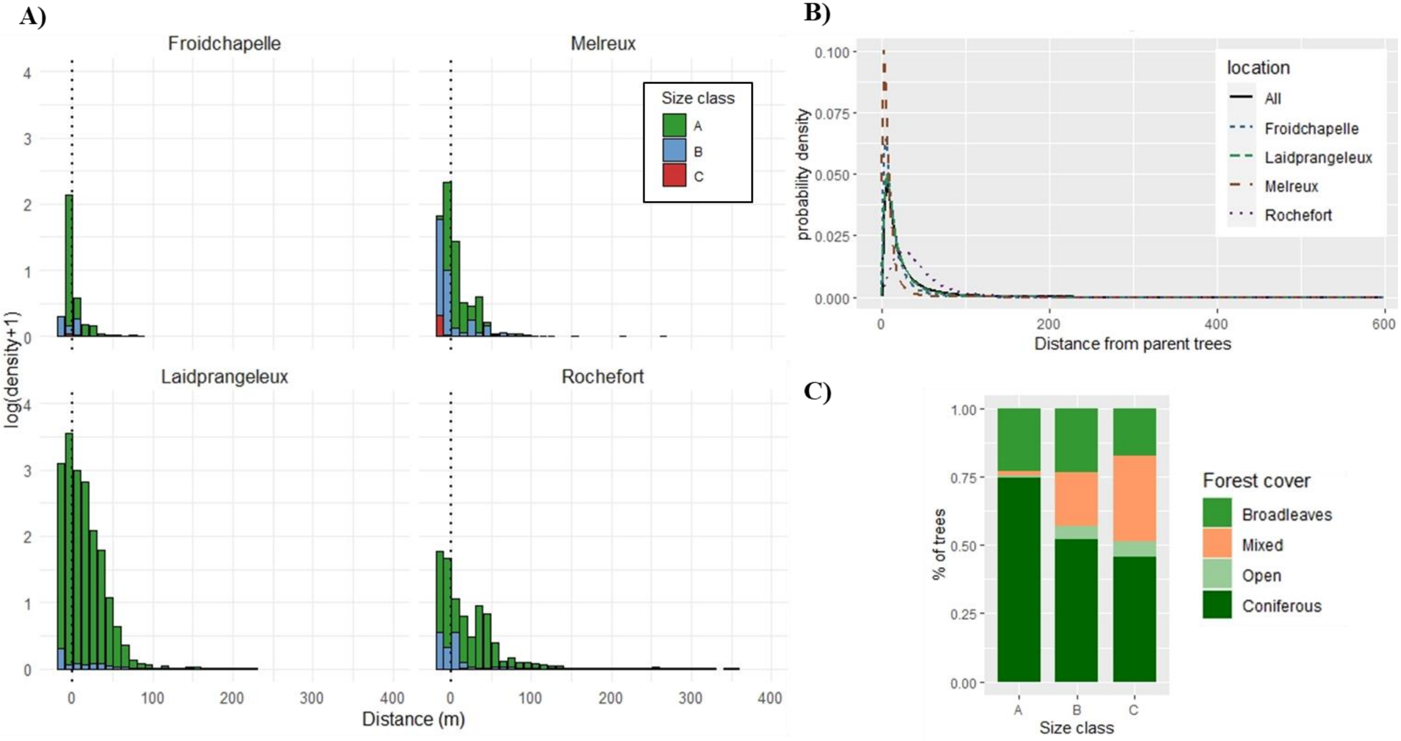


Figure 4-5: **A)** Raw data of dispersal of *Abies grandis* per site. Y axis is the mean of the logarithm of regeneration density between three sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the three size classes: A for seedlings less than 0.3 m, B for saplings between 0.3 and 1.5 m, C for young trees above 1.5 m. **B)** Comparison of predicted values of dispersal (probability density functions) for each site and for the combination of all sites. Best model, based on AIC, is used each time. **C)** Proportion of trees found under each forest cover type.

Thuja plicata

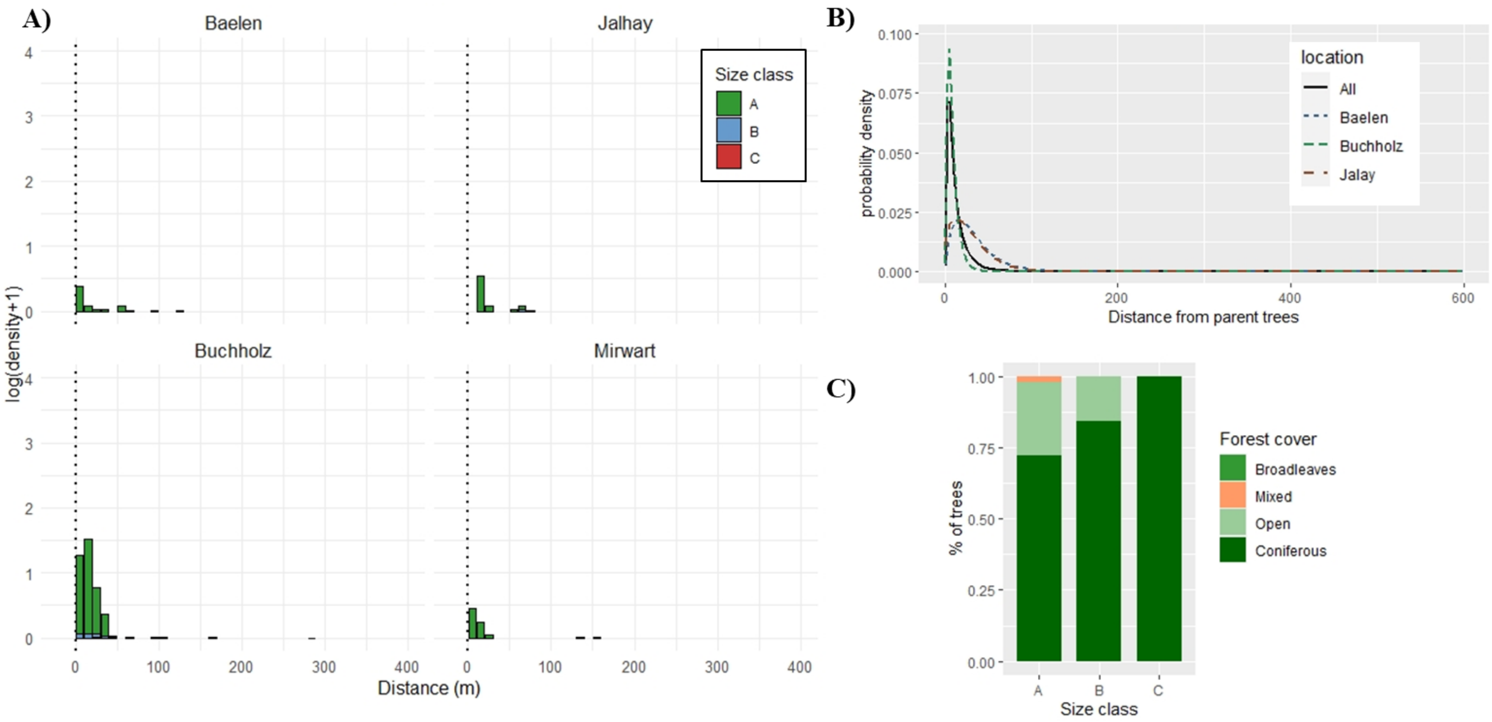


Figure 4-6: **A)** Raw data of dispersal of *Thuja plicata* per site. Y axis is the mean of the logarithm of regeneration density between three sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the three size classes: A for seedlings less than 0.3 m, B for saplings between 0.3 and 1.5 m, C for young trees above 1.5 m. **B)** Comparison of predicted values of dispersal (probability density functions) for each site and for the combination of all sites. Best model, based on AIC, is used each time. **C)** Proportion of trees found under each forest cover type.

Table 4-3: Description of the sites where the dispersal of the three species was investigated. GPS coordinates in World Geodetic System 84 (WGS84) and elevation of the sites are given. "Date" is the date of planting. Realized dispersal is described with the mean, median, 95th percentile and maximum distance. "N tot" is the total number of trees measured on the site. "Max density" is the maximum density (trees.m^{-2}) observed on a site. WER is the Wave Expansion Rate, FER is the Frontier Expansion Rate.

Sp.	**Site**	**North**	**East**	**Elev.**	**Date**	**Mean Disp.**	**Median Disp.**	**Max Disp.**	**0.95 Disp.**	**N tot**	**Max density**	**WER**	**FER**
				(m)		(m)	(m)	(m)	(m)		(trees.m^{-2})	(m.year^{-1})	(m.year^{-1})
Tsuga heterophylla	Gedinne	49.994760	4.989154	453	1919	84.1	35	355	265	244	1.28	0.46	4.67
	Mirwart	50.008066	5.270249	455	1962	210.1	205	565	445	3593	1.35	6.21	17.12
	Saint Michel	50.080360	5.344957	349	1929	5.9	5	25	15	261	5.27	0.08	0.38
	Vecmont	50.149503	5.477421	539	1970	23.1	15	255	75	361	1.31	0.60	10.20
	Vielsalm	50.314571	5.980918	523	1959	68.6	35	495	245	375	1.28	0.97	0.42
	Viroinval	50.002262	4.60635	376	1958	18.8	5	115	75	55	0.55	0.14	13.38
Thuja plicata	Baelen	50.578992	6.023314	418	1967	33.9	35	105	78	19	0.09	1.06	3.18
	Buchholz	50.369946	6.31839	634	1956	11	5	265	15	333	3.02	0.11	6.02
	Jalhay	50.567341	6.021211	428	1963	30.5	45	55	45.5	20	0.09	1.22	1.49
	Mirwart	50.037305	5.251675	401	1962	45	5	135	130	6	0.07	0.13	3.55
Abies grandis	Froidchapelle	50.141721	4.361153	286	1966	16	5	85	49	213	1.26	0.17	2.93
	Laidprangeleux	50.222638	5.571007	403	1959	22.1	15	225	55	12485	55.2	0.42	6.25
	Melreux	50.300219	5.447739	197	1965	11.3	5	265	35	1694	28.7	0.17	8.83
	Rochefort	50.172900	5.171326	250	1960	43.6	35	355	105	3955	11.9	1.00	10.14

Table 4-4: Estimates of parameter and moments for the best dispersal model on every site. These values were calculated by the “dispfit” R package.

Species	**Site**	**Distribution**	**Parameter 1**	**Parameter 2**	**Mean**	**Std deviation**	**Skewness**	**Kurtosis**
Tsuga heterophylla	Mirwart	2Dt	1069.74	22.34	208.94	15.40	262.47	285.68
	Gedinne	Wald	84.20	18.09	84.20	181.66	117.09	69.81
	Saint-Michel	Log-normal	5.46	0.32	5.74	1.88	1.01	1.88
	Vecmont	Wald	23.08	18.48	23.08	25.79	61.96	18.73
	Vielsalm	Wald	68.69	19.18	68.69	129.99	108.90	53.72
	Viroinval	Wald	18.83	12.45	18.83	23.15	45.94	22.68
	All	Weibull	171.30	1.10	165.10	149.76	1.72	4.31
Abies grandis	Laidprangeleux	Wald	22.08	20.12	22.08	23.13	63.23	16.46
	Froidchapelle	Wald	15.99	16.53	15.99	15.72	48.78	14.50
	Melreux	2Dt	6.17	1.93	10.69	inf	inf	inf
	Rochefort	2Dt	57.35	3.14	42.73	7.32	68.92	107.09
	All	Wald	25.65	19.10	25.65	29.75	66.33	20.18
Thuja plicata	Baelen	Exponential	16.97	NA	16.97	16.97	6.00	24.00
	Buchholz	Log-normal	7.96	0.65	9.81	7.06	2.53	13.23
	Jalhay	Weibull	33.09	1.39	30.21	22.07	1.22	1.91
	All	Wald	13.70	15.10	13.70	13.05	43.14	13.61

Table 4-3: Mean, median, maximum and 95th percentile of distance (m) from parent trees for the three size classes. A is for seedlings under 0.3 m high, B is for saplings between 0.3 and 1.5 m high and C is for trees over 1.5 m high. Values are given for each site, and the mean per species is also calculated. Total number of seedlings per size class and site is also given.

Species	**Site**	**NB**			**mean**			**median**			**perc 95**			**max**		
		A	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Tsuga heterophylla	Gedinne	112	47	85	26.6	152.9	121.9	15	155	145	119.5	295	265	235	355	335
	Mirwart	861	2495	237	176.8	202.2	414.1	205	195	395	275	435	555	335	545	565
	StMichel	237	2	22	5.4	20.0	10.0	5	20	5	5	24.5	15	25	25	25
	Vecmont1	10	192	155	33.0	26.4	18.9	40	15	15	45	105	35	45	255	145
	Vielsalm	38	233	105	19.2	66.2	91.4	5	25	65	86.5	265	235	125	495	495
	Viroinval	19	9	25	13.4	31.7	15.8	15	5	5	27	87	67	45	95	115
	Mean				**45.7**	**83.2**	**112.0**	**47.5**	**69.2**	**105.0**	**93.0**	**201.9**	**195.3**	**135.0**	**295.0**	**280.0**
Abies grandis	Froidchapelle	149	57	7	17.3	10.3	33.6	15	5	5	35	55	82	75	65	85
	Laidprangeleux	12132	353	0	21.8	30.7	NA	15	25	NA	55	75	NA	225	175	NA
	Melreux	1557	134	3	9.3	34.6	28.3	5	25	25	35	88.5	43	265	125	45
	Rochefort	3563	387	3	45.7	23.4	55.0	35	5	15	95	125	123	355	265	135
	Mean				**23.5**	**24.7**	**39.0**	**17.5**	**15.0**	**15.0**	**55.0**	**85.9**	**82.7**	**230.0**	**157.5**	**88.3**
Thuja plicata	Baelen	16	3	0	26.3	75.0	NA	35	75	NA	37.5	102		45	105	
	Buchholz	305	26	2	10.1	18.5	40.0	5	5	40	15	75	71.5	265	145	75
	Jalhay	16	4	0	26.9	45.0	NA	35	45	NA	47.5	45	NA	55	45	NA
	Mirwart	5	1	0	27.0	135.0	NA	5	135	NA	93	135	NA	115	135	NA
	Mean				**22.6**	**68.4**	**40.0**	**20.0**	**65.0**	**40.0**	**48.3**	**89.3**	**71.5**	**120.0**	**107.5**	**75.0**

Table 4-4: Results of the zi-gamma regressions performed on the density of regeneration (log) as a function of the distance from plantation (m) and forest cover type. “Deciduous cover” is the base type used for comparison. Variance of the random effect “site” is also given.

		Covariate	**Estimate**	**Std. Error**	**Z value**	**P value**
Tsuga heterophylla	Conditional Model	Deciduous	-	-	-	-
		Coniferous	1.026	0.226	4.533	**< 0.001**
		Mixed	0.872	0.437	1.997	0.046
		Open	1.310	0.300	4.384	**< 0.001**
		Distance	-0.011	0.001	-16.120	**< 0.001**
	ZI model	Distance	0.007	0.001	11.970	< 0.001
		Random effect variance (site): 1.18				
Abies grandis	Conditional Model	Deciduous	-	-	-	-
		Coniferous	1.317	0.348	3.79	< 0.001
		Mixed	-0.325	0.334	-0.973	0.331
		Open	-0.476	0.326	-1.46	0.144
		Distance	-0.022	0.001	-21.14	**< 0.001**
	ZI model	Distance	0.016	0.001	11.81	< 0.001
		Random effect variance (site): 0.37				
Thuja plicata	Conditional Model	Deciduous	-	-	-	-
		Coniferous	0.080	1.050	0.077	0.939
		Mixed	0.811	1.151	0.704	0.481
		Open	1.780	1.134	1.569	0.117
		Distance	-0.019	0.002	-7.130	**< 0.001**
	ZI model	Distance	0.025	0.005	5.400	< 0.001
		Random effect variance (site): 0.53				

The effect of the forest cover type (deciduous, coniferous, mixed or open) over the density of regeneration was tested with Gamma regressions. Deciduous covers were mainly beech- or oak-dominated stands while coniferous covers mainly consisted in Norway spruce plantings. Open areas were clear-cuts or small forest clearings. There was a significant effect of the forest cover type on the density of regeneration after accounting for distance and sites, except for *Thuja plicat*a (Table 4-3). Even if the latter seems to favor open areas, the smaller number of saplings counted led to higher errors and did not allow to identify a clear pattern. For *Tsuga heterophylla*, regeneration densities are higher under open and coniferous covers (Fig. 4-4 C). *Abies grandis* clearly favors coniferous covers (Fig 4.5 C).

10. Discussion

For an exotic tree species to be invasive according to the definition by Richardson et al. (2000), a species must produce offspring over 100 m in less than 50 years, which corresponds to a spread of 2m/year. It must also be abundant in the established regeneration (Nygaard and Øyen 2017). Finally, its offspring must be capable of reaching maturity and reproduce in turn, creating new populations. Looking at the values of Wave Expansion Rate (WER), the 2m/year benchmark is only crossed once for *Tsuga heterophylla* in the site of Mirwart. However, if we consider the Frontier Expansion Rate, the three species cross the invasive threshold in at least three sites. *Tsuga heterophylla* even reaches the rate of 17m/year in Mirwart and 13m/year in Viroinval. *Abies grandis* maximum rate hits 10 m/year, against 6/m year for *Thuja plicata*. As the maximum distance used for the calculation of FER may represent a rare LDD event, we also calculated the FER with values of the 95th percentile; yet again, the three species cross the threshold of 2m/year at least once. Taking only the rate of spread into account, the three studied exotic conifers meet the criterion for a categorization of invasion.

High densities of regeneration were sometimes observed for our three conifer species, especially for *A. grandis* for which the maximum density measured was 55 trees/m². These high values are usually observed in the first 50 meters after the planting edge, except on the site of Mirwart where high densities of *T. heterophylla* were still observed 200 meters from plantings, probably due to very favorable abiotic and/or biotic conditions for the germination and survival of seedlings. If a high number of stems of *T. heterophylla* and *A. grandis* were found in our sampling sectors (11077 and 26435 respectively), only 1070 stems of *T. plicata* were identified across the four sites.

For *T. heterophylla*, 61 % of the stems were saplings between 0.3 and 1.5 m high, and 13 % were above 1.5 m. Amongst these were cone-bearing mature trees. For Abies grandis, trees over 1.5 m high represent less than 1% of the regeneration (13 individuals) and saplings 5% (931 individuals nonetheless). Finally, only 2 trees over 1.5 m were found for Thuja plicata (<1%) and 34 saplings (9%), against 342 seedlings. The mortality of seedlings seems to be far more important for *A. grandis* and *T. plicata* than for *T. heterophylla*.

Not only are recruited trees present for *T. heterophylla* and *A. grandis*, but taller trees are found further from plantings. The probability of recruitment of seedlings is therefore higher with increased distance from parent trees, which validates the escape hypothesis for our studied species. The shape of the recruitment curves is therefore supposed to be quite dissimilar to the seed shadow, both because of varying favorable micro-sites availability and distance-dependent survival rates. However, we don't have the necessary data to clarify the process under this escape effect; is it due to a reduction of intra-species competition, or a reduction of herbivory and pest pressures? We notice that the regeneration is also very dense inside the plantations, under the parent trees, but most of this regeneration was under 0.3 m high. Maybe the dense planting densities and lack of light reaching the understorey hinder the recruitment of seedlings.

The density of regeneration of the three exotic conifer species varied greatly from site to site. Wald and 2Dt were the most selected functions, two distributions that tend to produce fat tails (Nathan et al. 2012). *T. heterophylla* displayed the most important dispersal distances, reaching 565 m in the site of Mirwart. This site was also characterized by a really flat dispersal curve, with half of the regeneration exceeding 200 m. For the rest of the sites and species, curves were very right-skewed with half of the regeneration in the first 50 meters around the plantings. This is consistent with other observations of recruited dispersal made in similar studies; in Amm et al. (2012), the mean of the realized dispersal distance of *A. alba* is 5 to 25 m from parent trees. In Nygaard and Øyen (2017), median spread distance of *Picea sitka* was often under 50 meters, except for a few sites where it reached up to 200 m.

Long-distance dispersal determines the rate of invasions by allowing the settlement of new populations at far distances. These events are not as rare as one might think (Horn et al. 2001). For wind-dispersed species, the occurrence of LDD events depends more on the characteristics of the winds than on variations in seed traits. LDD is nearly impossible to detect on dispersal experimental setups and samplings. However, we did find some regeneration at far distance from the plantings, exceeding 200 m for *T. plicata*, 300 m for *A. grandis* and even 500 m for *T. heterophylla.*

As our three species are wind-dispersed, it is more than likely that wind and topography affect the maximum dispersal distance, and therefore that our observations vary according to the chosen sampling direction. We did expect dispersal at further distance in the direction of strongest winds during the period of seeds release, and we tested this assumption (data not shown). However, the test was inconclusive because of the great variations in the direction of strongest winds between years and sites. However, considering this effect, we did sample at least three sectors per site in varying directions and managed to have a balanced representation of directions for each species.

Both seed dispersal and environmental characteristics play an important role in the recruitment of seedlings (Amm et al. 2012). The great variation of spread observed in the different sites is probably due to abiotic and biotic filters. On the seed dispersal stage, time since fecundity, topography and local wind conditions can influence the seed rain spatial distribution. Availability of favorable microsites (vegetation type, disturbances…) affects the germination of seeds, while the recruitment stages is highly dependent on the resource availability and the structure and composition of the receiving community (competition, herbivory, pests…). The invasibility of the habitats surrounding the plantings of exotic species therefore plays a critical role in the spread of an exotic tree species (Nygaard and Øyen 2017). In a study conducted by Fanal et al. (2021) on the regeneration of exotic conifers in old arboreta, it appeared that the density of regeneration was higher under coniferous stands and in forest clearings than under deciduous tree species. In Amm et al. (2012), the regeneration of *Abies alba* was affected by tall beech trees but facilitated by pine plantations. Calviño-

Cancela and Rubido-Bará (2013) demonstrated that native forests are more resistant to invasions from exotic eucalyptus species than pine plantations. In our study, we found that regeneration of *A. grandis* is facilitated by conifer plantations, while *T. heterophylla* favors open areas (such as forest clearings) and coniferous stands as well. Climax native beech forest appear to be particularly resistant to invasions from exotic conifers, that struggle to find favorable germination conditions. *T. plicata* also displayed low regeneration in the region of the "Hautes Fagnes" (sites of Jalhay and Baelen) because of dense layers of graminoids, mainly purple moor-grass (*Molinia caeruleae*). This detrimental competition with graminids was also observed for Sitka spruce in Coastal Norway (Nygaard and Øyen 2017).

Nygaard and Øyen (2017) describe 3 stages of the range expansion: the establishment and lag phase (0 – 25 years), a rapid population growth rate (25-60 years) and finally a reduced population growth and slowed spread of the geographic area occupied (> 60 years). Given the age of our studied plantations, our three conifers are likely in the second stage of population growth. Based on the recruitment curves, densities and proportion of tall trees, we can affirm that *T. heterophylla* is, amongst our three studied conifers, the one displaying the most rapid population growth and spread. *A. grandis* also presents an important growth rate, but slower spread, while *T. plicata* struggles to spread and survive in surrounding ecosystems. The dispersal and recruitment limitations of *T. plicata* will likely mitigate its invasiveness.

Figure 4-7: regeneration of *Thuja plicata* and *Tsuga heterophylla* next to planted stands in Mirwart (© Aurore Fanal)

Performing an exhaustive data collection of the realized dispersal around isolated, mature plantings provides valuable information on the dispersal process and potential of a species, which is an indubitable asset in assessing its invasive potential. However, this method is particularly time-consuming. Almost 100 man/days were necessary to conduct this study, and the important variation between locations emphasizes the need of multiplying monitoring sites. Yet, management of an exotic species must be undertaken before its exponential spread to be effective. Given the urgency to detect species at risk at an early stage of invasion, simplified protocols must be developed to assess the potential of regeneration and spread. Wyse and Hulme (2021) demonstrated that modelled dispersal potential is the strongest predictors of spread rates of exotic pines in New-Zealand, far more efficient that currently used risk assessment tools. Dispersal models could become part of risk assessment combining on-site monitoring of mature plantings with simpler predictors such as species traits or introduction pathways.

Growth and dispersal traits have already been identified as predictors of invasiveness (Grotkopp et al. 2002, Richardson and Rejmánek 2004, van Kleunen et al. 2010a, Fanal et al. 2022). In 2014, Tamme et al. demonstrated that reasonable predictions of maximum dispersal are possible with a simple model comprising the growth form, dispersal syndrome and mean seed mass (R^2=0.53). They developed the “dispeRsal” R package to estimate maximum dispersal distances of species based on simple traits. We tested the model on our three species to predict their maximum dispersal distance and compared the results to our observations. Maximum dispersal distances estimated were 408 m (CI = 234 – 712 m) for *T. heterophylla*, 325 m (CI = 189 – 558 m) for *A. grandis* and 274 m (CI = 150 – 502 m) for *T. plicata*. These predictions are close to our maximum observed distances (585, 375 and 285 m respectively) and most of our observations within sites fall into the confidence interval. This result reaffirms that simple traits can help predict the spread of exotic species in the environment and be used in risk assessments. Examined in parallel with the vulnerability of the receiving ecosystem, such risk assessment tools would provide helpful information for a smart selection of species used in future forest plantings.

11. Conclusion

Given the numerous post-germination events affecting the recruitment of seedlings and the spatial heterogeneity of micro-sites suitable for germination, multiplying sites and transects is a necessity to assess the invasive potential of exotic conifers based on their spread. *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata* all present spread rates above 2m/year, but considering the measured size classes and regeneration densities, *Tsuga heterophylla* is the species the most at risk of becoming invasive in suitable receiving communities. Models predicting maximum dispersal distances based on functional traits may prove useful when on-site monitoring is not feasible.

5

Can we foresee future maple invasions? A comparative study of performance-related traits and invasiveness of eight *Acer* species.

Can we foresee future maple invasions? A comparative study of performance-related traits and invasiveness of eight *Acer* species.

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12. Abstract

Determining traits correlated with invasiveness in order to identify potentially invasive species remains a priority in the field of invasion ecology. In trees, relative growth rate (RGR), specific leaf area (SLA) or plant height under optimal growing conditions have been identified as performance traits allowing pioneer exotic species to out-compete native species. However, few studies investigated the link between these traits and invasiveness on a continuous scale. Here, we compare the RGR, SLA, height, shoot-root ratio and number of leaves of seedlings of eight maple species (*Acer spp.*) with their invasiveness at the global level. Seedlings were grown in non-limiting conditions indoor in Gembloux, Belgium, and harvested after 2, 4 or 8 weeks. Global invasiveness was quantified using a combination of the number of regions and countries invaded in the GBIF database, the number of citations in the Global Compendium of Weeds (GCW) and the risk score estimated in the GCW. RGR, SLA, height and number of leaves after 8 weeks were positively correlated with invasiveness. We conclude that invasive maple species could benefit from an acquisitive strategy and that high growth and light capture also favors invasiveness of shade-tolerant species. Finally, we recommend a close monitoring of *Acer rufinerve* in western Europe due to its high RGR and SLA, comparable to other highly invasive maple species.

13. Introduction

The increasing number and extent of invasive species is one of the main drivers of biodiversity loss (IPBES 2019) and their impacts and management represent a great cost to society (Cuthbert et al. 2021). Invasive trees have the potential to greatly modify the structure of ecosystems and alter biological diversity and ecosystem services (Brundu and Richardson 2017, Dyderski and Jagodziński 2021). A species must go through several abiotic and biotic barriers to become invasive in natural habitats, and this process can take decades (Richardson et al. 2000). The lag-phase between introduction and actual impact on native habitats has been estimated to last about 170 years for trees in Germany (Kowarik 1995). A key goal in invasion ecology is to identify which species will progress through this invasion continuum and become invasive. Knowing which functional traits are associated with invasiveness can increase the efficacy of risk assessments (Gallagher et al. 2014) and allow early management actions before the problematic species become widespread.

The risk of naturalization of exotic trees increases with residence time and propagule pressure (Von Holle and Simberloff 2005, Pyšek et al. 2009b, Fanal et al. 2021). To reach the final stage of the invasion process, invasive species possess a combination of traits that allows them to invade a given environment by outcompeting native species (Divíšek et al. 2018, Moravcová et al. 2015). Several studies compared traits between native *vs.* invasive species, trying to identify which traits allow the latter to outcompete native species in an area (Pyšek et al. 2009b, Godoy et al. 2011, Funk 2013, Wang et al. 2018, Dyderski and Jagodziński 2019a, Mazzolari et al. 2020, Kumar and Garkoti 2021). Fewer studies compared invasive *vs.* non-invasive exotic species to investigate what traits distinguish successful invaders from the other exotic species. In a meta-analysis of trait comparison, van Kleunen et al. (2010) attested that for comparison between invasive species and native species being invasive elsewhere, performance-related traits are not significantly different. This is why it is important to consider the invasiveness of species at a global scale and to differentiate between invasive and less-invasive or naturalized non-invasive species in order to bring the strategy of invasive species to light (Divíšek et al. 2018).

Compared to non-invasive exotic species, invasive species seem to be positioned further along the leaf economics spectrum, towards an acquisitive strategy with rapid growth (Grotkopp et al. 2002, Tecco et al. 2010, Gallagher et al. 2014, Shouman et al. 2020). Species with leaf and other traits that allow faster growth should be more successful invaders when introduced into resource-rich environments (Leishman et al. 2007).

Relative growth rate (RGR) has often been cited as a key trait in explaining the success of invasive tree species. RGR in optimal conditions shortly after germination provides a good measure of growth potential (Turnbull et al. 2008). Several studies demonstrated that invasiveness is related to how fast species can grow in optimal conditions after germination (Grotkopp et al. 2002, 2010, Dawson et al. 2011b, Gallagher et al. 2014, Erskine-Ogden et al. 2016). However, in other studies, invasive species did not have a higher RGR than non-invasive ones (Bellingham et al. 2004, Van Echelpoel et al. 2016).

Specific leaf area (SLA) represents how fast a species can acquire resources through photosynthesis (Leishman et al. 2007). It encompasses both leaf construction costs (thickness and density) and leaf development. In Grotkopp et al. (2002), SLA was the main driver of differences in RGR between seedlings of invasive and non-invasive pine species. A seedling rapidly producing new leaves will have a higher SLA overall than a species producing the same leaves at a lower rate (Grotkopp et al. 2002). Gallagher et al. (2014) encourage the addition of SLA into screening procedures for invasive plants. However, differences in SLA between non-invasive and invasive plants is inconsistent (Grotkopp and Rejmanek 2007, Gallagher et al. 2011, Wang et al. 2018). The fast-growing strategy associated with a high SLA may only be advantageous in early-successional, resource-rich or highly disturbed environments (Leishman et al. 2007, Gallagher et al. 2014). Under water stress, a smaller SLA may lead to greater water use efficiency.

In 2011, van Kleunen et al. determined that herbaceous invasive species produced more biomass and had a higher shoot-root ratio than non-invasive congeneric species, notably in shaded conditions. In Porté et al. (2011), *Acer negundo* outperforms native species by allocating more resources to the development of aerial structure over roots, leading to a higher shoot-root ratio. However, Wang et al. (2018) found that invasive plants might gain a competitive advantage in nutrient and water uptake by having a small shoot-root ratio. The importance of resources allocation to roots may be dependent on the receiving environment. In a Mediterranean climate for example, increased root allocation may be critical for invasive species to survive summer droughts (Grotkopp and Rejmanek 2007, Erskine-Ogden et al. 2016).

Overall, the functional syndrome emerging from previous studies reflects that invasive species display an acquisitive strategy, with higher values for traits related to performance such as RGR, SLA, height and shoot allocation than non-invasive exotic species in resource-rich environments (Grotkopp and Rejmanek 2007, Herron et al. 2007, van Kleunen et al. 2010a, Dawson et al. 2011b, Lamarque et al. 2011, Gallagher et al. 2014, Mathakutha et al. 2019). Global change, especially nitrogen deposition, may amplify this syndrome.

To compare species with different levels of invasiveness, global databases are often used to retrieve traits. However, these traits have to be measured on species grown in the same environmental conditions to allow a fair comparison (van Kleunen et al. 2010a). Most studies use pairs of congeneric species to test the difference between functional traits (Bellingham et al. 2004, Grotkopp et al. 2010, Dawson et al. 2011, Gallagher et al. 2014, Moravcová et al. 2015). Fewer studies compared a large number of congeneric species. Gallagher et al. (2011) found that invasive Acacias in Australia were taller than non-invasive ones. Invasive pine species also had higher RGR and SLA values (Grotkopp et al. 2002, Matzek 2012). Furthermore, examining the invasiveness along a gradient, instead of a “non-invasive” – “invasive” dichotomy, can allow an even better understanding of the relationship between invasiveness and functional traits.

Here, we focus on temperate deciduous tree species from the *Acer* genus. Maples are forest species that have been widely introduced around the world for centuries for their ornamental or sylvicultural qualities. Their phylogeny has also been intensively studied (Li et al. 2019, Gao et al. 2020) and several maple species are highly invasive. These invasions have been widely documented for decades, especially for *Acer negundo* in Europe or *A. pseudoplatanus* and *A. platanoides* in North America (Webb et al. 2000, Galbraith-Kent and Handel 2008, Sikorska et al. 2019).

Our aim is to test the functional syndrome of invasiveness promoted by performance traits (RGR, SLA, shoot-root ratio, plant height, number of leaves), by testing whether differences in functional traits of seedlings can be explained by the recorded global invasiveness of eight maple species. To allow a finer analysis of these relationships, we used a gradient of global invasiveness instead of the dichotomous “non-invasive” and “invasive” categorization often used in comparative studies.

14. Material and method

14.1. Species selection and quantification of invasiveness

Eight species were selected for this study, originating from three different continents (Europe, Asia and North America – see Table 1) and varying in observed global invasiveness. Four proxies of invasiveness were chosen, based on literature (Dawson et al. 2011b, Erskine-Ogden et al. 2016): number of regions invaded in the Global Biodiversity Information Facility (GBIF 2022); number of countries invaded in GBIF; number of citations in the Global Compendium of Weeds (GCW, Randall 2017); and the “global risk score” used in the GCW. The regions are delimited as the 11 global regions presented in the GCW. The global risk score is a scoring system developed by Randall (2016) that quantifies a plant species invasive potential based on a combination of several characteristics: the types of human-mediated pathways of entry, the most significant dispersal mechanisms and the (potentially) significant impacts. To count the number of citations for each species in the GCW, we considered studies where the species is cited as “environmental weed”, “weed”, “invasive”, “agricultural weed” or “noxious weed” in the introduction range. As Erskine-Ogden et al. (2016) also stated, we understand that the GCW has uneven species coverage and sometimes redundant or lacking citations, but it is the most exhaustive source available on invasive species worldwide.

A Principal Component Analysis was performed on the four proxies of invasiveness with the “ade4” package (Dray and Dufour 2007) in R (R Core Team 2022). Number of citations was log-transformed. The coordinate of each species on the first PCA axis was defined as the global invasiveness score.

14.2. Seeds collection and planting

Seeds were collected from mature individuals in 4 arboreta and parks in Southern and Central Belgium, in the localities of Seraing, Profondeville, Gembloux and Tervuren. At least 3 different parent trees were used for seed collection. Additional seeds of *Acer lobelii* were graciously furnished by Hugh Angus from The Maple Society, England. Supplementary seeds of *A. palmatum* and *A. saccharum* were purchased from a French supplier.

Seeds were washed with 1% sodium hypochlorite solution for three to five minutes, then rinsed with water. They were then put in wet, oven-sterilized river sand and stored in the fridge at 4°C for three months to break dormancy.

According to the number of available seeds, 4 to 8 seeds of each species were sown in 1-liter pots filled with seed-starting soil mix (DCM – ECOTERRA®) in late March. Pots were organized in 15 blocks, each block containing three randomly arranged pots for each species, one for each harvest – 2, 4 and 8 weeks after germination. These time intervals were chosen because it appears that relative growth rate within a few weeks after germination might be predictive of the overall growth potential and invasive risk (Grotkopp et al. 2002, Grotkopp and Rejmanek 2007, Dawson et al. 2011b). The experiment took place in a heated laboratory with temperatures ranging from 18 to 25 °C. Pots were positioned in bright indirect sunlight, with light intensity varying from 3 000 to 30 000 lux at noon depending on the cloud cover. Seedlings were watered weekly, when the surface of the soil was dry, and additional seedlings were removed after one week to keep one seedling per pot. Each germination was dated so every seedling was the same age for each harvest time.

At harvest time, seedling height was measured as the height of the highest leaf tip, then pots were cut open and roots carefully washed in water. Leaves were spread out on white sheets of paper and scanned directly after harvest. The seedlings were separated into four parts – leaves, cotyledons, stems and roots – and dried in the oven at 60°C for 48h, then weighted to the nearest 10^{-4} g with an analytical balance (XA105 DualRange, Mettler Toledo®, Viroflay, France).

14.3. Growth analysis

Relative growth rates (RGR) was measured for the intervals 2-4 weeks, 4-8 weeks and 2-8 weeks. We used the formula proposed by Hunt (1982), where W is the biomass at time *t*:

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1}$$

Leaf areas were measured using the ImageJ software (Rasband n.d.). SLA at each harvest time was calculated as the ratio of leaf area (cm²) to leaf dry mass (g) (Cornelissen et al. 2003). Cotyledons were included in the calculation of the SLA as they are photosynthetic organs. Shoot-root ratio was calculated as the ratio of the above-ground biomass (leaves, stems and cotyledons) to the root biomass.

14.4. Statistical analyses

Closely related species tend to resemble each other, hence comparative studies generally investigate the phylogenetic signal between species to ensure a correlation between traits is not only due to the phylogeny (Freckleton et al. 2002, van Kleunen et al. 2010a). In case of non-independence to phylogenetic structure, phylogenetically independent contrasts (PICs) are used to control the phylogenetic effect (Felsenstein 1985, Grotkopp et al. 2010, Dawson et al. 2011b, Pyšek et al. 2014). We used a phylogenetic tree of 84 Acer species constructed with nuclear ITS and three cpDNA fragments by Gao et al. (2020) to identify the common ancestors and construct a sub-tree for our 8 studied species (Fig. 5-1).

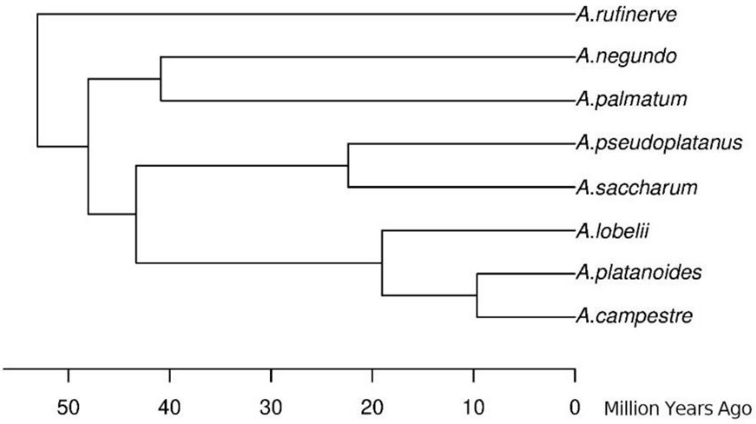


Figure 5-1: Chronogram showing the relationship between our 8 studied Acer species, based on the phylogenetic tree by Gao et al. (2020). X axis is in millions of years. The tree was coded in Newick format and drawn with the "ape" package.

We calculated the K parameter from Blomberg et al. (2003), which indicates if there is a strong phylogenetic signal ($K > 1$) or a random pattern (K close to zero). We used the "picante" package in R for calculation of the phylogenetic signal and its significance (Kembel et al. 2010).

Differences between species for each trait 8 weeks after germination were first investigated with ANOVA's and Tukey's post-hoc tests. Species were used as fixed factor and block as random effect. Significance threshold was p=0.05. Assumption of normality was tested with Shapiro-Wilk tests and visual interpretation of normal probability plots. A correlation matrix was built with non-parametric Spearman's rank correlation coefficients on the functional traits after 8 weeks. Linear mixed effect models were fitted to test the relationship between global invasiveness and RGR with harvest times as fixed effect (2-4 weeks, 4-8 weeks, 2-8 weeks), SLA with harvest times as fixed effect (4 and 8 weeks), and number of leaves, height and shoot-root ratio after 8 weeks, separately, with the “lme4” package (Bates et al. 2015). Each model was run with and without the random block effect, and we selected the model with the lowest AIC. Linear models were also fitted for each harvest time separately for RGR and SLA to allow a better comparison of the time intervals. The traits were treated as response variables and the invasiveness as fixed effect, so the variances of traits could be incorporated into the analyses. All the analyses were performed in R (R Core Team 2022).

15. Results

15.1. Quantification of invasiveness

To quantify the invasiveness of the eight maple species, a PCA was performed on the four proxies of invasiveness. The first component captured 81.1 % of the variance, and the second one 14.4 % (Fig. 5-2). All the proxies were highly correlated to the first axis, and each species’ coordinate on this axis was assigned as its value of global invasiveness, which allows a quantitative analysis of invasiveness on a continuous scale (Table 5-1).

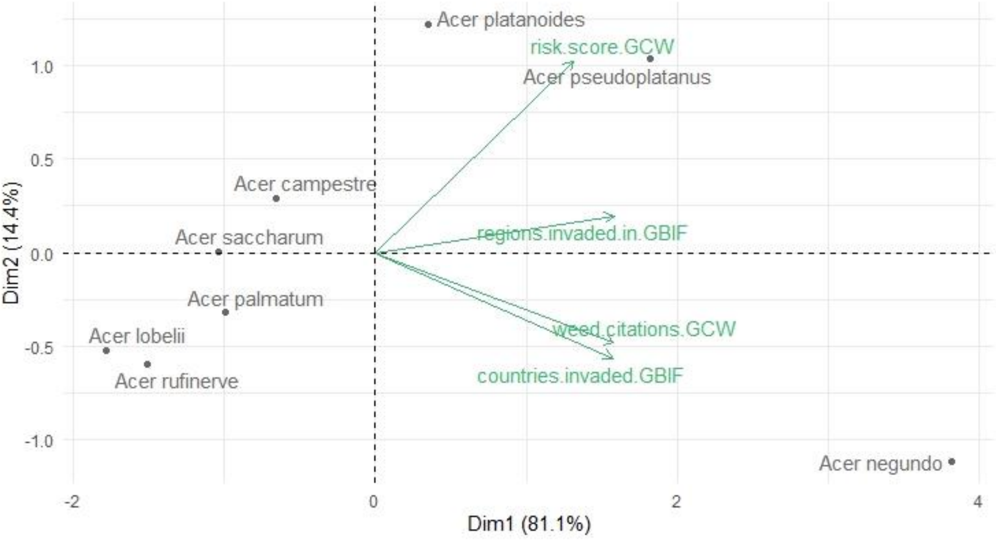


Figure 5-2: PCA on the 4 proxies of invasiveness for the eight studied maple species.

Table 5-1: Eight chosen maple species, origin, value of invasiveness proxies and global invasiveness determined as the coordinate on the axis 1 of the PCA. The global risk score and the number of citations are retrieved from the Global Compendium of Weeds, number of regions and countries invaded are retrieved from the GBIF database. Region names according to the GCW are EU: Europe, NA: North America, SA: South America, AF: Africa, EA: Eastern Asia, WA: Western Asia, CA: Central Asia, AU: Australasia.

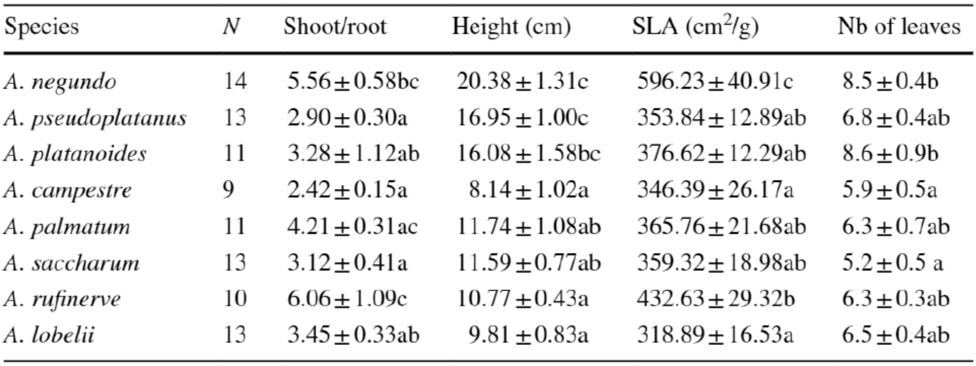
Species	**Origin**	**Global risk score**	**Number of citations**	**Regions invaded**	**Countries invaded**	**Global invasiveness**
A. negundo	NA	34.56	165	7 (EU, AF, EA, WA, CA, AU, SA)	45	3.82
A. pseudoplatanus	EU	43.32	48	7 (NA, AU, CA, SA, AF, WA, EU)	18	1.82
A. platanoides	EU	43.2	43	3 (NA, AU, EU)	5	0.35
A. campestre	EU	21.6	13	2 (NA, EU)	7	-0.66
A. palmatum	EA	4.8	15	3 (NA, EU, WA)	3	-0.99
A. saccharum	NA	12.96	5	2 (EU, WA)	5	-1.04
A. rufinerve	EA	2.16	8	1 (EU)	5	-1.51
A. lobelii	EU	0	2	1 (EU)	1	-1.78

15.2. Analyses of traits

The number of seedlings harvested per species varied between 28 and 42, because of variation in germination and mortality rates. Nine to 14 RGR values were calculated per species for the 2-8 week interval, and 8 to 14 values per species for the 2-4 week and 4-8 week intervals. Mean values and standard errors of the traits for each species are available in tables 2 and 3, as well as pair-wise significance from Tukey’s test.

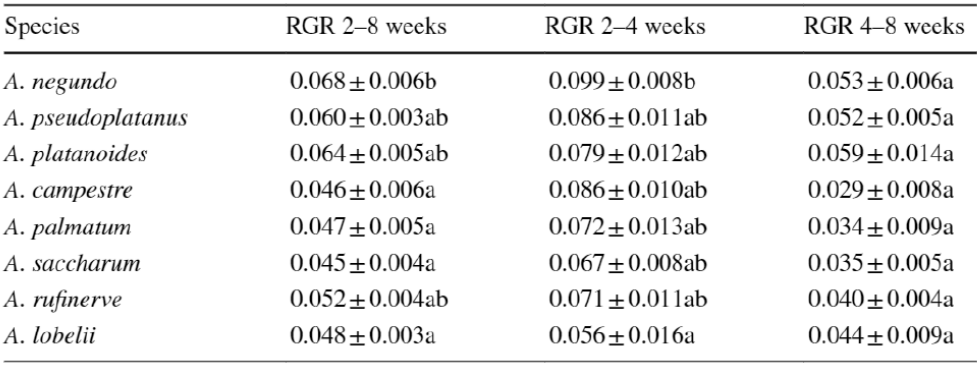
Relative growth rates between weeks 4 and 8 did not vary significantly between species (Table 5-3), but RGR between weeks 2 and 4 and between weeks 2 and 8 did (p<0.001 for both), as well as SLA after 8 weeks (p<0.001). *Acer Negundo* displayed the highest value of SLA after 8 weeks, followed by *Acer rufinerve* (Table 5-2). Overall, SLA values presented a great variation according to time and between species, but *A. negundo* had the greatest values during the whole experiment.

Table 5-2: mean values and standard errors of functional traits for each species after 8 weeks. N is the number of seedlings measures 8 weeks after germination. Significance letters obtained after Tukey's test are also given for each species and each trait.



Species	*N*	Shoot/root	Height (cm)	SLA (cm^2/g)	Nb of leaves
A. negundo	14	5.56 ± 0.58bc	20.38 ± 1.31c	596.23 ± 40.91c	8.5 ± 0.4b
A. pseudoplatanus	13	2.90 ± 0.30a	16.95 ± 1.00c	353.84 ± 12.89ab	6.8 ± 0.4ab
A. platanoides	11	3.28 ± 1.12ab	16.08 ± 1.58bc	376.62 ± 12.29ab	8.6 ± 0.9b
A. campestre	9	2.42 ± 0.15a	8.14 ± 1.02a	346.39 ± 26.17a	5.9 ± 0.5a
A. palmatum	11	4.21 ± 0.31ac	11.74 ± 1.08ab	365.76 ± 21.68ab	6.3 ± 0.7ab
A. saccharum	13	3.12 ± 0.41a	11.59 ± 0.77ab	359.32 ± 18.98ab	5.2 ± 0.5 a
A. rufinerve	10	6.06 ± 1.09c	10.77 ± 0.43a	432.63 ± 29.32b	6.3 ± 0.3ab
A. lobelii	13	3.45 ± 0.33ab	9.81 ± 0.83a	318.89 ± 16.53a	6.5 ± 0.4ab

Table 5-3: mean values of RGR ($g.g^{-1}.d^{-1}$), standard errors and significance letters for each time interval.



Species	RGR 2–8 weeks	RGR 2–4 weeks	RGR 4–8 weeks
A. negundo	0.068 ± 0.006b	0.099 ± 0.008b	0.053 ± 0.006a
A. pseudoplatanus	0.060 ± 0.003ab	0.086 ± 0.011ab	0.052 ± 0.005a
A. platanoides	0.064 ± 0.005ab	0.079 ± 0.012ab	0.059 ± 0.014a
A. campestre	0.046 ± 0.006a	0.086 ± 0.010ab	0.029 ± 0.008a
A. palmatum	0.047 ± 0.005a	0.072 ± 0.013ab	0.034 ± 0.009a
A. saccharum	0.045 ± 0.004a	0.067 ± 0.008ab	0.035 ± 0.005a
A. rufinerve	0.052 ± 0.004ab	0.071 ± 0.011ab	0.040 ± 0.004a
A. lobelii	0.048 ± 0.003a	0.056 ± 0.016a	0.044 ± 0.009a

The Spearman correlation analysis performed on traits after 8 weeks shows that the RGR is highly correlated to height (rk=0.7). A higher shoot-root ratio is also correlated to higher SLA values (rk=0.5) (Fig. 5-3).

Figure 5-3: Correlation plot (Spearman coefficient) between traits. SLA at week 8, shoot-root ratio, number of leaves and height are measured 8 weeks after germination. RGR is measured between weeks 2 and 8.

The K parameter for phylogenetic signal was calculated for each trait; RGR 2-4 weeks: K=0.609 (p=0.56), RGR 4-8 weeks: K=0.298 (p=0.99), RGR 2-8 weeks: K=0.422 (p=0.85), SLA after 4 weeks: K=0.298 (p=0.99), SLA after 8 weeks: K=1.115 (p=0.15), height: K=0.479 (p=0.77), shoot-root: K=1.43 (p=0.05) and the number of leaves after 8 weeks: K=0.484 (p=0.72). As there was no phylogenetic signal detected, the phylogenetic structure was not accounted for in the following regression analyses.

Results from the linear regressions indicated that RGR was positively associated with the global invasiveness ($p<0.001$, t value=4.12, adj r^2=0.26; Fig. 7-4). Moreover, there was a significant effect of the time interval ($p<0.001$). Looking at the time intervals separately, we find a stronger effect of global invasiveness for RGR values measured between 2 and 8 weeks ($p<0.001$, t value=4.60) and between 2 and 4 weeks (p=0.004, t value=2.94) than for the 4 to 8 weeks interval (p=0.028, t value=2.23). Invasive species were significantly taller ($p<0.001$, t value=9.31, adj r^2=0.48) and grew more leaves ($p<0.001$, t value=3.95, adj r^2=0.14). A higher SLA was significantly associated with increased invasiveness ($p<0.001$, t value=9.74, marginal r^2=0.47, conditional r^2=0.55) after both 4 weeks ($p<0.001$, t value=10.44) and 8 weeks ($p<0.001$, t value=8.41). However, the relationship between the shoot-root ratio and invasiveness was not significant (p=0.08, adj r^2=0.01).

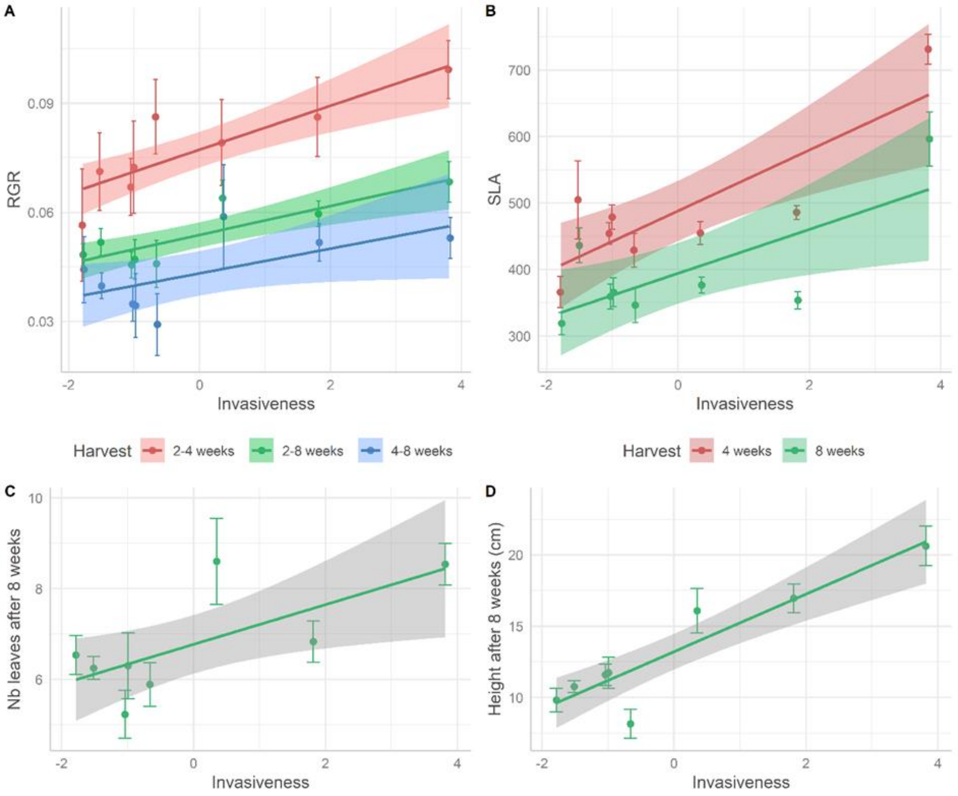


Figure 5-4: Predicted values for functional traits with significant relationship to global invasiveness. Mean values and standard errors are represented for each trait. Units are g.g^{-1}.d^{-1} for RGR (A), cm^{2}.g^{-1} for SLA (B) and cm for height after 8 weeks (D).

16. Discussion

Because of their ornamental or wood production properties, maples have been widely introduced around the world for centuries in temperate forests, arboreta, parks and gardens. However, only a few species have become invasive in natural habitats. Predicting which tree species are more likely to become invasive is essential, and performance traits were correlated to invasiveness in studies performed on acacias and pines (Grotkopp et al. 2002, Gallagher et al. 2011, Matzek 2012). In this study, among the eight maple species we studied, we did find a positive relationship between relative growth rate at the seedling stage and the global invasiveness. Height was also highly correlated to RGR, which indicates that invasive species favor fast vertical growth. SLA and number of leaves were also higher for invasive species, reflecting allocation of resources preferably to leaf construction and light capture. These results confirm a tendency towards an acquisitive trait syndrome for the most invasive species in favorable growth conditions, *i.e.* with sufficient nutrients and light.

To ensure the phylogenetic independence of our traits, we calculated the K parameter of phylogenetic signal for each of the studied trait. We did not find any significant signal, and therefore we conducted the analyses without taking the phylogenetic structure into account. The use of phylogenetically independent contrasts is mostly needed when species from different genera are compared. In their study on pines, Grotkopp et al. (2002) analyzed the difference of traits between invasive and non-invasive species with and without phylogenetic control, and arrived at the same conclusions. Even when the traits are phylogenetically constrained, from a manager's point of view, the predictive value of traits contributing to invasiveness remains useful regardless of the underlying evolutionary process (Pyšek et al. 2014).

The timing of the harvests is important to highlight differences in trait values. Differentiation of RGR values between our species was most significant on the 2 to 8 and 2 to 4 weeks periods. However, RGR values between 4 and 8 weeks did not significantly differ between species. Most comparative studies that found a relationship between RGR, SLA and invasiveness used a 1 to 3 months time span. A longer period might blur the differences between species. In a study conducted in New Zealand on woody plants, Bellingham et al. (2004) found no relationship between RGR and observed invasiveness, but their growth period lasted for 5 to 11 months. However, other factors could explain their results, such as the invasiveness defined at a local scale and the stage of invasion considered.

Compared to pines and acacias, both light-demanding pioneer species, the studied maple species differ in their shade tolerance and intermediate position in forest succession (Lei and Lechowicz 1990, 1998, Wada and Ribbens 1997, Petit et al. 2017). All studied species can tolerate shade and usually exploit small gaps in the forest cover. Porté et al. (2011) and Lamarque et al. (2015) already highlighted *A. negundo*'s ability to outperform native species and spread in temperate resource-rich forests due to its high SLA. *Acer pseudoplatanus* invades native forests by means of its resource-use efficiency, especially its high photosynthetic rates in shady conditions (Shouman et al. 2020). *Acer platanoides* is also a forest species that combines high growth rates with moderate shade tolerance, a unique combination of traits that allows it to invade established North-American forests (Martin et al. 2010b). Our study supports that rapid growth and fast light acquisition as early as on the seedling stage are important sources of invasiveness for invasive maples, even in shaded environments.

We found no pattern for the relationship between shoot-root ratio and invasiveness. *Acer negundo* and *A. rufinerve* both had the highest values, which indicates they invest more resources into their above-ground development, as it has already been observed for *A. negundo* in a study by Porté et al. (2011). However, other invasive species such as *A. pseudoplatanus* and *A platanoides* did not show the same pattern.

In our study, *Acer rufinerve* was assigned a rather low global invasiveness value, because of the low number of regions invaded and low number of citations as invasive. However, it shares similar trait values to the very invasive *A. negundo*, particularly SLA and RGR values. The species has recently been added to the European and

Mediterranean Plant Protection Organization (EPPO) list of invasive species because of its regeneration in three Belgian forests, where it outcompetes native plants and already represents an important management cost (EPPO 2022). It is described as an early-successional forest species that occupies small gaps and edges of oak-dominated forests (Branquart et al. 2011). In shaded or semi-shaded areas, *A. rufinerve* is taller than *A. pseudoplatanus* at the same age, and their radial growth is comparable (De Ruyver 2021). If *A. rufinerve* has the capability to maintain populations under forest cover, its high SLA values in our experiment indicate that the species probably has the potential to display rapid growth when put to light by clearings or other perturbations. This maple species also presents prolific resprouting, and vegetative regeneration is an important driver of invasiveness, making the control and eradication extremely challenging (Nunez-Mir et al. 2019). This "sit-and-wait" strategy, mixing shade tolerance and self-maintenance in the understories with rapid growth in canopy gaps and resprouting capacities, has already been described as the "recipe for success" of the invasive *Prunus serotina* in European woodlands (Closset-Kopp et al. 2007). We therefore suggest that *A. rufinerve* might not have completed the invasion process yet, which could explain its low invasiveness value in our study. We recommend a close monitoring of the species in other temperate countries, to identify invasions of natural habitats at early stages.

A limitation of our study is the origin of the collected seeds. All seeds were collected in western Europe, which is the native range for some species and the introduced one for others. If genetic differentiation has been observed in the invaded area for *A. negundo*, it is not the case for *A. platanoides* (Lamarque et al. 2015). This could be due to the life-strategy or the stage of invasion – genetic differentiation appears in the latest stages, when the trees spread from established populations (Lamarque et al. 2015). A meta-analysis by Bossdorf et al. (2005) concluded that some sort of genetic drift was often observed in the introduction range of invasive plants, sometimes leading to enhanced growth. Choosing seeds exclusively from invaded ranges would therefore probably have only sharpened the distinction between less-invasive and highly invasive species. Also, we did not test the plasticity of the species for the studied functional traits. However, previous studies stated that species traits, not plasticity, most explain the variations in invasion success (Palacio-López and Gianoli 2011, Matzek 2012). High plasticity seems to be more important in the naturalization process (Pyšek et al. 2009a, Gallagher et al. 2011, Lamarque et al. 2015). However, we must keep in mind that our experiment was conducted in particular lab conditions, while exotic species might present higher growth rates and shade tolerance in their introduced range compared to their native one, irrespective of any genetic differentiation. Indeed, some tree species might benefit from reduced carbon costs because of enemy release (herbivory, pathogens, etc.) and lesser environmental stress (Fridley et al. 2023). For example, *Acer pseudoplatanus* displays a better shade tolerance and higher growth rates in its invasive range (New Zealand) than in its native range, at any light condition. This functional shift allowed the sycamore maple to escape the growth-survival trade-off and become invasive (Shouman et al. 2017).

From our results, it appears that invasive maples favor fast growth, rapid leaf production and high SLA, promoting efficient light capture. As shown for pioneer species such as pines and acacias, this acquisitive trait syndrome also applies to shade-tolerant species such as maples. Because most introduced exotic tree species are pioneer species, traits relative to the invasion of shady established forests have long been neglected (Martin et al. 2009, 2010b). Yet more conservative traits such as shade-tolerance may play an important role in the invasion of ecosystems with low disturbance regimes. Fridley et al. (2022) recently stated that a “fast-but-steady” functional syndrome, implying both fast growth capacity and persistence in the shaded understorey might promote invasion success in forests. A comparison of these traits on a larger sample of pioneer, intermediate and closed-canopy invasive tree species might help build a more comprehensive profile on the strategies of invasive trees.

17. Conclusion

Our study contributes evidence that performance-related traits such as RGR, SLA, leaf production and height of the seedlings can help predict which species are invasive, even for shade-tolerant species such as maples. Once naturalized, species that become invasive present an acquisitive trait syndrome characterized by fast growth, rapid leaves production and efficient light capture *via* high SLA. *Acer rufinerve*, an early-successional maple invasive in a few western European countries, displays trait values close to *A. negundo* and should be monitored carefully.

6

Fast height growth is key to non-native conifers invasiveness in temperate forests

Fast height growth is key to non-native conifers invasiveness in temperate forests

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This paper is submitted in Biological Invasion.

18. Abstract

Many exotic conifer species have been introduced for wood production in temperate regions. Some of these species can display an invasive behavior and negatively impact native ecosystems. It is therefore crucial to identify potentially invasive species before they are widely planted. Seedling high Relative Growth Rate (RGR) and Specific Leaf Area (SLA) have been associated with enhanced invasiveness of trees in previous studies. However, it has been mainly demonstrated for light-demanding species in disturbed habitats, less for shade-tolerant species in closed forests. Here, we investigated the link between seedlings growth traits of 15 exotic conifer species and invasiveness considered at both global and local scale. Seedlings were grown outdoor, under a shade net, and harvested after 4 and 10 weeks. RGR, SLA, Shoot-Root ratio, Shoot Relative Growth Rate (SRGR), Relative Height Growth Rate (RHGR) and Relative Needles Production Rate (RNPR) were measured. We developed a continuous approach to position each species along a gradient of invasiveness. Local invasiveness consists of a value based on regeneration densities and dispersal distances observed in forest arboreta in Southern Belgium, and is therefore related to the ability of species to invade closed forest ecosystems. Global invasiveness was calculated based on the GBIF Database and the Global Compendium of Weeds, and encompasses all potentially invaded habitats. It appeared that RHGR was positively related to both local and global invasiveness, while SLA was positively related to local invasiveness only. However, RGR was not significantly related with local nor global invasiveness. This study indicates that preferential investment in rapid vertical growth associated with fast resource acquisition is a strategy enhancing invasiveness of non-native conifers, also in closed, shaded temperate forests.

19. Introduction

Forestry is one of the main pathways of introduction of invasive trees (Pyšek 2016). Species selected for wood production usually present high growth rates and climatic suitability in the introduced range (Pyšek et al. 2009a, Essl et al. 2010). They are also planted on large scale, which increases propagule pressure, with sylvicultural methods enhancing survival rates (Mack 2005, Křivánek et al. 2006, Pyšek et al. 2014). Invasion by trees are often under-estimated because of the long lag-phase, about 170 years in Germany according to Kowarik (1995), between the introduction and the actual spread of populations. In temperate Europe, numerous programs are implemented to test non-native tree species in order to diversify planted forest and secure timber supply. It is therefore important to understand the processes underlying invasion success of invasive trees to better predict which species are at risk of becoming invasive in this region before large-scale plantations start.

Conifers in particular have been widely introduced for timber production in temperate regions for decades, for example *Pinus radiata* in New Zealand and Chile, *Pseudotsuga menziesii* in Western Europe, or *Picea sitchensis* in Great-Britain (Moore et al. 2009, Bindewald et al. 2021a, Wyse et al. 2022). Some of these species have become invasive in the introduced range and caused great ecological damage, such as modification of soil nutrients, greater occurrence of fire, reduced water availability, or negative impacts on native biodiversity (Simberloff et al. 2010, Mason et al. 2017, Edwards et al. 2021, Nuñez et al. 2021). Although invasions by conifers are intensively studied in the Southern hemisphere, especially in South Africa and New Zealand, it is less the case in Continental Europe. However, recent studies have demonstrated that several non-native conifer species display an invasive behavior in European temperate forests, for example *Pseudotsuga menziesii*, *Tsuga heterophylla*, or *Pinus strobus* (Oyen 2001, Reichard et al. 2001, Bindewald et al. 2021). Fanal et al. (2021) found that, in old forest arboreta in Belgium, 17% of studied planted conifer species present an important natural regeneration, with dispersal exceeding 100 m from planted trees, which indicates an invasive behavior (Richardson et al. 2000, Nygaard and Øyen 2017).

Residence time and propagule pressure are major factors increasing the probability of naturalization of exotic tree species (Pyšek 2016). Once naturalized, their invasiveness in a given ecosystem is enhanced by a combination of traits. Invasive trees would present higher growth rates, higher specific leaf area or shorter juvenile period compared to non-invasive exotic trees (Pyšek et al. 2014, Hodgins et al. 2018, Shouman et al. 2020). This has been demonstrated specifically for pine species (Richardson et al. 1994, Grotkopp et al. 2002). In a meta-analysis from Lamarque et al. (2011), the relative growth rate appeared to be the most efficient predictor of trees invasiveness. Overall, it emerges from previous studies that invasive woody species display an acquisitive strategy, with higher values than non-invasive exotic species for traits such as RGR, SLA, height and shoot-root ratio (Porté et al. 2011, Gallagher et al. 2014, Shouman et al. 2020). However, different traits might promote invasiveness in various environments, thus approaches at a local scale are also interesting to focus on the success of invasive species in a specific region or habitat (Palacio-López and Gianoli 2011). Most of the studies comparing traits and invasiveness of trees focused on light-demanding species, such as pines and acacias (Grotkopp et al. 2002, Gallagher et al. 2011), but the syndrome of traits enhancing invasiveness of shade-tolerant species in less-disturbed habitats such as closed forests might be different and needs more investigation. For example, In 2019, Dyderski and Jagodziński suggested that both acquisitive and conservative strategies might allow exotic trees to outcompete native species, either by a general investment in foliage or by the roots carbon allocation and overall tree's growth rate.

Many studies compared traits between invasive and native species in an area, trying to explain why the non-native species successfully established in a given ecosystem and which trait gave it an advantage over native species. However, if one wishes to identify traits linked to invasiveness at a global scale, they would better compare exotic species that became invasive to non-invasive exotic species in the introduction range (van Kleunen et al. 2010b). A limitation to this method is that non-invasive species might still be in a lag-phase, or given insufficient opportunity to invade; it is therefore important to select species with similar introduction history (Pyšek et al. 2015b).

Among studies comparing traits values of exotic species, most used pairs of congeneric species with a dichotomous "invasive" and "non-invasive" categorization (Bellingham et al. 2004, Grotkopp et al. 2010, van Kleunen et al. 2010a, Gallagher et al. 2014, Moravcová et al. 2015). A few studies compared a large number of species from the same genus, for example Grotkopp et al. (2002) on pines and Gallagher et al. (2011) on acacias, but they still divided species in two groups – invasive vs. non-invasive. However, invasion is a process and exotic species occupy different positions along a gradient of invasiveness from casual to naturalized and finally more-or-less invasive (Richardson et al. 2000). Traits involved in the invasive success might differ according to the stage and success of invasion, therefore a continuous approach using a gradient of invasiveness can help to better understand the contribution of traits.

The aim of the present study is to test whether the invasiveness of 15 non-native conifers used in forest plantations can be explained by a set of seedlings development traits. Based on previous studies, we expect increasing values of invasiveness to be related to increased values of performance traits such as RGR, Relative height growth Rate or SLA. We considered both the global invasiveness worldwide and the local invasiveness in Southern Belgium. Global invasiveness represents the propensity of conifers to invade diverse habitats globally, including treeless ecosystems, while local invasiveness is related to the invasive potential of conifers in closed, shaded temperate forests. We only selected species that are not naturally present in continental Europe and share a similar introduction history in Belgium as they were planted in small patches in public forests at the end of the 19th century. The invasiveness was calculated as a continuous variable to allow finer analyses.

20. Material and method

20.1. Species selection and invasiveness

Fifteen conifer species non-natives in Europe were selected (Table 6-1). These species have all been introduced in Southern Belgium in forest trials for at least one century (Fanal et al. 2021). The requirements for the 15 chosen species were: (1) they were on the list of species introduced in old Belgian forest arboreta studied by Fanal et al. (2021), with available data on local invasiveness, (2) seed supply from Belgian plantations was sufficient, (3) a gradient of invasiveness was represented and (4) attention was paid to have invasiveness contrasts within phylogenetic groups when possible.

Defining this gradient of invasiveness at a global scale is not an obvious procedure. On a study performed on 105 plant species in the UK, Dawson et al. (2011) used the number of references in the Global Compendium of Weeds (Randall 2017) as a proxy of invasiveness. The number of citations as invasive can be tricky to use, as the effort of research can be unbalanced between species according to the place of study, available research funding and economic impacts of the studied plant (Matzek et al. 2015). Moreover, the GCW has sometimes redundant or lacking citations. However, as stated by Erskine-Ogden et al. (2016), it is the most comprehensive source available on invasive and naturalized species worldwide. We can also consider a species more invasive when it is listed as invasive in many biogeographic regions. Dawson et al. (2011) also used the number of regions invaded based on the records in the GCW as a proxy of invasiveness. Multiplying proxies enables to compensate for their varying weaknesses and to better capture the overall invasiveness of species. Fanal et al. (2022) used a combination of proxies in a study on maples, by integrating the risk score and number of references in the GCW as well as the number of regions and countries invaded listed in the Global Biodiversity Information Facility (GBIF 2022) in an principal component analysis. A similar method will be used in this study. Here, Global invasiveness was calculated using occurrences in databases and the literature, following the same method performed on maples in Fanal et al. (2022). Four proxies of invasiveness were selected: (1) the number of regions invaded in the Global Biodiversity Information Facility (GBIF 2022), (2) the number of countries invaded in GBIF, (3) the number of citations in the Global Compendium of Weeds (GCW, Randall 2017), and (4) the risk score provided in the GCW. Citations in the GCW were counted when the species was referred to as “weed”, “environmental weed”, “agricultural weed”, “noxious weed” or “invasive” out of its native range. The risk score provided in the GCW is calculated with the pathway of introduction, dispersal mechanisms and potential impacts of the species in question. The “invaded regions” are based on the 11 biogeographical regions delimited in the GCW. The Principal Component Analysis of the four proxies was retrieved and the coordinate of species on first component (70.3 % of explained variance) was used to assign a value of global invasiveness (Fig 6-1).

At a local scale, in a given ecosystem, it is easier to compare exotic species with similar planting history. In Richardson et al. (2000), invasive plant species are defined as "Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants". The degree of invasiveness can therefore be inferred from data on the natural regeneration density and the dispersal distance observed on site (Fanal et al. 2021). Even if natural regeneration is found only under the parent trees, it would indicate that the species is naturalized and able to produce offspring, having therefore fewer barriers left to overcome to become invasive (Richardson and Rejmánek 2004). We calculated local invasiveness using the natural regeneration mean density and the 95th percentile of dispersal distances observed across eight forest arboreta in Southern Belgium by Fanal et al. (2021). This sampling was performed mainly in closed forest stands of dense plantation trials, spruce plantations or native oak- or beech-dominated forests, punctuated with canopy gaps and logging sites. The two variables were scaled and centered, and a Principal Component Analysis (PCA) was performed with the "ade4" package (Dray and Dufour 2007) in R (R Core Team 2022). The first component represented 76.3 % of variance, therefore the coordinate of each species on the axis was used to assign a value of invasiveness (Fig. 6-1). Five species showed no regeneration on the studied sites; they were all assigned the same value of local invasiveness.

Table 6-1: List of selected species, origin (NA = North America, EA = Eastern Asia, WE = Western Asia), taxonomic grouping, local and global invasiveness values equal to the species’ coordinate on the first PCA axis. High values indicate high invasiveness.

Species	**Group**	**Origin**	**MRD**	**0.95 DD**	**Local invasiveness**	**Risk score**	**Citations**	**Regions**	**Countries**	**Global invasiveness**
Abies grandis	*1*	NA	1493.84	67.42	**1.26**	4.32	13	2	8	**-1.08**
Abies nordmanniana	*1*	WA	688.27	5.80	**-0.38**	6.72	13	3	12	**-0.31**
Abies procera	*1*	NA	20.73	0.00	**-1.10**	1.68	8	1	4	**-2.07**
Chamaecyparis lawsoniana	*6*	NA	279.45	126.72	**0.93**	10.08	27	4	15	**0.98**
Cryptomeria japonica	*5*	EA	0.00	NA	**-1.12**	8.64	25	7	22	**2.27**
Larix kaempferi	*2*	EA	136.60	74.30	**0.05**	6.72	20	3	11	**-0.12**
Picea rubens	*3*	NA	0.00	NA	**-1.12**	2.16	1	0	0	**-2.95**
Picea sitchensis	*3*	NA	104.15	36.49	**-0.51**	12.96	22	3	10	**0.22**
Pinus ponderosa	*4*	NA	0.00	NA	**-1.12**	20.16	23	4	10	**0.93**
Pinus strobus	*4*	NA	357.78	124.16	**0.97**	25.92	44	3	18	**2.56**
Pseudotsuga menziesii	*2*	NA	248.77	87.00	**0.34**	19.44	53	2	21	**2.56**
Thuja plicata	*6*	NA	637.78	90.34	**0.76**	25.92	23	3	11	**1.08**
Tsuga canadensis	*1*	NA	0.00	NA	**-1.12**	12.96	12	1	5	**-1.17**
Tsuga heterophylla	*1*	NA	2794.03	124.31	**3.30**	12.96	14	2	6	**-0.74**
Xanthocyparis nootkatensis	*6*	NA	0.00	NA	**-1.12**	3.36	1	1	5	**-2.15**

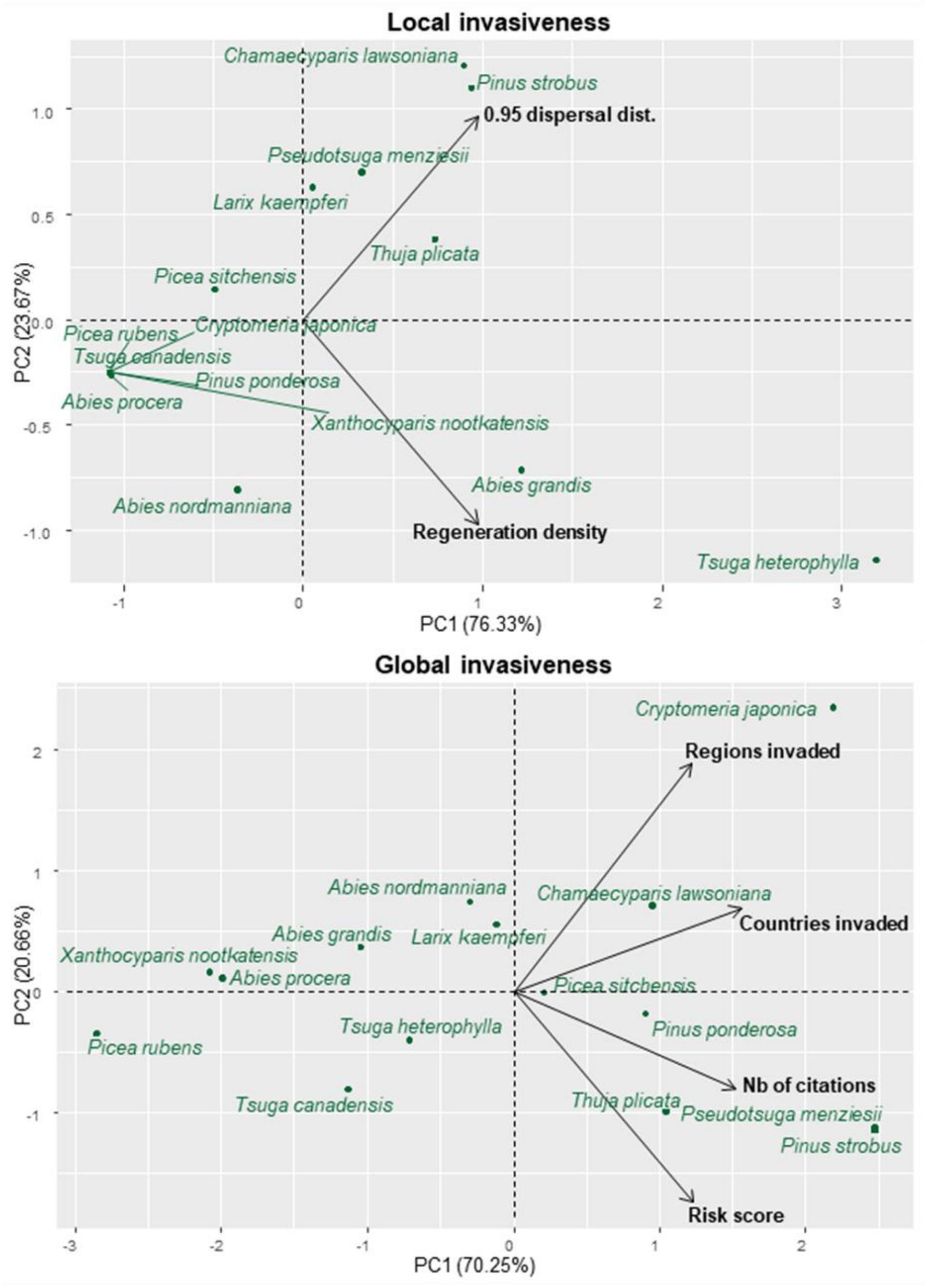


Figure 6-1: Biplots of the PCA's performed on the 2 proxies of local invasiveness and the 4 proxies of global invasiveness for the 15 studied conifer species.

To control for the phylogenetic effect in traits comparisons, we created a phylogenetic tree for the fifteen conifer species using the package “V.PhyloMaker2” (Jin and Qian 2022). This package uses the phylogeny from Jin and Qian (2019), which combines data from Smith and Brown (2018) and Zanne et al. (2013), resulting in a phylogeny of 74,531 species of vascular plants in 10,587 genera. We then used the resulting tree to group the conifer species in six taxonomic groups numbered from 1 to 6 (Fig. 6-2).

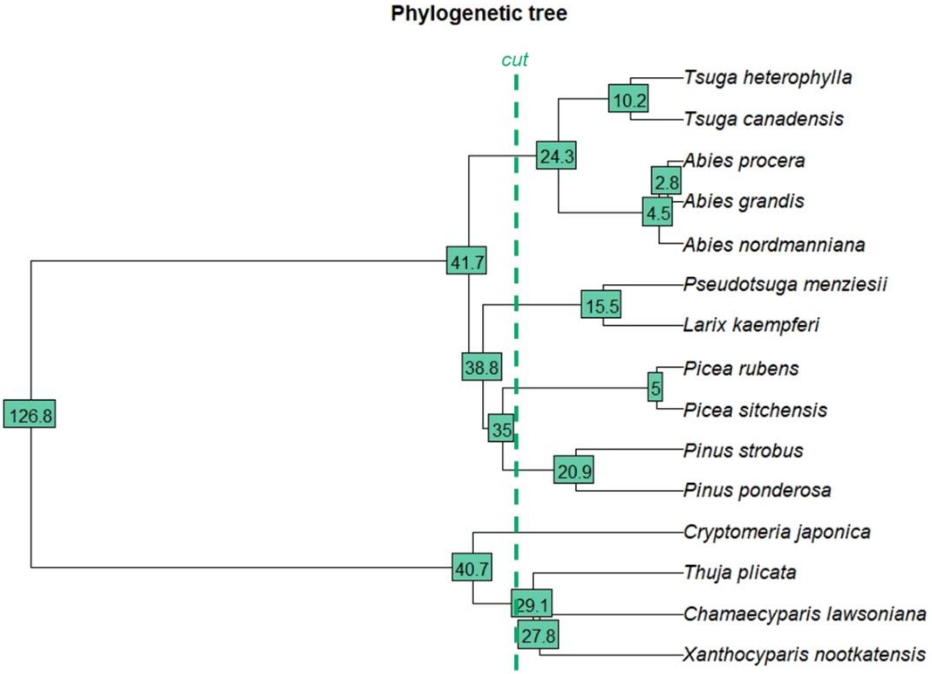


Figure 6-2: Phylogenetic tree constructed for the 15 studied conifer species with the” V.PhyloMaker2” package (Jin and Qian 2022) and the cutting line defining phylogenetic groups.

20.2. *Seeds collection, planting and harvest*

Seeds of the 15 species were collected in >80 years old forest plantings in good health conditions, in the public arboreta of Seraing, Spa, Gedinne and Saint-Michel, Southern Belgium (Fig. 6-3A). Seeds were collected with seed traps placed under the focus species in autumns 2020 and 2021, from September to December, and collected every month. Seeds were also collected directly from cones for *Abies*, *Pinus* and *Picea* species. Additional seeds were provided by the public Walloon Counter of forest reproductive material and also originated from Belgian public plantings. The public

Walloon Counter selects several plantings with good sylvicultural potential, but the seeds are not sorted except for the removal of empty ones.

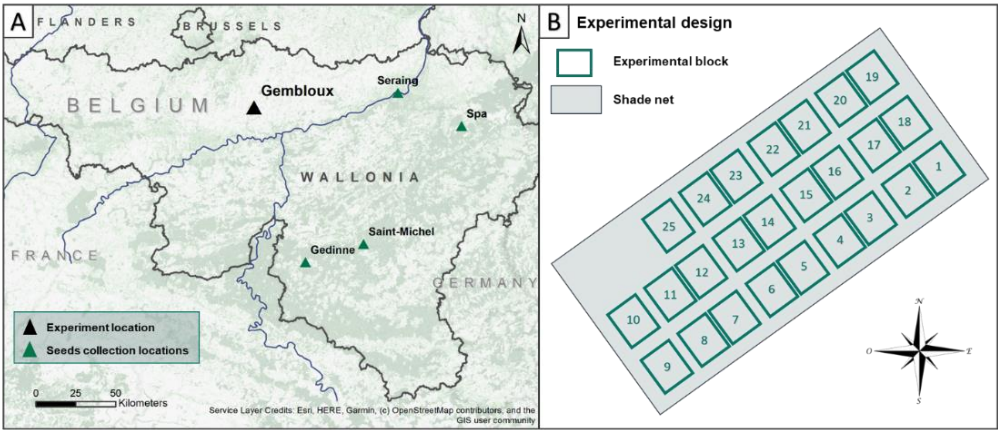


Figure 6-3: **A)** Location of the experiment field and the arboreta where seeds were collected. Background on the map is the tree cover in 2000 (Hansen et al. 2013). **B)** Experimental design with 25 blocks, each one containing 2 pots of each species.

Seeds were washed with a 1% sodium hypochlorite solution for 3 minutes and rinsed three times with water. They were then soaked in water for 24h and kept in a fridge at 4°C for at least 3 months. Seeds of *Abies* spp., *Picea sitchensis* and *Pseudotsuga menziesii* required moist stratification, and were stored in moist oven-sterilized river sand in the fridge.

Twenty-five blocks of 30 pots each (with 2 pots per species) were randomly arranged in an experimental field under a UV-stabilized polyethylene knitted shade net of 50% light transmittance (60 g/m²) mounted on a tunnel greenhouse structure (Fig. 6-3B). The 6-liters pots were filled with a mix of peat (70%), perlite (20%) and sand (10%) and sown in late March 2021 with 5 to 12 seeds, according to the quantity of available seeds per species. Each germinated plant was identified, labelled and dated. Pots were watered when the soil was dry on 1 cm. Precipitations during the experiment ranged from 26 to 166 mm per month. After 2 weeks, only one seedling was kept per pot (the first that germinated except if damaged or diseased). In every block, one seedling per species was harvested at 4 weeks old and another at 10 weeks old. We harvested the trees at the seedling stage, as previous studies found a relationship between growth rate during the first few months after germination and the observed invasiveness (Grotkopp et al. 2002, Dawson et al. 2011b, Fanal et al. 2022). Also, growth rates in optimal conditions measured shortly after germination provide a good estimate of the overall growth potential (Turnbull et al. 2008).

20.3. *Traits measurements*

We selected growth traits that were already identified as predictors of the invasiveness of trees in the literature: relative growth rate (Lamarque et al. 2011), SLA (Hodgins et al. 2018), shoot-root ratio (Porté et al. 2011), relative height growth rate (Porté et al. 2011, Tan et al. 2018) and the relative needles production rate (Grotkopp et al. 2002). High values for these traits are linked to an acquisitive strategy of fast growth and efficient light capture, with less allocation to defense mechanisms or structures enhancing resistance to stresses. On the contrary, species with low SLA and important allocation to roots biomass rather display a conservative strategy of better resistance to stress, such as water scarcity, herbivory and shade (Wright et al. 2004, Grotkopp and Rejmanek 2007, Dyderski and Jagodziński 2019a).

At harvest time, vegetative height was measured to the nearest mm with a ruler and the seedling was carefully uprooted and washed. Needles were removed, counted and scanned directly for SLA measurement with ImageJ (Rasband n.d.). Roots and stems were also separated and the three parts were dried in the oven at 60°C for 48 hours. They were then weighted to the nearest 10^{-4} g with an analytical balance (XA105 DualRange, Mettler Toledo®, Viroflay, France).

Growth rates were measured for the 4 to 10 weeks' time interval (*i.e.* between 28 and 70 days), based on the measurements on the two conspecific seedlings per block. Relative Growth Rates (RGR: $g.g^{-1}.d^{-1}$) were calculated with the formula proposed by (Hunt 1982), where W is the dry biomass at time t. All formulas are displayed in Table 6-2. The Shoot Relative Growth Rate (SRGR) is calculated with the same formula, using only the shoot biomass (stems and needles). Relative Height Growth Rate, used in Porté et al. (2011), is derived from Hunt's formula and consists in the relative increment in height over time ($cm.cm^{-1}.d^{-1}$). Relative Needle Production Rate is the increment in needles number over time and is calculated with the same formula, the number of needles replacing height. The shoot-root ratio is calculated as the shoot biomass divided by the root biomass of the 10-weeks old seedlings. SLA is the ratio of the total needle area (cm^2) to the total needle dry biomass (g) 10 weeks after germination.

20.4. *Statistical analysis*

Differences in traits between species was first investigated with a variance analysis (ANOVA) and a Tukey's post-hoc test. The phylogenetic grouping and blocks were used as random effects, species as fixed effect. Significance α risk used for all analyses is 0.05. Spearman's rank-order correlation (r_S) between traits was calculated. To test the relationship between invasiveness and traits, linear mixed effects models were fitted with the "lmerTest" package (Kuznetsova et al. 2017). A stepwise selection with the "dredge" function from the MuMIn package (Bartoń 2009) was performed to select explanatory traits based on AIC value. Local and global invasiveness were treated as response variable and traits as fixed effect after scaling and centering. The phylogenetic group was nested as random effects.

Models were then run with the selected variables to extract p values and R². Analyses were performed in RStudio (R Core Team 2022).

Table 6-2: Name, acronym, formula and units of measured traits. t1 and t2 are the consecutive times of harvesting at weeks 4 and 10 after sowing, respectively. H and W correspond to total height and dry weight (or per compartment needles, shoots and roots). A is the leaf area. N is the number of needles.

Name		Formula	Unit
Relative Growth Rate	RGR	$\frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1}$	g.g^{-1}.d^{-1}
Shoot Relative Growth Rate	SRGR	$\frac{\ln(W_{shoot\ 2}) - \ln(W_{shoot\ 1})}{t_2 - t_1}$	g.g^{-1}.d^{-1}
Relative Height Growth Rate	RHGR	$\frac{\ln(H_2) - \ln(H_1)}{t_2 - t_1}$	cm.cm^{-1}.d^{-1}
Relative Needle Production Rate	RNPR	$\frac{\ln(N_2) - \ln(N_1)}{t_2 - t_1}$	Leaf.leaf^{-1}.d^{-1}
Specific Leaf Area	SLA	$\frac{A_{needles}}{W_{needles}}$	cm^2.g^{-1}
Shoot-Root Ratio	Shoot/root	$\frac{W_{shoot}}{W_{roots}}$	-

21. Results

Between 10 and 22 values were obtained per species for the studied traits. Mean and standard errors for each species are given in Table 6-3. All traits varied significantly between species: RGR ($p=0.03$), RHGR ($p < 0.005$), SRGR ($p = 0.025$), RNPR ($p < 0.005$), SLA ($p < 0.005$) and shoot-root ratio ($p = 0.020$). As shown in Fig. 4, RGR and SRGR are positively correlated ($r_s=0.97$), as well as RNPR and SRGR ($r_s=0.69$), RNPR and RGR ($r_s=0.68$), RHGR and SRGR ($r_s=0.64$) and RGR and RHGR ($r_s=0.61$). On average, *Tsuga canadensis* has the lowest values of RGR, SRGR, RNPR and shoot-root ratio, while *Abies nordmanianna* has the lowest values of RHGR, RNPR and SLA. *Thuja plicata* has the highest mean value of RGR, RHGR and SRGR, while *Abies grandis*, *Chamaecyparis lawsoniana* and *Picea sitchensis* have the highest mean value of RNPR, SLA and shoot-root ratio, respectively. Boxplots of traits values for each species are available in Appendix 3.

Results from the linear mixed effects models are given in Table 6-4. After the stepwise procedure, only RHGR and SLA are significantly positively related to local invasiveness. The same traits stand out when the taxonomic group is not considered (see Appendix 4). For the global invasiveness, a significant relationship is only found for RHGR. Here also, a faster relative increase in height is related to a higher invasiveness value (Fig. 6-5).

Table 6-3: Number of measurements, mean values, standard errors and significance letters (Tukey's t test) of traits for each species. Units are g.g^{-1}.d^{-1} for RGR and SRGR, cm.cm^{-1}.d^{-1} for RHGR, needles.needles^{-1}.d^{-1} for RNPR and cm^{2}.g^{-1} for SLA.

Species	N	RGR		RHGR		SRGR		RNPR		SLA
Abies grandis	18	0.026 ± 0.003	a	0.009 ± 0.002	ab	0.027 ± 0.003	a	0.026 ± 0.003	b	169.4 ± 6.6
Abies nordmanniana	21	0.016 ± 0.002	a	0.001 ± 0.001	a	0.015 ± 0.002	a	0.011 ± 0.003	ab	104.78 ± 3.9
Abies procera	17	0.029 ± 0.003	a	0.007 ± 0.002	ab	0.028 ± 0.003	a	0.025 ± 0.005	b	150.4 ± 6.5
Chamaecyparis lawsoniana	13	0.018 ± 0.005	a	0.008 ± 0.002	ab	0.018 ± 0.005	a	0.017 ± 0.003	ab	243.4 ± 19.4
Cryptomeria japonica	15	0.022 ± 0.003	a	0.012 ± 0.002	ab	0.022 ± 0.003	a	0.022 ± 0.002	ab	202.3 ± 8.1
Larix kaempferi	22	0.029 ± 0.004	a	0.010 ± 0.002	ab	0.029 ± 0.005	a	0.022 ± 0.003	ab	222.0 ± 7.9
Picea rubens	17	0.022 ± 0.003	a	0.005 ± 0.002	ab	0.020 ± 0.003	a	0.018 ± 0.001	ab	162.4 ± 7.7
Picea sitchensis	14	0.025 ± 0.003	a	0.010 ± 0.002	ab	0.025 ± 0.003	a	0.020 ± 0.003	ab	191.0 ± 10.9
Pinus ponderosa	12	0.021 ± 0.004	a	0.005 ± 0.002	ab	0.020 ± 0.004	a	0.013 ± 0.002	ab	185.5 ± 4.9
Pinus strobus	19	0.022 ± 0.003	a	0.007 ± 0.002	ab	0.020 ± 0.003	a	0.021 ± 0.002	ab	186.5 ± 5.4
Pseudotsuga menziesii	15	0.028 ± 0.004	a	0.014 ± 0.002	ab	0.028 ± 0.004	a	0.021 ± 0.004	ab	182.1 ± 11.0
Thuja plicata	18	0.031 ± 0.004	a	0.017 ± 0.003	b	0.031 ± 0.005	a	0.018 ± 0.002	ab	210.9 ± 9.5
Tsuga canadensis	17	0.014 ± 0.003	a	0.004 ± 0.002	ab	0.013 ± 0.004	a	0.011 ± 0.003	ab	214.6 ± 13.2
Tsuga heterophylla	17	0.024 ± 0.003	a	0.010 ± 0.002	ab	0.024 ± 0.003	a	0.020 ± 0.003	ab	223.0 ± 14.5
Xanthocyparis nootkatensis	10	0.020 ± 0.003	a	0.009 ± 0.002	ab	0.020 ± 0.003	a	0.019 ± 0.003	ab	209.5 ± 10.1

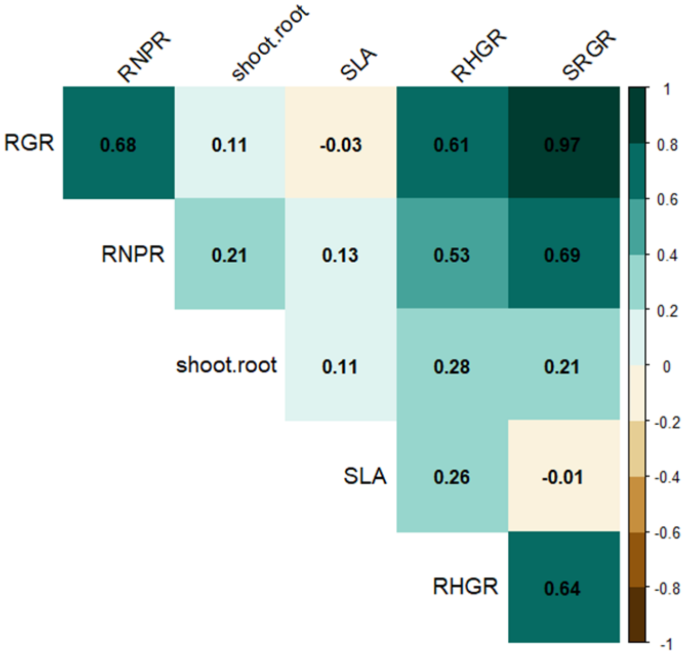


Figure 6-4: correlation plot of the six studied traits with Spearman coefficient values.

Table 6-3: Regression summary of the two models selected by stepwise regression on growth traits. Response is either local or global invasiveness. P values, estimates, t values, standard errors, variance of the taxonomic group and conditional r² are given for each trait.

	Significant predictors	**P Value**	**Estimate**	**t value**	**Std error**	**Taxa var.**	**Cond. R^2**	**Marg. R^2**
Local	RHGR	0.018 *	0.180	2.38	0.076	0.39	0.31	0.08
	SLA	< 0.001 ***	0.276	3.56	0.077			
Global	RHGR	0.021 *	0.166	2.32	0.072	2.27	0.67	0.01

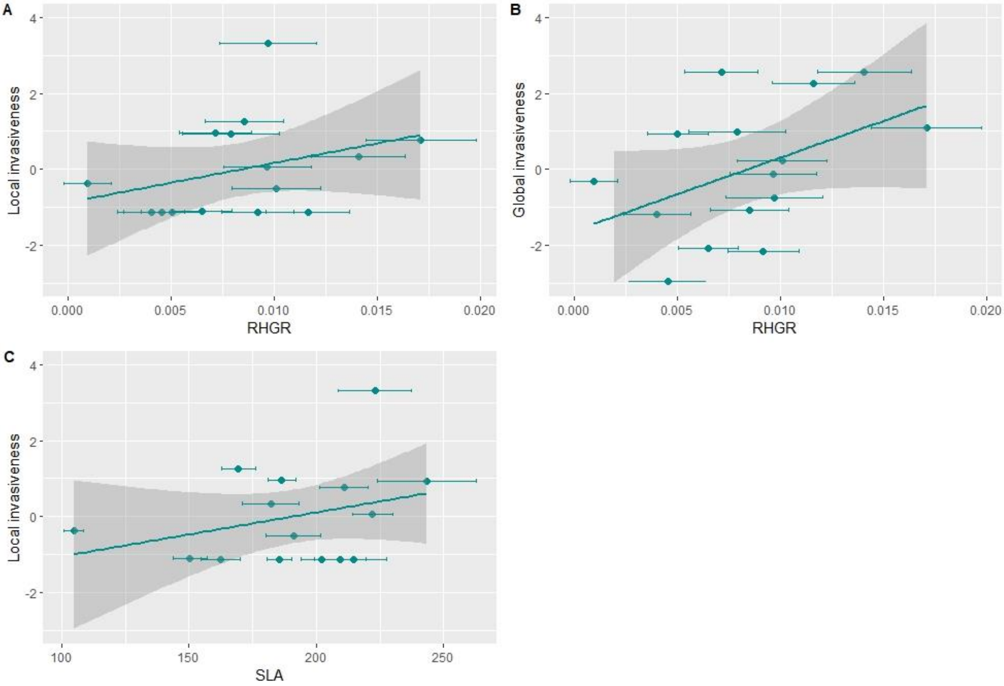


Figure 6-5: Predicted values for growth traits significantly related to invasiveness for both local and global invasiveness: (A) for RHGR and local invasiveness, (B) for RHGR and global invasiveness, (C) for SLA and local invasiveness. Mean values and standard errors of traits values are represented for each species. Units are cm.cm^{-1}.d^{-1} for RHGR and cm2.g^{-1} for SLA.

22. Discussion

The relative increment in height (RHGR) consistently emerges as a key trait at both local and global scales. Our study contributes evidence that rapid height growth at the seedling stage is a determinant factor of invasiveness for conifer species. Fast vertical growth has also been identified as a key strategy allowing woody plants to become invasive in Porté et al. (2011) and Tan et al. (2018). Global invasiveness gives a broad picture of the potential the species have to invade in various environments, while local invasiveness is defined based on observed invasiveness in shaded Belgian forests. Therefore, values assigned to a same species for local and global invasiveness can be fairly different. However, RHGR remains a consistent predictor of invasiveness at both scales, which indicates that a strategy of fast height increment is an advantage for invasive species in both open and closed habitats. This supports the interest of using a trait-based approach in the determination of invasiveness and of varying the studied scales.

The specific leaf area (SLA) is also positively correlated to local invasiveness. SLA has already been identified as the main driver of growth rate variation between invasive and non-invasive pines (Grotkopp et al. 2002) and a key trait in explaining maples' invasion (Porté et al. 2011, Fanal et al. 2022). As the local study took place in closed forests, SLA might play a more important role for light acquisition in this ecosystem type. Indeed, SLA represents how fast species can acquire resources through photosynthesis (Leishman et al. 2007). For seedlings, SLA is related to the rate of new leaves production. However, SLA and RNPR were not highly correlated, which indicates that, in our case, higher SLA is not necessarily due to a higher needles production rate of the seedlings.

Previous studies have found relationships between invasiveness of trees and seedlings' RGR. In a meta-analysis by Lamarque et al. (2011), RGR was identified as a key-trait in predicting the invasiveness of tree species. In this study, we did not find a significant relationship between RGR and local nor global invasiveness, regardless of its positive correlation with RHGR. The high intraspecific variability observed for RGR and other growth traits might have led to non-significant relationships with invasiveness, despite sometimes high correlations with RHGR.

In a two-dimensional representation of trade-offs between major traits critical to survival and growth, Díaz et al. (2015) identified the "leaf economic spectrum" or "acquisitive-conservative" continuum, a dimension in traits variation running from species with "acquisitive" leaves (nitrogen-rich, high SLA) to species with "conservative" leaves (nitrogen-poor, low SLA). Fast-growing species with high SLA replace their leaves more often, transferring their resources to better-lit new foliage. They also exhibit lower wood density (Yeboah et al. 2014) and invest less resources into defenses and hydraulic architecture (Brienen et al. 2020). On the contrary, more stress-tolerant species will allocate more resources to robust leaves with low palatability and longer lifespan and to defense mechanisms (Wright et al. 2004).

The recent study used to calculate our local invasiveness took place mainly in closed broadleaves or conifer forest ecosystems (Fanal et al. 2021). Therefore, species which displayed important regeneration and dispersal were mainly shade-tolerant species. We see in our experiment that an acquisitive strategy favors invasiveness not only in disturbed habitats, but also in closed forest ecosystems – even though it is rather in vertical growth and not in total biomass increment. This defies the usual trade-offs expected for shade-tolerant species in closed forest habitats. Ligot et al. (2020) already observed that saplings of *Tsuga heterophylla*, which has highest value of local invasiveness, had an annual height increment twice as fast as other frequently planted conifers such as *Picea abies, Abies alba,* and *Larix kaempferi* in Belgian forests. Outcompeting other tree species for light acquisition through rapid vertical growth and high SLA seems to be an effective strategy for shade-tolerant invasive trees. Fridley et al. (2022) suggested that a combination of fast growth and persistence in the shaded understory may enhance invasion success in forests. *Tsuga heterophylla* is the perfect example of this strategy, remaining in the understorey in anticipation of favorable light conditions and outcompeting co-occurring tree species in canopy gaps (Bellingham et al. 2018, Ligot et al. 2020). This strategy has also been highlighted for

Acer platanoides in North-American temperate forests (Webb et al. 2000, Martin et al. 2010a).

In our study, we selected a majority of North-American species, as Asian conifer species have been less imported for timber production in Europe, except for a few species from Japan and Caucasus such as *Cryptomeria japonica*, *Abies nordmanniana* and *Larix kaempferi*. Asian species had therefore less opportunity to invade, which creates a bias in the provenance of the studied species (Richardson and Rejmánek 2004). For conifers, most available studies present a taxonomic bias towards *Pinaceae*, as pines are among the most widely planted conifers worldwide and many invasion successes have been recorded (Richardson and Rejmánek 2004). In this study, we broadened the investigated taxa by including *Cupressaceae* species. We see that the traits related to invasiveness are similar for both families.

Cryptomeria japonica was attributed a high value of global invasiveness, but no regeneration was found in Belgian arboreta and its local invasiveness value is the lowest. It is probably because the abiotic conditions suitable for this species were not met in the studied Belgian sites: *C. japonica* regenerates mainly in full light and favors a > 2000 mm annual pluviometry (Pardé 1983), while annual mean rainfall on the studied sites ranges between 885 and 1280 mm (RMI n.d.). On the other hand, *Tsuga heterophylla,* a shade-tolerant hemlock native from western North America, displayed the most abundant local natural regeneration and dispersal, but was attributed a low global invasiveness value. This species has not been introduced in many regions of the world yet; its occurrences in GBIF, out of the native range, are scattered in 3 regions (as defined in the Global Compendium of Weeds), while *Cryptomeria japonica,* for example, is present in 9 regions (GBIF: The Global Biodiversity Information Facility 2022). The two pine species, *P. ponderosa* and *P. strobus*, had much higher scores of global invasiveness than local invasiveness. It is not surprising, as pines distinguish from most other conifers in their efficiency in aggressive post-disturbance colonization, and have proved to be very successful invaders in open habitats (Richardson and Rejmánek 2004).

Other functional traits may play a role in the invasion success of conifer species, such as reproductive traits. Richardson and Rejmánek (1996) identified a short juvenile period, a small seed mass and short intervals between large seed crops as key traits promoting invasiveness in conifers. These traits are indeed associated with an early and consistent reproduction, and with a large amount of better dispersed seeds, increasing the rate of spread of exotic conifers in natural habitats. Richardson and Rejmánek (2004) used mean values of these traits to build “Z scores” of invasiveness for a large number of conifer species. We were able to retrieve Z scores for all of our studied conifers, except for *Picea rubens* (Appendix 5). However, we noticed weak to no correlation between the Z scores and local ($r = 0.02$) or global ($r = 0.21$) invasiveness. Some species with high Z scores, such as *Xanthocyparis nootkatensis,* had very low scores of global and local invasiveness in our study. While it may be due to a lower planting intensity or a more recent history of introduction, it seems that reproductive traits alone may not be sufficient to explain the invasion success of some conifers. However, combining reproductive traits and the syndrome of fast height increment and high SLA in shaded conditions might improve our understanding of the invasion process in forests and the identification of species with high inherent invasive potential.

The invasibility of the habitat and anthropogenic factors are important factors to consider as well: woodlands are more prone to invasions when exposed to a higher disturbance regime, and intensive commercial plantations of conifers facilitate the dispersal and establishment of other non-native conifers (Wagner et al. 2017, Fanal et al. 2021). Therefore, sylvicultural practices play an important role in mitigating invasions by exotic trees. In Southern Belgium for instance, plantations of non-European conifers already represent about 8% of the forest area. A high number of planted reproductive exotic trees, resulting in an enormous propagule pressure, may accelerate invasion events (Simberloff et al. 2010) and overwhelm ecological resistance of ecosystems to invasions (Von Holle and Simberloff 2005). Non-native species introduced in adaptative forest management programs should undergo a thorough risk assessment, and monitoring sites should be established for early detection of invasive tree species (Carrillo-Gavilán and Vilà 2010, Wagner et al. 2017, Brundu et al. 2020)

Finally, climate change is likely to affect the invasion risk of many conifers in temperate Europe. It may lower some barriers to naturalization and invasion of exotic trees, including pine species (Richardson and Rejmánek 2004). On the contrary, changes in the precipitation regime and more frequent heat waves will likely mean that environmental niches of many conifers will shift northwards and northeastwards and be reduced: for example, the ranges of *Abies grandis* and *Larix kaempferi* in Europe are expected to decrease by 52 and 60 % respectively by 2070 (Thurm et al. 2018, Puchałka et al. 2023). Dyderski et al. (2018) labeled conifer species as “losers” in the future climate scenarios in Europe, because of the lack of available suitable areas at northern latitudes. A conservative strategy of higher carbon allocation in the root biomass and mechanisms of resistance to water stress might therefore become more advantageous in future forest ecosystems in temperate Europe (Funk 2013). However, conifers with high inherent invasiveness might still be problematic in their new northern range if not too limited in their water intake (Thurm et al. 2018).

23. Conclusion

Our results support the interest of using a trait-based approach to understand the determinants of invasiveness and the benefit of using different scales. Our study brings elements to better understand the drivers of exotic conifers invasions in closed forest ecosystems, and supports the hypothesis that an acquisitive strategy of fast resource acquisition through fast height increment and high SLA is also an advantage for shade-tolerant gymnosperms invading forests understories. However, more conservative strategies might become more efficient compared to acquisitive strategies in future years, as water resources are likely to become more limited in temperate Europe.

7

Discussion

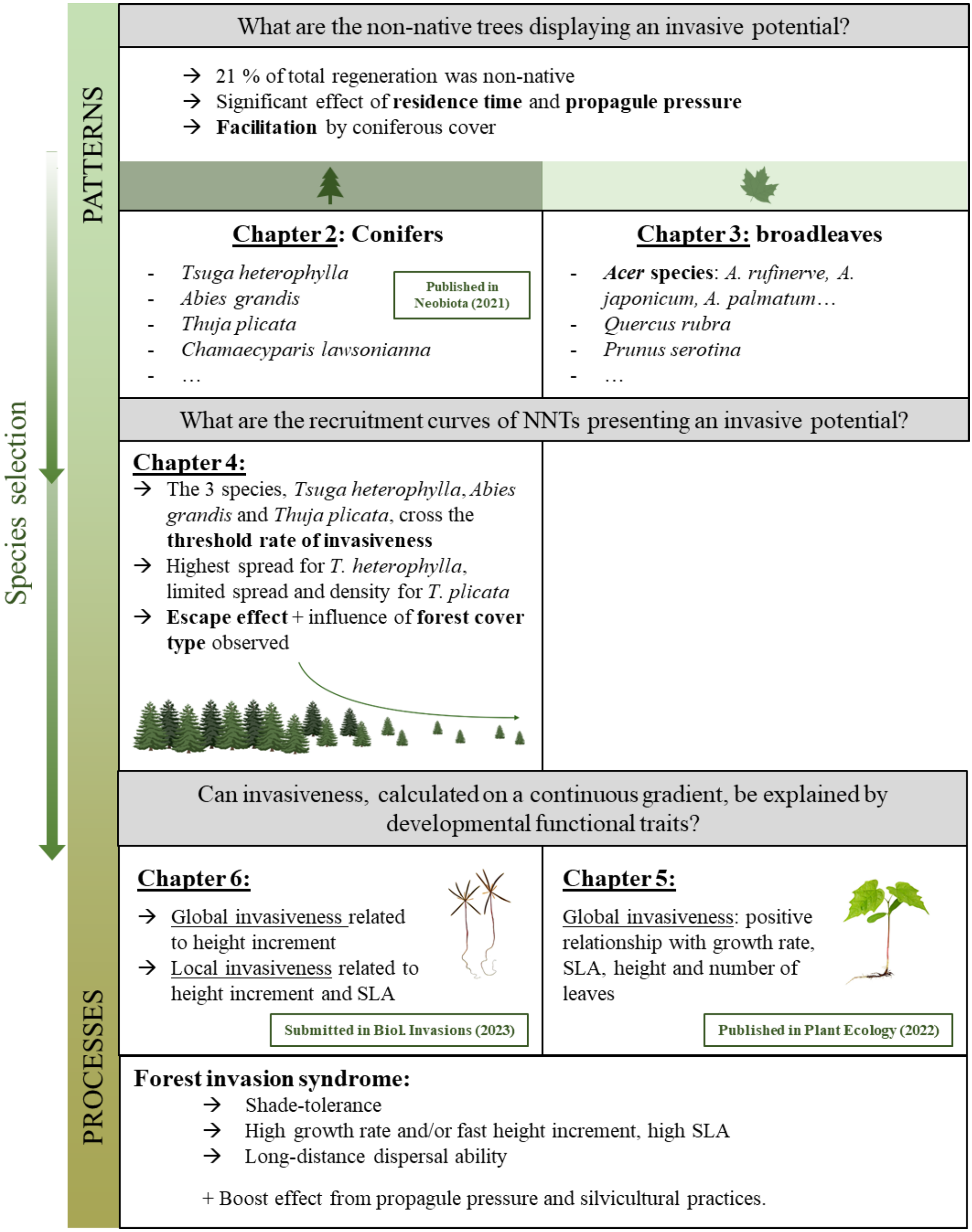
24. The process of NNTs invasions in European forests

24.1. Determining a species' invasion potential

There is a considerable invasion debt existing in Europe regarding invasive plant species (Rouget et al. 2016), and it is likely to increase with the current afforestation programs promoting the use of non-native trees. In this thesis, I bring elements to better understand the invasion process of NNTs into European temperate forests and identify species at risk. A summary of the results of chapters 2 to 6 is presented in Figure 7-1.

In Chapters 2 and 3, we used old forest arboreta as natural experiments to identify non-native tree species (NNT) displaying an invasive potential. We observed several NNTs regenerating in the arboreta, some being already well-known invasive species, such as *Quercus rubra*, *Prunus serotina* and *Robinia pseudoacacia*. *Acer rufinerve,* still not a widely spread invasive species in Europe but already listed in Belgium, also stood up in our results as a species with high potential to spread into forest ecosystems. Other maple species were also found in dense regeneration patches, such as *Acer japonicum*, *Acer palmatum*, *Acer lobelii* or *Acer rubrum*. However, the most striking finding was the important density of regeneration of several conifer species, especially *Tsuga heterophylla* which creates dense, impenetrable stands. Seventeen percent of the widely planted conifers we studied displayed important regeneration and dispersal potential, and could be part of the invasion debt threatening European forests. Our monitoring of recruitment curves of three of these conifer species confirms the invasive risk of *Tsuga heterophylla* and *Abies grandis* if planted in favorable sites. However, it mitigates the risk for *Thuja plicata*, the species displaying more important dispersal and regeneration limitations.

Chapters 2, 3 and 4 confirm the interest of using old forest trials to monitor the risk of invasion by NNTs. If some of the monitored NNTs only displayed low natural regeneration at short distances, more plantings of these species might create a massive propagule pressure accelerating their progression on the naturalization-invasion continuum. Thorough monitorings of existing plantings, arboreta and botanical gardens are therefore critical to prevent new invasions by NNTs (Carrillo-Gavilán and Vilà 2010, Brundu and Richardson 2016, Culley et al. 2022). More recently, a code of conduct produced on behalf of the Bern Convention recommended the use of sentinel sites to identify species presenting an invasive potential (Brundu and Richardson 2017). The network of old arboreta set in Belgium more than a century ago in various environmental conditions offered a unique opportunity to test monitoring protocols for NNTs and to study factors of the invasion process on-site.



What are the non-native trees displaying an invasive potential?

→ 21 % of total regeneration was non-native
→ Significant effect of **residence time** and **propagule pressure**
→ **Facilitation** by coniferous cover

Chapter 2: Conifers

- *Tsuga heterophylla*
- *Abies grandis*
- *Thuja plicata*
- *Chamaecyparis lawsonianna*
- …

Published in Neobiota (2021)

Chapter 3: broadleaves

- ***Acer*** **species**: *A. rufinerve, A. japonicum, A. palmatum*…
- *Quercus rubra*
- *Prunus serotina*
- …

What are the recruitment curves of NNTs presenting an invasive potential?

Chapter 4:

→ The 3 species, *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata*, cross the **threshold rate of invasiveness**
→ Highest spread for *T. heterophylla*, limited spread and density for *T. plicata*
→ **Escape effect** + influence of **forest cover type** observed

Can invasiveness, calculated on a continuous gradient, be explained by developmental functional traits?

Chapter 6:

→ Global invasiveness related to height increment
→ Local invasiveness related to height increment and SLA

Submitted in Biol. Invasions (2023)

Chapter 5:

Global invasiveness: positive relationship with growth rate, SLA, height and number of leaves

Published in Plant Ecology (2022)

Forest invasion syndrome:

→ Shade-tolerance
→ High growth rate and/or fast height increment, high SLA
→ Long-distance dispersal ability

+ Boost effect from propagule pressure and silvicultural practices.

Figure 7-1: Summary of the main results of the experiments presented in Chapters 2 to 6.

Our results concerning the determinants of invasiveness are consistent with previous studies. Both time since planting and area planted of a species increased its observed density of regeneration (Pyšek et al. 2009b, Dyderski and Jagodziński 2018).

In order to test the relationship between invasiveness and functional traits, a continuous approach of invasiveness was developed and used in chapters 4 and 6 on the two groups of species that emerged in our field sampling, conifers and maples. It is interesting to note that the *Aceraceae* and *Pinaceae* families have been precisely highlighted in Richardson and Rejmánek (2004) as two of the most "weedy" families (*i.e.* families with the highest proportions of invasive species, for predominantly woody species). Indeed, a dichotomous invasive/non-invasive categorization misses the array of possible positions of species on the "introduced-naturalized-invasive" continuum. At the local scale, we chose to use data recorded in old arboreta as proxies of invasiveness, in relation to the definition of an invasive plant presented in Richardson et al. (2000): the density of regeneration and the 95th percentile of distance from potential parent trees. For invasiveness at a global scale, however, the choice of proxies is not so obvious. The number of citations in the scientific literature is biased in favor of highly-studied, impactful species, mainly in countries with more funding available. The number of regions invaded is often used as a proxy, but depends on the introduction effort. Moreover, there is sometimes confusion between introduced, naturalized and invasive species in national databases. Finally, risk scores are often computed based on general models and are not always representative of the actual invasiveness of a species. Each of these proxies has advantages and limitations – therefore, we combined them to better capture the actual invasiveness of the studied species. The four proxies we used for both maples and conifers (risk score and number of citations in Randall (2017), number of invaded countries and regions in GBIF (2022) were positively correlated and brought a more nuanced picture of the species' invasiveness, which confirms the coherence of our approach. However, the limitations of the proxies still apply, and we suggest to use this procedure with caution and with a critical gaze as this is mainly effective to compare several species with similar introduction histories.

24.2. Rate of spread into natural habitats and recruitment

Dispersal curves of wind-dispersed trees are usually strongly right-skewed, most of the propagules landing close or under the parent trees, even if the median varies strongly according to the seed morphology and dispersal vectors (Clark et al. 2005, Säumel and Kowarik 2013). Most of the regeneration observed in our arboreta and isolated sites was, indeed, situated in the first 30 meters around the plantings. The invasion success depends on the ability of a species to spread at far distances. For trees, there must be "clear evidence that it regenerated naturally and recruited seedlings more than 100 m from parent plants" according to Richardson et al. (2000). We did find several species exceeding this distance in less than 50 years after maturity of parent plants. Some were already known invasive trees, such as *Robinia pseudoacacia*, *Quercus rubra* and *Prunus serotina*. However, recruited regeneration of several non-native conifers was also observed at far distance (*Tsuga heterophylla, Pseudotsuga menziesii, Abies grandis, Chamaecyparis lawsonianna, Larix kaempferi,* and *Thuja plicata*), as well as a few saplings of exotic maples (*Acer rubrum, Acer saccharinum, Acer rufinerve, Acer lobelii* and *Acer japonicum*). These species are therefore likely capable of creating new satellite populations, accelerating the expansion rate.

Rare LDD events and fat-tailed dispersal kernels can have an overwhelming effect on the rate of expansion of trees, accelerating the speed of spread up to an exponential function of time (Nathan et al. 2008, Hui and Richardson 2017). There is also strong evidence that there is a constant selection pressure on dispersal-related traits at the range front through spatial sorting, which results in stronger dispersers at the edge of the occupied area (Monty and Mahy 2010). These two phenomena are important drivers of boosted range expansion (Hui and Richardson 2017). The tendency towards fat-tailed dispersal kernels observed for *Tsuga heterophylla* and *Abies grandis* planted in favorable sites indicates that the spread of these two species, which already reaches up to 17 m/years and 10 m/years respectively, may accelerate in the near future.

Growth abilities of trees at the range front and initial propagule pressure can also increase the rate of spread (Ramanantoanina et al. 2014) and overwhelm ecological resistance of ecosystems to invasions (Von Holle and Simberloff 2005).Therefore, high planting intensities may override dispersal limitations of species such as *Thuja plicata* or *Chamaecyparis lawsonianna*.

In chapter 4, accurate recruitment curves of established trees were hard to model for *Thuja plicata* and *Abies grandis*, as these two species presented few stems over 150 cm in the natural regeneration. This might be due to the fact that these two species are highly palatable for herbivores and susceptible to browsing even in the introduced range, contrary to *Tsuga heterophylla* (Petit et al. 2017). We observed a slight escape effect for the three species, the mean distances of dispersal being displaced further from the parent trees with each successive recruitment stage. This escape effect may be due to a density-dependent impacts of natural enemies – however, it is unlikely that large herbivores are responsible. Herbivorous vertebrates are indeed highly mobile, and the Janzen-Connell effect relies on the relative dispersal abilities of natural enemies (Song et al. 2021). Predation pressure from pests and herbivores is not enough to explain the observed recruitment patterns, as the strongest escape effect was observed for *Tsuga heterophylla*, and this species is less subject to browsing, pests and pathogens in its introduced range. Despite the three species being shade-tolerant conifers, the recruitment of established seedlings may be dependent on small disturbances allowing light to reach the understorey (Howe and Miriti 2004, Martin and Canham 2010). As forest trials usually consist in dense plantings, more favorable sites are probably available at increasing distance from the parent trees, which results in a temporal shift of the recruitment curves.

24.3. Towards a forest invasion syndrome

Chapters 5 and 6 highlighted the strategy of fast resource acquisition as a key component of the invasion process in forests for tree species. While we could expect different strategies for angiosperms and gymnosperms, they are actually similar. For maples, this strategy appears through higher growth rates in biomass and height for invasive species, as well as a higher SLA and number of leaves. For conifers, it mainly consists of higher height increment, presumably in a strategy of fast light acquisition, which is also observed locally in dense forests with higher SLA values for more invasive species.

This syndrome of fast resource acquisition has already been tested intensively in the literature. However, most of these studies concerned pioneer, light-demanding species, often in highly disturbed habitats, such as the studies performed on pines and acacias by Grotkopp et al. (2002) and Gallagher et al. (2011). Here, we confirm the traits syndrome of fast resource acquisition is also applicable for shade-tolerant species displaying an invasive behavior in forests. However, for conifer species, it was not expressed by differences in biomass increment, but rather in height. The ability to outcompete other tree species for light acquisition through rapid growth and high specific leaf area (SLA) confers an advantage in closed forest ecosystems, even for late-successional species. Fridley et al. (2022) suggested that a "fast-but-steady" functional syndrome, combining fast growth and persistence in the shaded understorey, may promote invasion success in forests. This surely explains the invasive success of some of our studied species, which have the capacity to remain in the understorey in anticipation of favorable light conditions, and which outcompete co-occurring species in canopy gaps (Galbraith-Kent and Handel 2008, Bellingham et al. 2018, Fridley et al. 2022). *Tsuga heterophylla* is the perfect example of this strategy, as it grows 2 to 3 times faster than co-occurring non-native conifers in mixed coniferous stands while being one of the most shade-tolerant species planted in Southern Belgium (Ligot 2011). This strategy has also been highlighted for *Acer platanoides* in North-American temperate forests (Webb et al. 2000, Martin et al. 2010b).

Combining the results from chapters 2 to 6, I portrayed a **“forest invasion syndrome”**, combining (1) shade-tolerance allowing seedlings persistence in the understorey, (2) high growth rate enhancing competitiveness in canopy gaps and (3) a long-distance dispersal ability. High planting intensities, resulting in high propagule pressure, and enhanced habitat invasibility through frequent disturbance or silvicultural practices (*eg* abundant coniferous cover) amplify this syndrome.

This combination of shade-tolerance (usually associated to S strategy) and high growth rates after disturbances (rather a C strategy) can be surprising. In forest ecosystems, a trade-off is usually expected between shade-tolerance and rapid growth of trees. For example, *Ailanthus altissima* displays high growth rates in high light levels, where it is highly competitive against native species, but its survivorship drops drastically in low-light conditions. Trade-offs also exist between high SLA and resistance to herbivory: fast-growing species tend to replace their leaves more often, transferring their resources to better-lit new foliage, while more stress-tolerant species will allocate more resources to robust leaves with low palatability and longer lifespan (Wright et al. 2004). Fast-growing species will also exhibit lower wood density (Yeboah et al. 2014) and invest less resources into defenses and hydraulic architecture (Brienen et al. 2020). In a “global spectrum of plant form and function”, a two-dimensional representation of trade-offs between six major traits critical to survival, growth and reproduction, Díaz et al. (2015) identify a dimension in traits variation running from species with “acquisitive” leaves (nitrogen-rich, low leaf mass per area) to species with “conservative” leaves (nitrogen-poor, high leaf mass per area and lower stem density), i.e. the “leaf economic spectrum” or “acquisitive-conservative” continuum. Another important dimension runs from species with small diaspores to tall species with larger diaspores, which might reflect the r-K continuum (colonization – exploitation) (Jones 1976). Most species lie at intermediate positions along these gradients (Fig. 7-2).

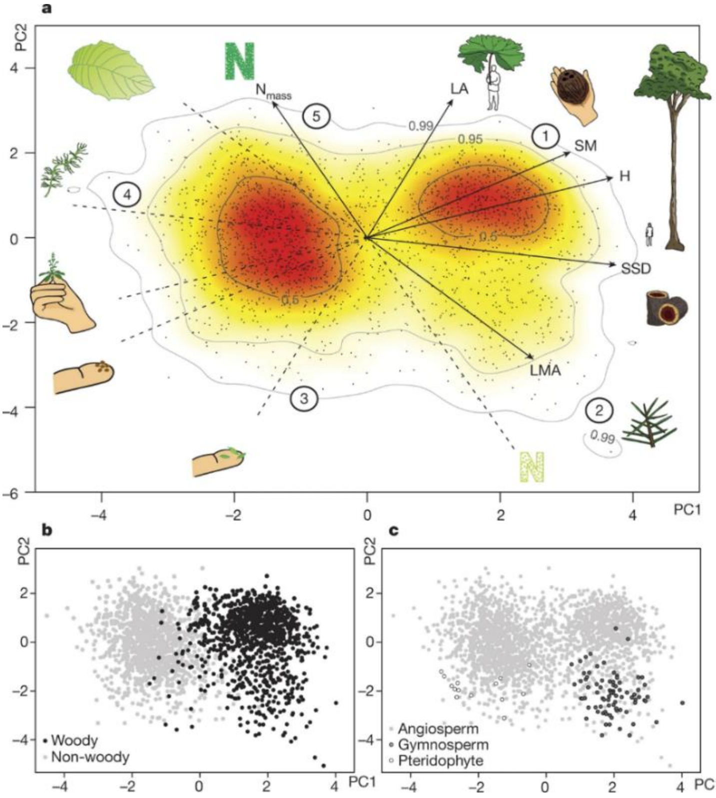


Figure 7-2: projection of global vascular plant species on the two-dimensional global spectrum of plant form and function. The color gradient indicates regions of highest (red) to lowest (white) occurrence probability of species. Circled numbers 3, 4 and 5 roughly correspond to the stress-tolerant, ruderal and competitor Grime’s strategies. **b** and **c** are the locations of different growth-forms and major taxa in the spectrum. Illustration from Díaz et al. Nature 1-5 (2015).

Recently, in early 2023, Fridley et al. made a statement similar to our forest invasion syndrome: exotic trees acting as “superinvaders” in forest ecosystems combine shade tolerance, rapid growth potential and high fecundity. As shade-tolerant species have traits that minimize tissue respiration and turnover, the same traits that prevent rapid growth and competitive abilities in high-light conditions, these invaders defy this trade-off expected for forest tree species. They develop the hypothesis that light availability and net carbon gain are the main factors driving forest invasions, using the concept of WPLCP (light level at which net growth is zero). As light is the main limiting resource in most of temperate forests, the process of forest invasions is mainly driven by the need to minimize energy costs in shaded conditions, making net carbon gain the primary driver of saplings survival in shade. Greater carbon costs, leading to an increase of WPLCP and a reduction of shade-tolerance, may be due to greater tissue loss from herbivory, greater wood investment per unit leaf mass, larger carbon investment in roots and defensive structures, or reproduction. At the opposite, lower carbon costs and reduced WPLCP can derive from reduced herbivory, longer tissue lifespan, fewer support structures or defense mechanisms, reduced below-ground investment or a shorter stature. Fridley et al. propose that the relationship between carbon costs, shade tolerance and growth rate can explain the forest “superinvader” phenotype, under the assumption that they experience fewer carbon costs, allowing more acquisitive NNTs to persist at lower light levels that they otherwise could in their native ranges.

Fridley et al. (2023) also identify several mechanisms that could explain this reduction in carbon costs for NNTs:

a) the enemy release hypothesis: a release from herbivores and pathogens in the introduction range can lead to an increased shade-tolerance. However, the advantages of enemy release usually decrease over time, as NNTs acquire new pathogens from the introduction area.

b) Environmental change and stress tolerance: if the environment changes and become less stressful (in terms of drought, extreme heat or freezing, nutrient scarcity…), native species might continue to expend carbon for adaptations for relatively uncommon stresses, while novel, more competitive exotic phenotypes can establish more easily.

c) Disharmonic native floras: some native floras have experienced more extreme climatic histories, eliminating taxa and creating more “empty niches”. For example, North American deciduous forests may be more vulnerable to invasions by East Asian species having more effective strategies for resources acquisition in an understory environment (Fridley 2013) or by European woody species differing in their extended phenology (Zohner and Renner 2017), which might explain the advantage of *Acer platanoides* over native North American species (Morrison and Mauck 2007). Conversely, a mid-successional “sit-and-wait” strategy of low-light survival and fast disturbance response is common amongst the North American woody forest flora, but lacking in Europe except for *Fagus sylvatica*, which might explain the success of *Prunus serotina* in European temperate forests (Closset-Kopp et al. 2007).

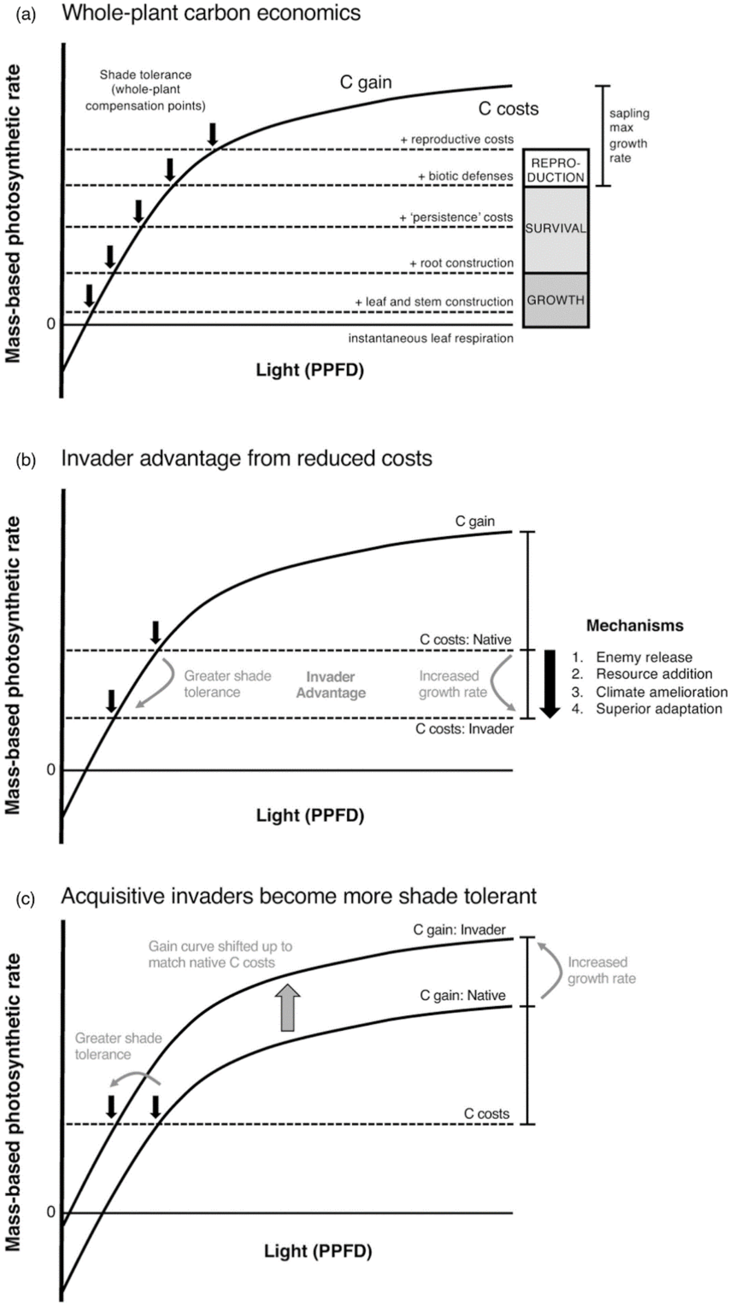


Figure 7-3: (a). WPLCP after accounting for carbon (C) costs. For a given light assimilation curve (C gain), C costs influence both growth rate in high light and shade tolerance. (b) Reduced C costs in invaders enhance both high-light growth rate and shade tolerance. (c) Invaders of high photosynthetic potential may still achieve greater shade tolerance than native species with similar C costs. Graph from Fridley et al. (2023).

Forest “superinvaders” therefore persist in shaded areas by increasing light capture, whether by prioritizing apical growth, through resprouting and clonal expansion. Examining several studies of photosynthetic function in native and invasive species, Funk (2013) found that invasive trees in shaded conditions achieved high photosynthetic rates at a lower respiratory cost than natives. In our growth experiment, we saw that species with higher invasiveness scores displayed higher growth rates in height, leaf production rates and SLA than less- or non-invasive species. Building cheaper leaves, invasive plants produce more photosynthetic structures, maximizing the whole-plant carbon gain (Heberling and Fridley 2013). Surplus carbon stored in shaded conditions is then rapidly mobilized when the light level increases after disturbance, which enables the production of new light-adapted leaves and rapid stem elongation. They later benefit from the increased rates of carbon gain to support reproduction, with copious propagules production. Such a plasticity in saplings physiology has been observed for several species, such as *Acer platanoides* in North America, the invasive tree fern *Sphaeropteris cooperi* in Hawaii, Quercus rubra in Poland, and *Micona calvescens* in Australia (Martin and Marks 2006, Murphy et al. 2008, Funk 2013, Dyderski and Jagodziński 2019a). High abundance of the invader in the sapling bank can further enhance invasion. In that regard, Horvitz et al. (1998) proposed a syndrome of “seedling-layer “oskar”-winner” for invasive plant species in forest communities, where NNTs dominate the oskar layer (suppressed saplings, receiving little to no direct sunlight) of the understory, establish in shade and outcompete native trees seedlings when light is available through superior physiological response.

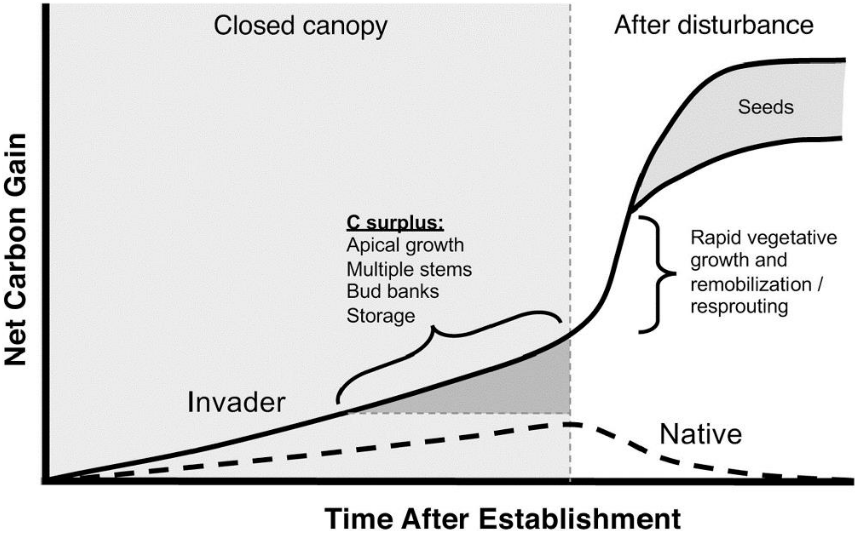


Figure 7-4: Carbon surplus from lower costs enables strategies in invaders allowing rapid exploitation of canopy gaps. Subsequent prolific production of small seeds at relatively small size classes is observed with many forest invaders, leading to rapid numerical dominance and high competition with native species. Graph from Fridley et al. (2023).

We focused primarily on growth traits in our experiments on maples and conifers, investigating the relationship between the position on the leaf-economic spectrum and invasiveness. Yet, the assemblage of traits associated with dispersal, called dispersal syndrome, is also relevant during the spreading stage of the invasion (Hui and Richardson 2017). For example, Pyšek et al. (2014) demonstrated that early start of flowering increased the probability of invasiveness of NNTs in Central Europe. Richardson and Rejmánek (2004) also indicated that a small seed mass and short time between large seed crops was positively correlated with invasiveness of conifers. Horvitz et al. (1998) described a "seed rain-of-terror" syndrome where invasive tree species dominate the seed rain from both internal and external native species. However, the relationship between seed mass and invasiveness can be complex. A trade-off between dispersal and survival based on seed mass has been tested among pine species: larger seeds disperse shorter distances but have a higher likelihood of successful recruitment (Wyse and Hulme 2022). In 2022, Dalling and Hubbell already stated that a seed-size dependent trade-off exists between dispersal success (large number of small seeds) and establishment success (fewer but larger seeds). We took advantage of our two growth experiments to dry and weigh a portion of the collected seeds. However, contrarily to other studies on invasive trees, we did not find any relationship between the mass of seeds and the invasiveness, neither for maples nor conifers.

24.4. Invasibility of the natural habitat and context-dependence of the invasion success

The context-dependence in invasions outcomes in European forests complicates the identification of future invasive species and the understanding of the underlying mechanisms of invasion. In addition to the species' inherent invasive potential, factors such as propagule pressure, time since introduction, habitat adequacy, management practices and the composition of the receiving community, act together in determining the invasion risk of an NNT in a specific site. It is therefore difficult to accurately infer the role of one factor in determining invasion risk without considering confounding factors. For example, a massive propagule pressure might override the effect of functional traits and dispersal or recruitment limitations. This complexity has significant implications when deciding whether to approve a species for introduction and planting. Therefore, it is essential to use models that analyze multiple factors simultaneously to properly assess the role of traits affecting species invasiveness (Pyšek et al. 2014, 2015a, Pyšek 2016, Bindewald 2021). The long time-lag between introduction and invasion by NNTs is also a difficulty in the assessment of their invasiveness. The duration of a time-lag varies with the age of maturity of a species, but also with the intensity of planting, habitat and management modifications or climate change (Duncan 2021).

The type of invaded forest ecosystem will also influence the traits associated with increased invasiveness in NNTs. For example, in dry forest ecosystems where water is a main limiting resources, more conservative NNTs allowing more carbon to below-ground biomass will have an advantage on purely acquisitive species (Funk 2013). Purely acquisitive species with low shade tolerance can also invade forest edges and clearings (Martin et al. 2010b, Dyderski and Jagodziński 2019a).

In both chapters 2 and 4, we saw that a coniferous forest cover facilitated the spread of non-native conifers, pointing on the influence of forest management practices in the invasibility of forest ecosystems. In Southern Belgium, more than 40% of the forest area is planted with conifer species, mainly monospecific plantings of *Picea abies*. This high proportion of coniferous stands may accelerate the invasion rate of shade-tolerant alien conifers (Jagodziński et al. 2015). On the other hand, deciduous stands, and particularly climax beech stands, hinders the regeneration of non-native conifers. Beech forests also impeded the regeneration of *Abies alba* in a study by Amm et al. (2012). We saw earlier that NNTs invasive in closed European forests might benefit from an empty niche, as “sit-and-wait” strategies are rare in the European flora (Closset-Kopp et al. 2007, Fridley et al. 2023). However, European beech (*Fagus sylvatica*) displays this same strategy (Laurent et al. 2017). Climax native beech forests could therefore be more resistant to invasions because of the lack of available niche for NNTs displaying our forest invasion syndrome. They could play a role as buffer zones, slowing down invasions of NNTs near protected or sensitive natural areas.

In brief, our forest invasion syndrome helps assess the potential to invade forests that NNTs possess. The capacity of NNTs to tolerate shade might differ between the native and the introduced range due to reduced carbon costs leading to an increased shade tolerance, therefore information on the ecology of NNTs in their native range might not be sufficient for risk assessments. Once introduced in a particular place, an NNT with high invasive potential will not systematically become invasive – it will depend on the propagule pressure, history of introduction, climate and abiotic suitability, invasibility of the receiving ecosystem, etc. Forestry practices can also favor invasive species: overstory harvest operations might facilitate their establishment and coppicing can stimulate the rejuvenation of some invasive NNTs (Sitzia et al. 2016, Liebhold et al. 2017). Forestry also directly influence the invasion risk by the choice of species applied (number of exotic species) and the diversity of native species maintained. An adapted management of tree cover and density can regulate inter-species competition and locally reduce the regeneration of NNTs, promoting native species (Sitzia et al. 2016). I summarized the distinction between invasive potential and invasion risk in Figure 7-5.

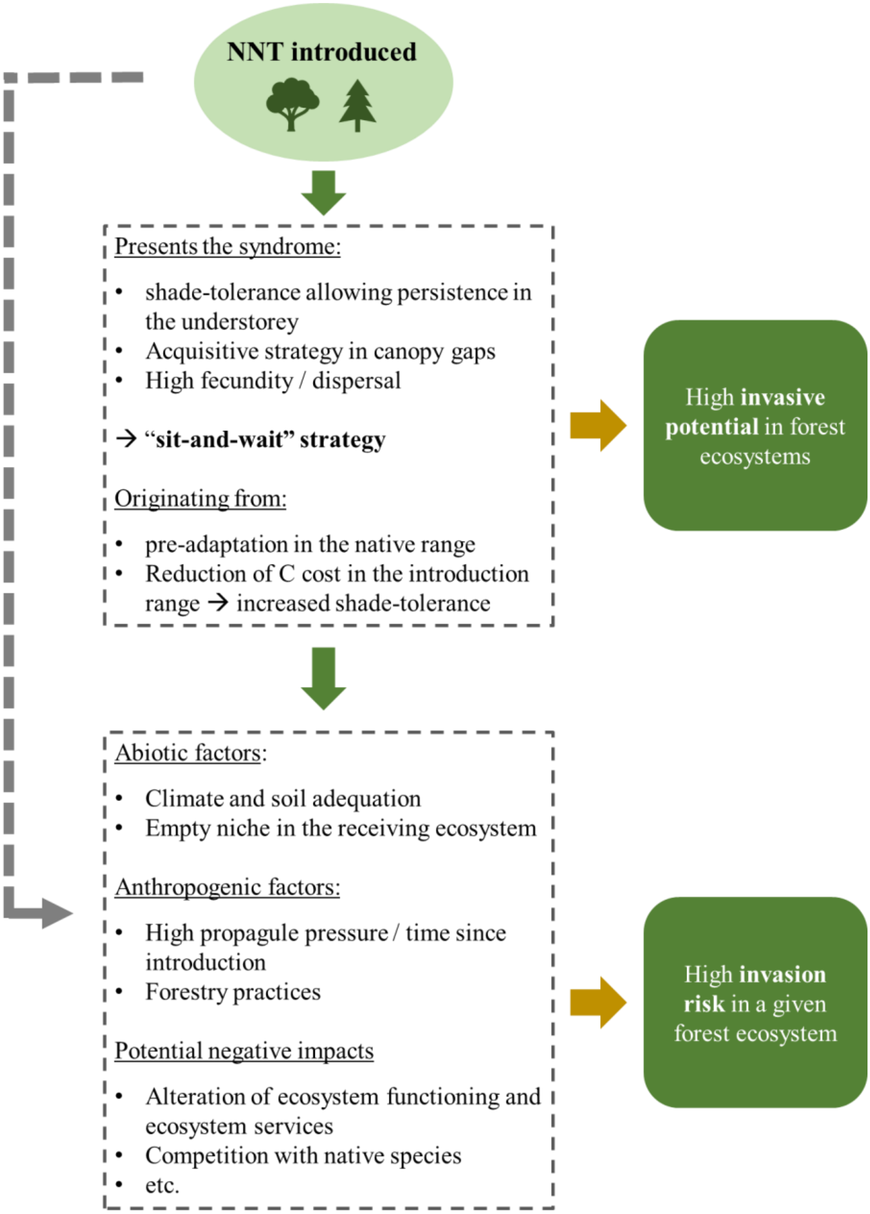


Figure 7-5: Factors influencing the invasive potential and invasion risk for shade-tolerant NNTs introduced in forest ecosystems. Introduced exotic tree species possess traits that enhance their **invasive potential**. A sit-and-wait strategy (persistence of saplings in the understory and high competitive abilities in canopy gaps following disturbances) has been associated to an increased invasion success in closed forests. In a specific area, several abiotic and anthropogenic factors will influence the **invasion risk** of a species. High propagule pressure due to high planting intensities can override establishment and dispersal limitations of a species and increase its invasion risk (grey dotted arrow).

25. The influence of climate change

The effect of climate change on European forests is difficult to predict, given the variety of processes and potential impacts. Higher productivity can be expected from the extension of the growing season and the increase of atmospheric carbon dioxide concentrations (Reyer et al. 2014), but at the same time decreased productivity and increased mortality will likely arise from frequent heat waves and storms, improved conditions for the reproduction of pests, extremes droughts or, conversely, flooding damages (Bolte et al. 2009). Climate change may also lower some barriers to naturalization of non-native species, increasing the naturalization potential and invasion risk of already introduced NNTs in Europe, therefore increasing the invasion debt in the European flora (Haeuser et al. 2018). On the contrary, the invasion risk of some NNTs might decrease as their environmental niche is no longer met in the new climatic conditions.

For example, in our studied arboreta, *Abies grandis* seemed to tolerate drier soils and was even met on a limestone hill in the arboretum of Nismes. While we expected this capacity to tolerate dryer soils to become an advantage in the coming years, given the expected consequences of climate change, it seems that the species is still greatly affected by successive droughts and *Armillaria sp.* attacks in many forests of Wallonia (OWSF 2019). While the intrinsic invasive potential of *Abies grandis* is high, climate change might reshuffle the cards regarding its invasion risk, as well as the invasion risk of many exotic conifers in temperate regions where droughts are becoming more frequent and intense. Thurm et al. (2018) predicted that, by 2070, the range of *Abies grandis* in Europe might decrease by 44 to 60 % according to the climate scenario, and the range of *Larix kaempferi* by 57 to 63%. On the contrary, distribution ranges of more drought-tolerant NNTs such as *Quercus rubra* and *Robinia pseudoacacia* wound increase, by about 68 % and 133 % respectively). In general, the range of most exotic conifers will contract in the near future, as they have limited possibilities to shift further north or at higher altitudes. As conifers are also frequently damaged by native or introduced pests and pathogens, a warming climate might enhance the risk of biotic hazards (Dyderski et al. 2018b, Puchałka et al. 2023). Only *Pinus* species might benefit from climate change in Europe and expand their potential range, especially *P. strobus*, an aggressive post-disturbance colonizer (Puchałka et al. 2023).

Dyderski and Jagodziński (2019a) have just highlighted that the strategy of *Quercus rubra* in forests of West Poland differed from other studied NNTs, with a rather conservative strategy of high belowground resource competition, allowing it to reach a high biomass and high projected leaf area. Conservative tree species allocating more resource to their below-ground biomass and to mechanisms of resistance to water stress might therefore dominate future forest ecosystems in temperate Europe (Funk 2013). Hanewinkel et al. (2012) predicted that, by 2100, between 21 and 60 % of European forests lands would be suitable for a Mediterranean forest type, dominated by slow-growing, drought-resistant oaks.

It is interesting to note that, according to Thurm et al. (2018), *A. grandis* would benefit from enhanced growth conditions in its more northern new expected distribution, while for *Q. rubra* the growth conditions would deteriorate. Temperate-forest NNTs of which potential range will shift further north might therefore display enhanced invasiveness in their future northern distribution, while the invasiveness of more drought-tolerant NNTs such as *Q. rubra* might decrease a little bit despite the expansion of their distribution range, due to the cost of adaptations to drier conditions (lower leaf-area index, higher leaf thickness, higher root-to-shoot ratio…). Also, the authors insist on the fact that their models on exotic trees might be too restrictive, as it is based on the low level of genetic biodiversity introduced in Europe. *Abies grandis* for example has a great native distribution, from moist coastal regions to drier interior mountainous areas. Mainly coastal provenances were selected for importation in Europe, while other provenances might allow a better drought-tolerance of the grand fir in temperate Europe.

26. Focus species: *Tsuga heterophylla*

Tsuga heterophylla (Raf.) Sarg. (Western hemlock) is a coniferous tree from the *Pinaceae* family that can reach a height of over 80 meters in its area of origin. This area extends from southern Alaska to northern California with a slight tendency to expand inland to the East (Christy and Mack 1984). It is highly sensitive to drought, which is why it develops preferentially under a mild and rainy climate (Gavin and Hu 2006). In North American forests, it appears mainly at the end of the species succession (Christy and Mack 1984), sharing the stand with the Sitka spruce or Douglas fir. Its relatively shallow root system makes it highly sensitive to windthrow caused by strong winds.

It is a very shade-tolerant specie, capable of regenerating under a dense tree cover. However, relative exposure to light is necessary for its development at a more advanced stage. This strong dependence on light creates a great variability in the relationship between age and height of individuals. Seedlings grow particularly well under their own cover (Schrader 1998), so their growth depends on the spatial distribution of the adults and the quantity of light received. Furthermore, numerous studies have shown that *Tsuga heterophylla* regenerates easily on dead wood (cases of epiphytism are even described) but also that the survival rate of its seedlings increases with the accumulation of litter of hemlock or spruce needles (Harmon 2011). Seedling growth also increases with litter thickness and canopy openness. They experience the highest mortality rate during the two first years.

Tsuga heterophylla disperses by anemochory. The mature tree produces seeds every year with a peak production appearing every three to four years (Christy and Mack 1984), and this, once it is between 25 and 30 years old (Galoux 1951).

Western hemlock was introduced in Belgium for its high growth rate in regions with sufficient water supply (Galoux 1951). Its appearance in Belgian arboreta dates back to the beginning of the 20th century. Despite a fairly sustained growth, this species was not popularized in Wallonia, probably because it was not already popular in its area of origin, where it is mainly used for paper production and a little bit for construction. Very few stands have been planted in public forests, mainly in the region of the Ardennes for site adequacy.

In its native range, the expansion of *Tsuga heterophylla* is hindered by natural low-intensity fire regimes destroying its regeneration, by the presence of competitive species (Gavin and Hu 2006) and by the lack of water in drier regions (Galoux 1951). However, such fire regimes do not exist in Wallonia. Moreover, there are not many species in competition with the western hemlock because of its early and rapid growth, which allows it to quickly outgrow other tree species in dense forests. It generally survives longer in the shade than spruce (Harmon 2011), and very few pathogens or pests threaten this species in Belgium (Petit et al. 2017). Furthermore, the western hemlock benefits from the Ardennes climate, where it meets a water regime adapted to its ecological requirements.

Global climate change is a very complicated factor to anticipate. In many cases, it can enhance the invasiveness of non-native species (Willis et al. 2010). *Tsuga heterophylla* could also benefit from climate change as it tends to reduce severe winters, which are the main cause of its mortality. Nevertheless, it remains sensitive to periods of drought, and an increase in their frequency and intensity could counteract this trend.

The comprehensive revision of woody species considered invasive based on regional and national databases and literature conducted by Richardson and Rejmánek (2011a) lists *Tsuga heterophylla* as an invasive species in Europe. An exuberant regeneration around the plantings is also observed in Scotland and Norway, with few native species able to survive underneath (Oyen 2001, Harmer et al. 2011, Forestry Commission Scotland 2015). In a German study, *Tsuga heterophylla* is said to present a vivid and dense regeneration, with expansion range up to 866 meters from a potential seed origin. It is also said to have a high adaptability with regard to light availability, outcompeting other native species, which is consistent with our forest invasion syndrome (Frischbier et al. 2017). In Belgium, the regeneration of western hemlock has become overwhelming in some areas such as Vielsalm, where seed-bearers are now systematically harvested (Thunus 2021). However, there is very little specific information about the dispersion of *Tsuga heterophylla* in Wallonia.

In our monitoring of old arboreta, *Tsuga heterophylla* displayed the highest combination of dispersal distance and regeneration density amongst the non-native conifers. Densities were higher on wet and acidic soils, which is consonant with the ecology of the species. Dense regeneration mats were present under the parent trees, and higher individuals were found in small forest gaps allowing more light to penetrate the forest cover. Ligot et al. (2020) found that western hemlock had a vertical growth up to twice as fast as other common conifers in forests of Wallonia. In our study of growth traits of conifers, *Tsuga heterophylla* grew faster than his congeneric *Tsuga canadensis*, which displayed almost no regeneration in the studied arboreta. Finally, we measured a maximal frontier expansion rate of 17 m/years in Mirwart, which is much higher than the threshold given by Richardson et al. (2000) for an invasive seed-dispersed plant species (2 m/year). In Vielsalm, seedlings of

Western hemlock have been found more than 900 m from the plantings (Thunus 2021). It is a perfect representative of the forest invasion syndrome, combining great shade-tolerance, high growth potential and capacity of long-distance dispersal.

Figure 7-6: regeneration of *Tsuga heterophylla* and *Chamaecyparis lawsonianna* in the "Hautes Fagnes – Eifel" Natural Park (© Aurore Fanal).

Based on this trait syndrome, the lack of natural enemies and the important area potentially favorable to this species in Wallonia, western hemlock is a species with high invasive risk in Belgian forests not subjected to water stress. However, climate change and the resulting changes in the precipitation regime might lead to a shifting of its area of high invasion risk further north.

I have personally observed regeneration of *Tsuga heterophylla* in wet heaths, a natural habitat of conservation concern (Figure 7-6). Its dense regeneration prevents any other native species from growing, forming mono-specific stands with a thick litter. Thankfully, Western hemlock does not appear in the list of species selected for the "Trees for Future" arboretum network recently set up in Belgium to test species for future forest diversification programs, because of its invasive behavior. However, small plantings are still made in both public and private forests. Given the highly invasive behavior and the potentially high impacts on the native biodiversity, western hemlock should not be considered for any forest planting anymore, and seed-bearers should be managed to avoid further spread of the species in natural habitats.

27. Focus species: *Acer rufinerve*

The *Acer* genus is rich of invasive species, with *A. rufinerve* and *A. negundo* in Europe, or *A. pseudoplatanus* and *A. platanoides* in North America. Shortly after our monitoring in the arboretum of Seraing, most of the natural regeneration of exotic maples was controlled by the Department of Nature and Forestry as a precautionary measure, especially as *Acer rufinerve* was present.

Acer rufinerve Siebold & Zucc., or red veined maple, or grey-bud snakebark maple is an early successional species of temperate forests of Japan. It has a short generation time, high rates of survival and growth, and can resprout quickly after cutting, which complicates its control in invaded forests (Branquart et al. 2011, Nunez-Mir et al. 2019). Despite being introduced as an ornamental plant in many countries, there are few reports of it invading other areas in scientific literature. However, it has been recently reported that the species has invaded three different broadleaved forests in Belgium, in Seraing, Brussels and Bon-Secours, which resulted in important management costs and its addition to the European and Mediterranean Plant Protection Organization's "List of Invasive Alien Plants" (EPPO 2022). In the forest of Bon-Secours, it is often found together with the invasive *Prunus serotina*, and both tend to avoid dense canopies dominated by beech trees. The species has colonized more than 50 ha of forest between 2000 and 2010 and the formation of dense thickets by young stems is likely to reduce plant diversity (Fig. 7-7). Populations of *A. rufinerve* in the three Belgian sites has been managed during the last decade by systematic felling of seed-bearers and uprooting of saplings.

In our study on the relationship between traits and invasiveness, *A. rufinerve* obtained a rather low global invasiveness value. It is listed as invasive in a few European countries: Belgium, Estonia, France, Germany and the United Kingdom (GBIF: The Global Biodiversity Information Facility 2022). However, it is one of the broadleaved species with the highest regeneration density and dispersal distance observed in our monitoring of old arboreta. The low invasiveness score might be due to the fact that *A. rufinerve* has already been introduced in many ornamental parks with high management pressure, but not yet in many low-managed forests where the natural regeneration could occur more easily.

Figure 7-7: dense regeneration of Acer rufinerve in Belgium, in the forest of Bon-Secours before management (© Etienne Branquart).

In our growth experiment, seedlings of *A. rufinerve* displayed high values of RGR and SLA, close to the very invasive *A. negundo*. An experimental study conducted in the forest of Bon-Secours revealed that, in shaded or semi-shaded areas, *A. rufinerve* is taller than the native *Acer pseudoplatanus* at the same age (De Ruyver 2021). Once again, the combination of shade-tolerance allowing persistence in the understories and high growth and SLA in canopy gaps resulting from small perturbations may explain the invasion success of the red veined maple in several oak-dominated Belgian forests. This sit-and-wait strategy coupled with resprouting capacities may be similar to the one expressed by *Prunus serotina* (Closset-Kopp et al. 2007), however cases of invasions by *A. rufinerve* remain rare so far compared to the black cherry. Investigations on the reproduction success of *Acer rufinerve* (number of seeds, dispersal distances, establishment success) might help explain this difference.

28. On risks and benefits of using NNTs in afforestation programs

As explained in the general introduction (Chapter 1), silviculture is an important introduction pathway of invasive tree species. Despite this information and the abundant regeneration of NNTs observed in old forest trials, it is concerning to note the limited consideration given to policy-level decisions until the last few years. As stated by Krumm and Vítková (2016), *« the discussion on biological invasions and forestry has been often dominated by prejudice and emotions »*. The black locust (*Robinia pseudoacacia*) for example is considered an invasive species by ecologists, the species spreading on long distances and invading open dry grassland of ecological interest, yet the species is still widely promoted in afforestation programs for its valuable wood (Orazio et al. 2013, Vítková et al. 2017).

In Wallonia, non-European conifers represent about 8% of the forest area (Lecomte 2017). Conifers represent almost half of the forest surface, mainly *Picea abies*, a spruce exotic from Belgium but native in France (OEWB 2021). Non-native broadleaves, such as *Quercus rubra*, represent a minimal portion of the forest area (< 1%), but their planting intensity is increasing, especially in areas where native oaks are declining (Hasenauer et al. 2017). If NNTs presenting the “forest invasion syndrome” of shade tolerance coupled with high growth rate and dispersal capacities in canopy gaps are further cultivated in Belgium, and in temperate Europe in general, cases of invasions in natural habitats would likely be more frequent. The high proportion of coniferous stands in Southern Belgium forests may also accelerate the spread of non-native conifers presenting this syndrome, such as *Tsuga heterophylla, Chamaecyparis lawsonianna*, *Thuja plicata* and *Abies grandis*.

NNTs were originally mainly managed in even-aged monocultures maximizing productivity, which could have led to an underestimation of their potential to support native biodiversity. Nowadays, to enhance resilience of planted forests, more and more forest managers turn to a “close-to-nature” forestry, maintaining a continuous cover and encouraging natural regeneration (Pro Silva 2012). A mix of native and exotic species might enhance the resilience and productivity of forests while maintaining the contribution to other ecosystem services such as supporting biodiversity (Pötzelsberger et al. 2020). However, non-native species displaying an abundant regeneration might therefore be favored by foresters, leading to a reinforcing feedback loop where human interventions exacerbate the ongoing invasion by economically valuable exotic tree species (Sinclair et al. 2020).

The concern of foresters regarding the composition of future forests under climate change is legitimate. In Belgium, the most productive tree species (beech, oaks and Norway spruce) suffer from diebacks caused by heat waves or emerging pests (OEWB 2021). Diversifying the plantings to maintain the productivity of forests is therefore a necessity. This diversification can come from underexploited native species (*Prunus avium*, *Sorbus torminalis*, *Acer platanoides*…), from southern provenances of native species (Aitken and Bemmels 2015), from other European species or from non-

European species. The impact on forest resilience and native biodiversity will not be the same according to the chosen approach.

If NNTs can have detrimental impacts on the receiving ecosystem, they can also provide a wide variety of ecosystem services: provisioning of timber, honey, nuts or firewood, nitrogen fixation, carbon sequestration, erosion control, ornament… (Dickie et al. 2014). In average, the productivity of the main NNTs used in Europe is superior to that of an equivalent native species, leading to an overall gain around 30 % for both broadleaves and conifers (Hasenauer et al. 2017). In the light of the current climate change, the use of NNTs adapted to the future climatic conditions could ensure economic stability in forest management (Puchałka et al. 2023).

Several recent studies analyzed the benefit/risk balance of using NNT species in forest plantings. In Great-Britain, Ennos et al. (2018) demonstrated that using NNTs for forests diversification presents great ecological and economic risks, potentially to the detriment of native tree species and their associated biodiversity. Novel exotic trees are likely to be vulnerable to native pests and pathogens, and their importation can also facilitate the unintentional introduction of pathogens which they host in their native range. For NNTs phylogenetically close to native species, there is also a risk of hybridization leading to the slow disappearance of the native tree species (Boissier et al. 2009). An assessment of the ecological risks related to the use of NNTs in Sweden's production forests concludes that there is a high risk of adverse ecological impacts, such as invasions, hybridization or a decrease in native biodiversity (Felton et al. 2013). In the Belgian country report of the COST action "Non-Native Tree Species for European Forests: Experiences, Risks and Opportunities", published in 2017, key risks associated with the introduction of NNTs in Wallonia are the introduction of exotic pests and hybridization (especially for poplars). Modification of the soil characteristics through nitrification (by *Robinia pseudoacacia*) or acidification (by conifers) is also a concern. In Czech forests, plantings of *Pinus strobus* caused an important soil acidification, which in turn led to a shift in the species composition of the herbal layer and a decrease of native biodiversity (Bednář et al. 2016). While some exotic tree species can provide shelter for native flora and fauna, their presence is mostly detrimental compared to their native counterparts (Hasenauer et al. 2017). In a review published in 2022, Wohlgemuth et al. suggest to use NNTs with caution as a majority of exotic trees frequently introduced in Europe have negative impact on local biodiversity, especially if they are phylogenetically distant from European tree species.

These risks are expected to be more important for species alien to Europe compared with exotic species originating from Europe. Indeed, the distribution ranges of European species has varied greatly with glaciations over the last millennia, and related tree species host a similar diversity of pathogens, insects, birds, fungi, etc. (Krumm and Vítková 2016, Wohlgemuth et al. 2022). Whether a species is "native" is therefore prone to discussion: should we consider a regional scale, or more a continental one? The Norway spruce (*Picea abies*) is the most planted conifer in Wallonia and is not native from Belgium. However, it is native in the neighboring countries of France et Germany, and pollen data attests its presence in Belgium during the Holocene (Latałowa and van der Knaap 2006). Should we therefore put the Norway spruce on the same level as the Douglas fir (*Pseudotsuga menziesii*), the second most planted conifer in Southern Belgium, which originates from North America and has no closely related species in Europe? Referring to the framework for biological invasions (Blackburn et al. 2011) and the definitions by Richardson et al. (2000), an exotic species is introduced in a new area as a result of human activity, beyond a major geographical barrier it could not have crossed alone. As there is no insurmountable mountain range or large bodies of water between the present natural distribution of *Picea abies* and Belgium, there is no reason why the species could not have come back with favorable climatic conditions. Given the lower risk of joint introduction of exotic pests and negative biodiversity impacts, a distinction should be made between NNTs originating from temperate forests of Western and Central Europe (in the same ecoregion exempted from major geographical barriers) and NNTs introduced from other continents (Decocq et al. 2021). This is the approach that I chose when defining non-native species in this thesis. However, a clear differentiation is still too rarely made in planting programs and guidelines, when it would probably facilitate discussions between ecologists and forest managers.

Recent global guidelines for the use of NNTs in forestry have been published in Europe (Brundu et al. 2020, Brundu 2022, Directorate-General for Environment 2023), yet plenty of afforestation programs don’t take these guidelines into account. Based on recently published European guidelines, scientific reviews, position papers by ecologists and forest owner associations (Richardson and Rejmánek 2004, Carrillo-Gavilán and Vilà 2010, Felton et al. 2013, Wagner et al. 2017, Brundu and Richardson 2017, Ennos et al. 2019, Pötzelsberger et al. 2020, Brundu et al. 2020, Bindewald 2021, Messier et al. 2021, Decocq et al. 2021, Di Sacco et al. 2021, Brundu 2022, Dassonville and Leruth 2023, Directorate-General for Environment 2023), and the results of this thesis, here is a short list of recommendations concerning the use of NNTs in European afforestation programs:

1. **Favor the use of southern origins of native species, or southern European species, over non-European NNTs:** negative risks associated with the use of NNTs are indeed higher for species which are not present in the same ecoregion, as these species do not share a similar association of species and might benefit from an enemy release in the introduction range.
2. **Adopt a close-to-nature forestry with continuous cover and mixed stands, avoid monocultures and large clearcuts:** favoring competition between a large number of tree species lowers the probability of empty niches and therefore the risks of invasions.
3. **Avoid planting NNTs proximate to sensitive natural areas and set up monitored buffer zones around protected areas**: native climax forests such as beech-dominated forests can act as effective barriers to the spread of NNTs.
4. **Apply thorough risk-assessments for all non-native species introduced in adaptative forest management programs:** this applies to species not yet

introduced as to species already present but of which planting surface is to be increased

5. **Establish monitoring sites for early detection of invasive tree species:** fast identification and rapid action is the safest way to prevent impactful invasions. More specifically, any species maintaining high densities of saplings in the understories and outperforming native species in canopy gaps and other favorable light conditions must be watched carefully as it presents the typical invasion syndrome in forest ecosystems (Closset-Kopp et al. 2007, Fridley et al. 2023), as reaffirmed by our observations in forest arboreta and experiments.
6. **Be aware of global and national guidelines and regulations and of reports of NNTs invasion cases**; guidelines are evolving quickly and must be incorporated promptly into local forest management plans.

There are numerous ways to enhance the resilience of forests by adapting management practices and varying provenances of native trees. The use of NNTs for production purposes can bring great economic incomes but should be considered on a limited scale and with caution, with prioritization of the use of native species mixtures and assisted migration of genotypes (Fig 7-8). For NNTs already introduced, the decision to maintain or even increase plantings or to eradicate the installed populations can be taken after an assessment of risks and impacts balanced with the benefits provided, such as timber production or cultural value (Figure 7-9). According to Pötzelsberger (2019), a “good” non-native tree to use in forestry features both a good potential for forestry (tolerance of a wide range of abiotic conditions, good productivity, desirable timber properties) and low impact risk (no major impact on ecosystem services and biodiversity and easy to confine or eradicate). For seldom-planted or not yet introduced species, risk assessments should always be performed before large plantings.

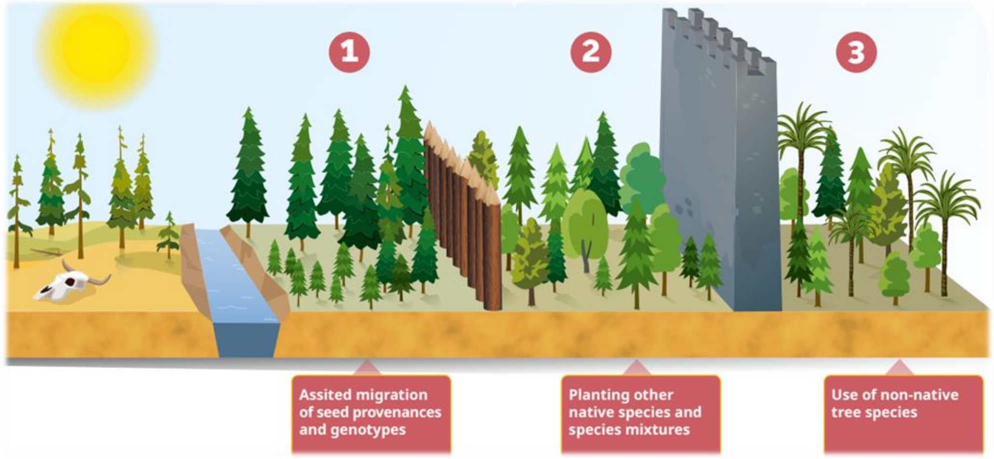


Figure 7-8 : The 3 lines of defense for sustaining ecosystem services provided by forests in the light of climate change, proposed by the SUSTREE INTERREG project for implementing assisted migration (Chakraborty et al. 2019).

Local data from forest inventories or monitoring of arboreta, such as the ones I performed for this thesis, are valuable for risk assessments of NNTs. Combining on-site monitoring of plantings with predictors such as species traits or introduction history can already give a good overview of the invasive potential of an exotic tree. Such risk assessments, examined in parallel with the vulnerability of the receiving area, can guide politics and forest managers in their species selection for planting programs.

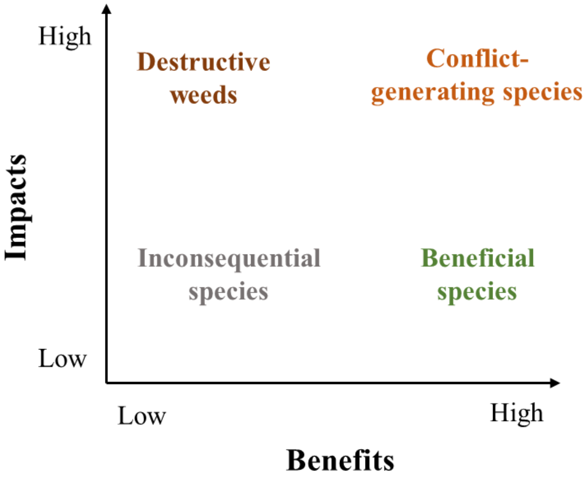
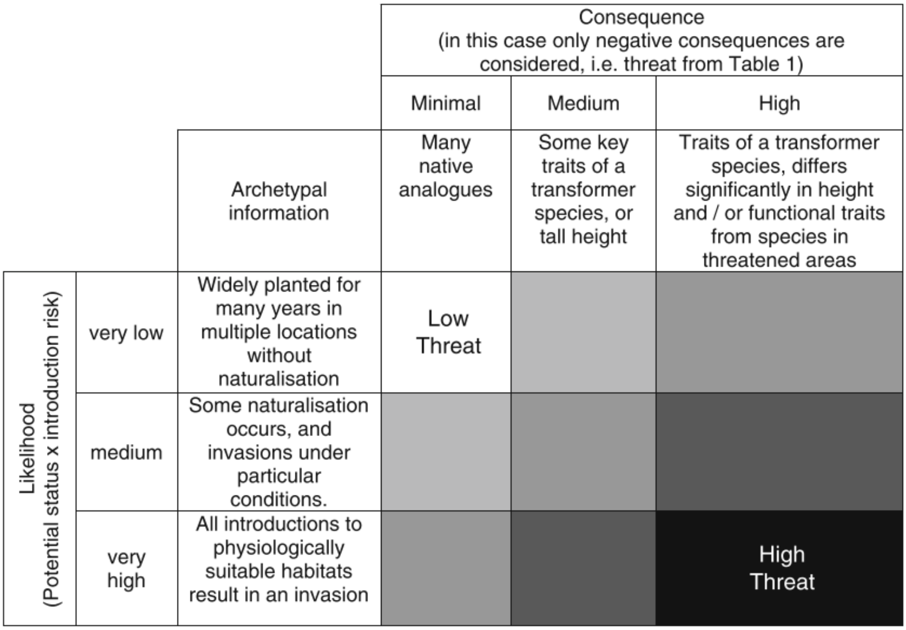


Figure7-9: Types of invasive NNTs based on the degree of impact on the environment and the benefits they provide adapted from van Wilgen and Richardson (2014).

Wilson et al. (2014) proposed a rapid assessment scheme based on the history of introduction and invasiveness of the NNT and its potential as a transformer species, *i.e.* a species capable of affecting ecosystem functioning (modifications in fire regimes, soil carbon storage, litter accumulation, excessive use of resources, etc.) (Figure 7-10). More recently, Bindewald et al. (2021c) presented a methodological framework at a site-specific level. The decision tree is presented in Figure 7-11. This assessment also considers the effectiveness of management strategies to lower the impacts of NNTs and can be used for both already established and not yet introduced species. Local data on regeneration and dispersal, such as the data we gathered in chapters 2, 3 and 4, are particularly useful in this type of site-specific assessment. More generic risk assessment protocols, such as Harmonia + (D'hondt et al. 2015), combining information on the likelihood of establishment and spread, and potential impacts on the environment, native species and human activities, are already proven very effective in the assessment of the invasive potential of trees (Branquart et al. 2011).



			Consequence (in this case only negative consequences are considered, i.e. threat from Table 1)		
			Minimal	Medium	High
		Archetypal information	Many native analogues	Some key traits of a transformer species, or tall height	Traits of a transformer species, differs significantly in height and / or functional traits from species in threatened areas
Likelihood (Potential status x introduction risk)	very low	Widely planted for many years in multiple locations without naturalisation	Low Threat	░	▒
	medium	Some naturalisation occurs, and invasions under particular conditions.	░	▒	▓
	very high	All introductions to physiologically suitable habitats result in an invasion	▒	▓	High Threat

Figure 7-10: A proposed system for rapidly assessing the threat posed by an introduced tree. The darker the shade, the higher the threat (Wilson et al. 2014).

The eight arboreta we selected for our study already provided a large amount of data, but several public or private arboreta and forest trials can still be monitored. More than data on natural regeneration, they also offer the opportunity to study the impact of NNTs on the native biodiversity, such as associated fungi, insects or diversity in the herbaceous layer. Indeed, quantitative data on the impact of NNTs on the environment is still lacking, especially in Europe (Felton et al. 2013, Bindewald 2021). Addressing the currently limited and potentially biased knowledge on invasiveness and impacts of NNTs is essential for establishing resilient forests. Therefore, supporting extensive collaborative efforts and incorporating a standardized European methodology for collecting data could facilitate a more informed decision-making process. Such an approach would be valuable to researchers, practitioners and policymakers alike (Dimitrova et al. 2022).

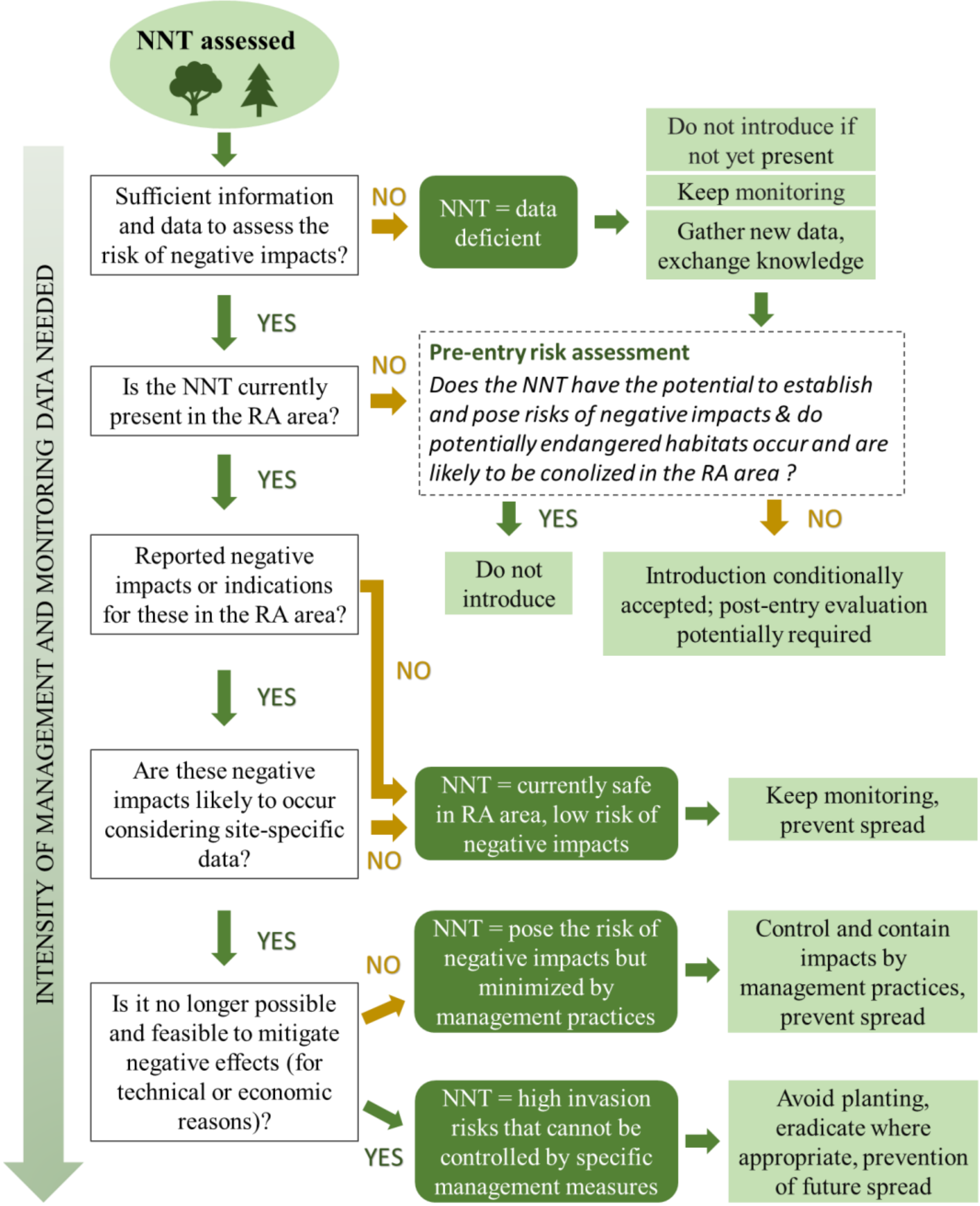


Figure 7-11: Decision tree demonstrating practical application of the site- specific risk assessment; NNT, non- native tree species; RA, risk assessment; SSRA, site- specific risk assessment. Adapted from (Bindewald et al. 2021b).

29. Conclusion

The invasion process of an exotic species is complex and highly context-dependent. Throughout this thesis, I brought elements to better understand the invasion process of non-native trees in European temperate forests. If a general "forest invasion syndrome" could be highlighted, it is still highly dependent on the recipient ecosystem, the introduction history and other human-mediated events. Moreover, climate change will likely influence both exotic species' invasiveness and habitats invasibility, challenging our current expectations on NNTs' behavior in temperate forests.

The introduction of NNTs for silviculture has become a highly controversial issue, with discussions dominated by emotions and preconceived ideas. The lack of common terminology between ecologists, forest managers and politicians further complicates the debate. However, unreasonable use of NNTs might create irreversible changes in ecosystems. Given the vulnerability of native forests in the face of global changes and the complexity of factors influencing forest resilience, it is unwise to increase the uncertainty weighting on forests with an abusive use of non-native trees of which impacts on ecosystems are still misunderstood.

NNTs considered for future plantings, whether they were already introduced for wood production in Europe or not, should undergo a thorough risk analysis and be tested in small trials before any exploitation on larger scales. Old forest trials and arboreta offer great opportunities to evaluate the invasive potential of NNTs across various regions, and to quantify the impact on native biodiversity and other ecosystem services. Simplified protocols and models relying on species traits can also help save time and provide proper assessments of the invasion risk of exotic trees. Nevertheless, introducing exotic species should never be taken lightly, and a better consideration of invasion biology in forests managements would help attain more sustainable and resilient forests in the future.

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Supplementary information

Appendix 1: Species composition of the eight studied arboreta. Information gathered from (Scholzen and Lhoir 2018).

Species	Saint-michel	spa	Virton	Seraing	Profondeville	Nismes	Bertrix	Gedinne
Abies alba Mill.	x	x	x	x	x	x	x	x
Abies amabilis Douglas ex J. Forbes	x							
Abies balsamea (L.) Mill.	x							
Abies bornmuelleriana Mattf.								x
Abies cephalonica Loud.	x	x			x			
Abies cilicica (Ant. et Kotschy) Carr.	x	x			x		x	
Abies concolor (Gord.) Hoopes		x		x	x		x	x
Abies delavayi (var fabri?)	x							
Abies fraseri (Pursh) Poir.	x	x						
Abies firma Siebold & Zucc.	x				x			
Abies grandis Lindl.	x	x	x	x	x	x	x	x
Abies homolepis S. et Z.	x	x		x	x		x	x
Abies koreana E. H. Wilson		x			x			x
Abies lowiana (Gordon) A.Murray				x		x		
Abies lasiocarpa (Hook.) Nutt.		x						x
Abies mariesii Mast.	x							
Abies nebrodensis (Lojac.) Mattei	x							
Abies nordmanniana (Stev.) Spach.	x	x		x		x	x	x
Abies numidica De Lannoy ex. Carr.		x			x		x	x
Abies pinsapo Boiss.	x	x						
Abies procera Rehd.	x	x		x			x	x
Abies recurvata Mast.		x						
Abies sachalinensis (F. Schmidt) Mast. ssp. mayriana Miyabe & Kud	x							
Abies veitchii Lindl.		x		x	x		x	x
Abies x borisii-regis Mattf.	x							x
Acer campestre L.			x					x
Acer cappadocicum Gled.					x			
Acer circinatum Pursh.		x		x				
Acer cissifolium S. et Z.				x				
Acer japonicum Thunb.				x				
Acer macrophyllum Pursh				x				
Acer lobelii Ten.	x				x			
Acer opalus Mill.	x							
Acer palmatum Thunb.				x				
Acer platanoides L.			x	x			x	
Acer pseudoplatanus L.			x	x				x
Acer rubrum L.	x	x	x	x	x		x	x
Acer rufinerve S. et Z.				x				
Acer saccharum Marshall	x			x			x	
Acer saccharinum L.	x	x	x	x	x			x
Acer tataricum L. ssp. ginnala (Maxim.) Wesm.				x				

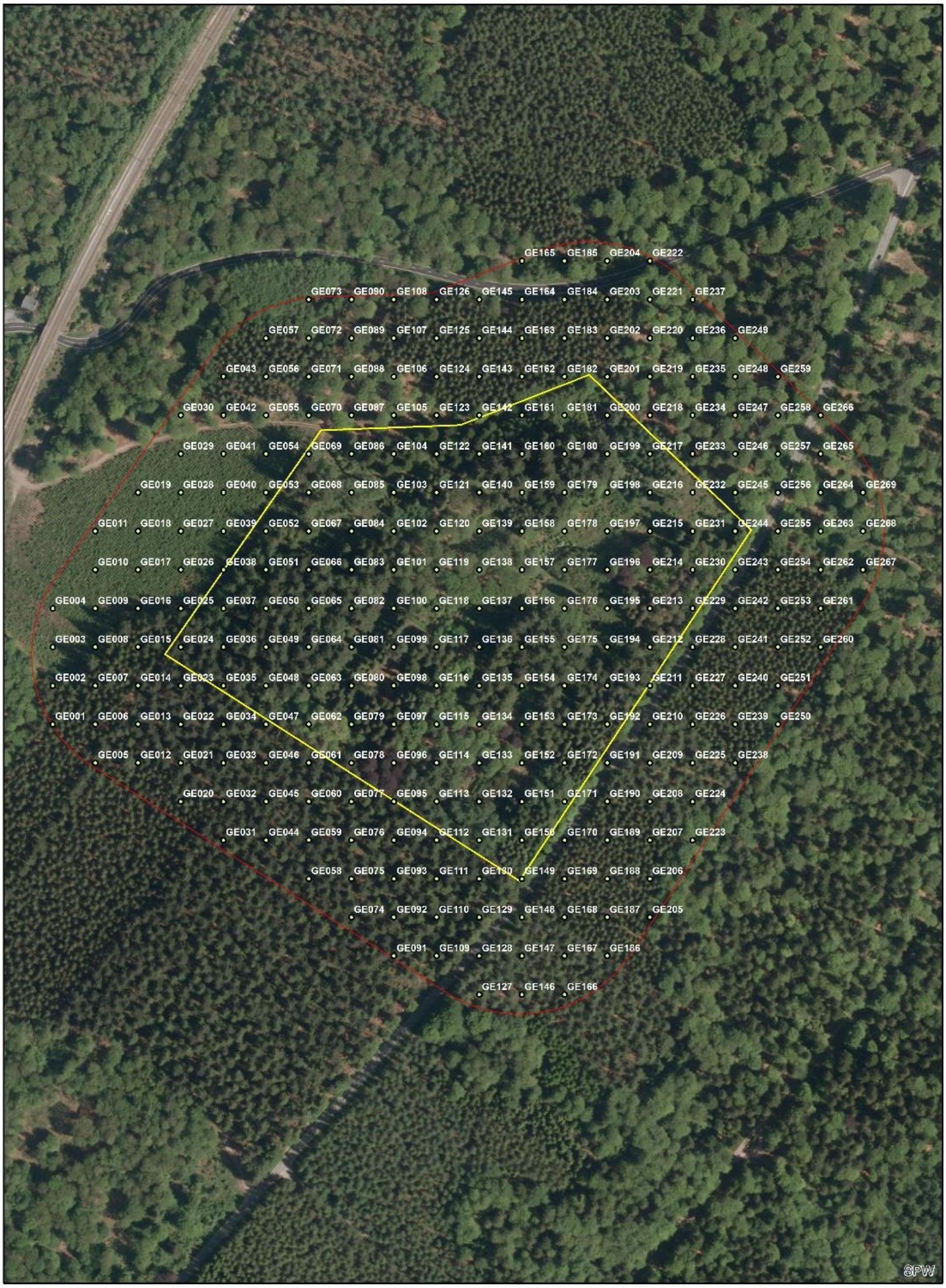
Species	Saint-michel	spa	Virton	Seraing	Profondeville	Nismes	Bertrix	Gedinne
Aesculus hippocastanum L.		x	x	x				x
Alnus cordata (Loisel.) Duby	x		x		x	x	x	x
Alnus glutinosa (L.) Gaertn.								x
Alnus incana (L.) Moench	x						x	x
Alnus rubra Bong.							x	
Alnus subcordata C.A.Mey.	x							
Alnus x spaethii Spaeth	x							
Betula alleghaniensis Britt.	x	x	x	x			x	
Betula ermanii Cham.	x							
Betula lenta L.	x	x			x		x	
Betula maximowicziana Regel.	x							x
Betula nigra L.	x							
Betula papyrifera Marsh.		x	x	x	x			x
Betula pendula Roth							x	x
Betula pubescens Ehrh.		x					x	x
Betula utilis D. Don	x							
Betula utilis D. Don var. jacquemontii				x				
Calocedrus decurrens (Torr.) Florin	x					x		
Carpinus betulus L.								x
Carpinus caroliniana Walter						x		
Carpinus japonica Blume			x	x				x
Carya cordiformis (Wangenh.) K.Koch	x						x	
Carya laciniosa (Mill.) K.Koch	x		x				x	
Carya ovata (Mill.) K.Koch	x		x					
Castanea crenata S. et Z.		x						
Castanea sativa Mill.		x	x	x	x			x
Cedrus atlantica (Endl.) Manetti ex Carrière	x	x		x				
Cedrus deodara (Lamb.) G. Don			x					x
Cedrus libani A. Rich.				x		x	x	x
Chamaecyparis lawsoniana (Murr.) Parl.	x	x	x	x	x	x	x	x
Chamaecyparis obtusa (Siebold & Zucc.) Endl.	x		x		x		x	x
Chamaecyparis pisifera (Siebold & Zucc.) Endl.	x	x	x	x	x		x	x
Cornus nuttallii Audubon			x					
Corylus avellana L.								x
Corylus colurna L.	x						x	x
Cryptomeria japonica Don D.	x	x	x	x	x	x	x	x
Fagus sylvatica L.	x	x	x	x	x	x		x
Fagus sylvatica L. 'Atropunicea'	x			x	x	x		x
Fagus sylvatica L. 'purpurea'		x						x

Species	**Saint-michel**	**spa**	**Virton**	**Seraing**	**Profondeville**	**Nismes**	**Bertrix**	**Gedinne**
Fraxinus americana L.				x	x			x
Fraxinus americana L. var. juglandifolia				x	x			
Fraxinus angustifolia Vahl								x
Fraxinus excelsior L.			x	x				
Fraxinus latifolia Benth.	x		x					
Fraxinus ornus L.				x			x	
Fraxinus pennsylvanica Marshall				x	x			
Fraxinus velutina Torr.							x	
Ilex aquifolium L.		x						
Juglans cinerea L.			x					
Juglans nigra L.			x					
Juglans regia L.								x
Juniperus virginiana L.				x		x		
Larix decidua Mill.	x	x	x	x	x	x	x	x
Larix kaempferi (Lamb.) Carr.	x	x				x	x	x
Larix x eurolepis Henry	x							x
Larix gmelinii (Rupr.) Kuzen.			x	x	x			
Larix kaempferi (Lamb.) Carr.			x	x	x			
Liquidambar styraciflua L.								x
Liriodendron tulipifera L.	x	x	x	x	x			x
Malus sylvestris (L.) Mill.								x
Metasequoia glyptostroboides Hu et Cheng.	x	x		x	x		x	x
Picea abies (L.) Karst.	x	x				x	x	x
Picea alcoquiana (Veitch ex Lindl.) Carrière	x	x						
Picea asperata Mast.		x						
Picea engelmannii (Parry) Engelm.	x	x		x				x
Picea glauca (Moench.) Voss.	x	x			x		x	
Picea jezoensis (Sieb&Zucc.) Carr.	x	x		x			x	x
Picea koyamae Shiras	x		x	x	x		x	x
Picea mariana (Mill.) B.S.P.		x		x	x			
Picea obovata Ledeb.		x		x				
Picea omorika (Panc.) Purkyne	x	x		x	x	x	x	x
Picea orientalis (L.) Link.	x	x	x		x	x	x	x
Picea pungens Engelm.		x			x			x
Picea rubens Sarg.	x	x		x	x			
Picea retroflexa Mast.		x						
Picea sitchensis (Bong.) Carr.	x	x		x				x
Picea torano (Siebold ex K.Koch) Koehne		x		x	x		x	

Species	Saint-michel	spa	Virton	Seraing	Profondeville	Nismes	Bertrix	Gedinne
Pinus banksiana Lamb.	x			x	x			
Pinus cembra L.		x						
Pinus contorta Dougl. ex Loud.				x				
Pinus mugo Turra 'Pumilio'		x						x
Pinus nigra Arn. ssp. nigra Neum.		x	x	x	x	x		x
Pinus nigra ssp. laricio (Poiret) Maire				x	x	x		x
Pinus nigra ssp. laricio (Poiret) Maire var. calabrica		x			x			
Pinus nigra ssp. laricio (Poiret) Maire var. calabrica 'Koekelare'								x
Pinus ponderosa Dougl. ex. Laws.		x	x	x		x		
Pinus peuce Griseb.	x	x						
Pinus strobus L.	x	x		x	x	x		x
Pinus sylvestris L.		x			x	x	x	x
Pinus wallichiana A. B. Jacks				x				
Pinus uncinata Ramond ex.DC	x							x
Platanus orientalis L.				x				x
Platanus x acerifolia (Aiton) Willd.								x
Populus tremula L.							x	
Prunus avium L.		x	x					x
Prunus serotina Ehrh.	x	x					x	x
Pseudotsuga menziesii (Mirb.) Franco	x	x	x	x	x	x	x	x
Pyrus calleryana Decne. 'Chanticleer'							x	
Quercus cerris L.			x	x	x		x	x
Quercus palustris Muenchh.	x	x		x			x	x
Quercus petraea (Mattuschka) Liebl.		x	x	x		x	x	x
Quercus pubescens Willd.							x	
Quercus robur L.	x	x		x			x	x
Quercus rubra L.	x	x	x	x	x	x	x	x
Quercus velutina Lam.	x		x		x	x		x
Robinia pseudoacacia L.			x	x		x		
Salix caprea L.			x					
Sciadopitys verticillata (Thunb.) Siebold & Zucc.	x							
Sequoia sempervirens (D. Don) Endl.	x							x
Sequoiadendron giganteum (Lingl.) Buchh.	x	x	x	x	x		x	x
Sorbus americana Marsh.		x						
Sorbus aria (L.) Crantz.	x	x					x	x
Sorbus aucuparia L.		x	x				x	x
Sorbus domestica L.								x
Sorbus latifolia (Lam.) Pers.			x					
Sorbus torminalis (L.) Crantz.		x	x				x	x
Sorbus x intermedia (Ehrh.) Pers.	x	x						x

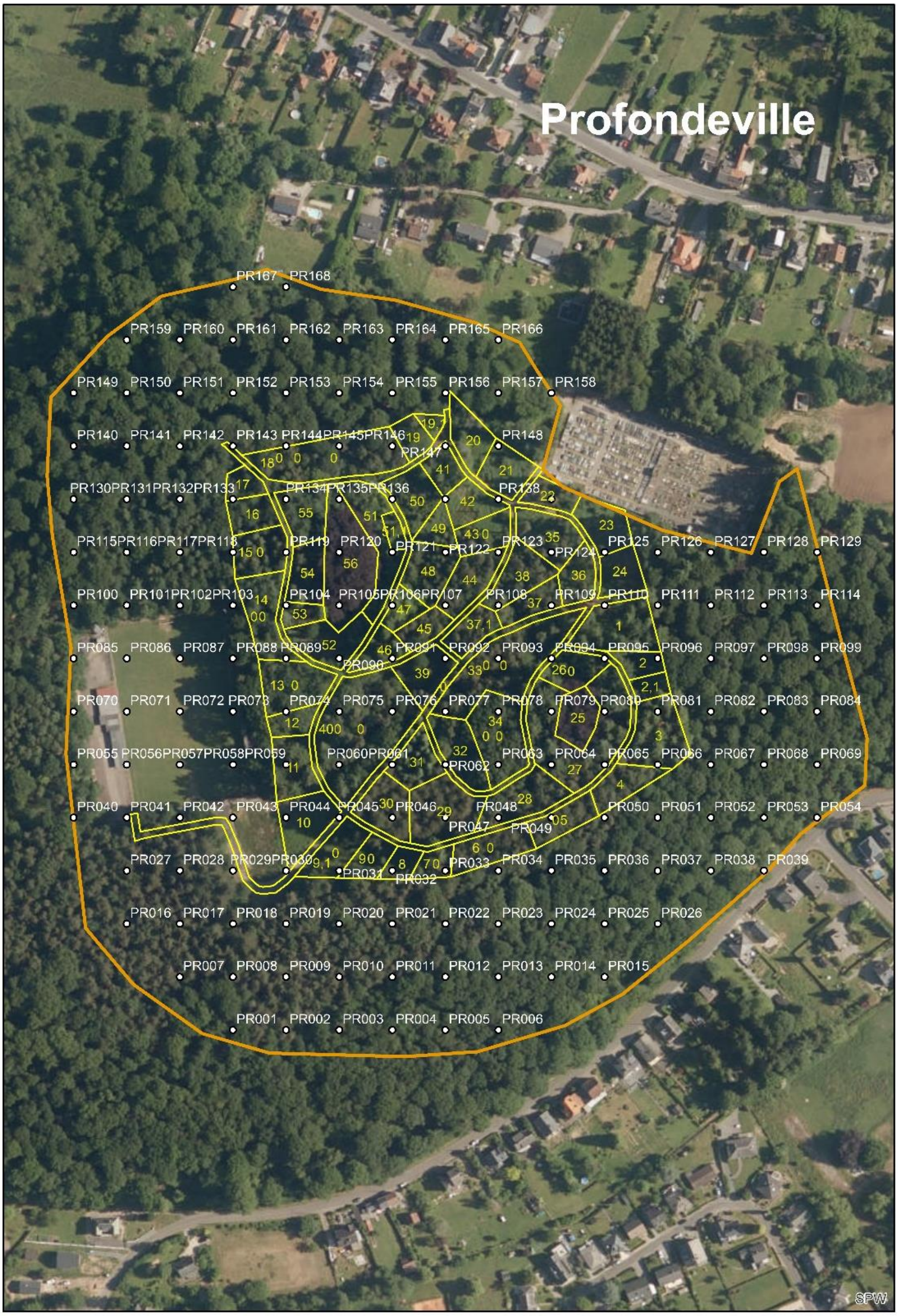
Species	Saint-michel	spa	Virton	Seraing	Profondeville	Nismes	Bertrix	Gedinne
Taxus baccata L.		x	x					x
Taxus canadensis Marsh.					x			
Taxus cuspidata Siebold & Zucc.						x		
Thuja occidentalis L.								x
Thuja plicata Don D.	x	x	x	x	x	x	x	x
Thuja standishii (Gordon) Carrière	x							
Thujopsis dolobrata (Thunb. ex L. f.) Siebold & Zucc.	x							
Tilia americana L.							x	
Tilia cordata Mill.			x				x	x
Tilia dasystyla Maxim.							x	
Tilia platyphyllos Scop.				x				x
Tilia tomentosa Moench						x		
Tilia x euchlora K. Koch					x			
Tsuga carolinana Engelmann		x			x		x	
Tsuga diversifolia (Maxim.) Mast.		x					x	
Tsuga canadensis (L.) Carr.	x	x		x			x	x
Tsuga chinensis (Franch.) Pritzel ex Diels.		x						
Tsuga heterophylla (Raf.) Sarg.	x	x	x	x	x	x	x	x
Tsuga mertensiana (Bong.) Carrière ssp. mertensiana	x						x	
Tsuga sieboldii Carr.		x					x	
Ulmus americana L.			x					
Ulmus glabra Huds.			x					
Ulmus laevis Pall.			x					
Ulmus glabra Huds.								x
Ulmus minor Mill.								x
Ulmus pumila L.								x
Xanthocyparis nootkatensis (D. Don) Farjon & Harder	x			x			x	x
Zelkova serrata (Thunb.) Makino			x	x				

Appendix 2: Maps of the sampled arboreta, with plantation parcels limits (yellow lines), buffer boundary (orange line) and sampling plots (white dots).



Arboretum de Gedinne Grids : 30 m

Total surface : 24,635 ha
arboretum surface : 9.3742 ha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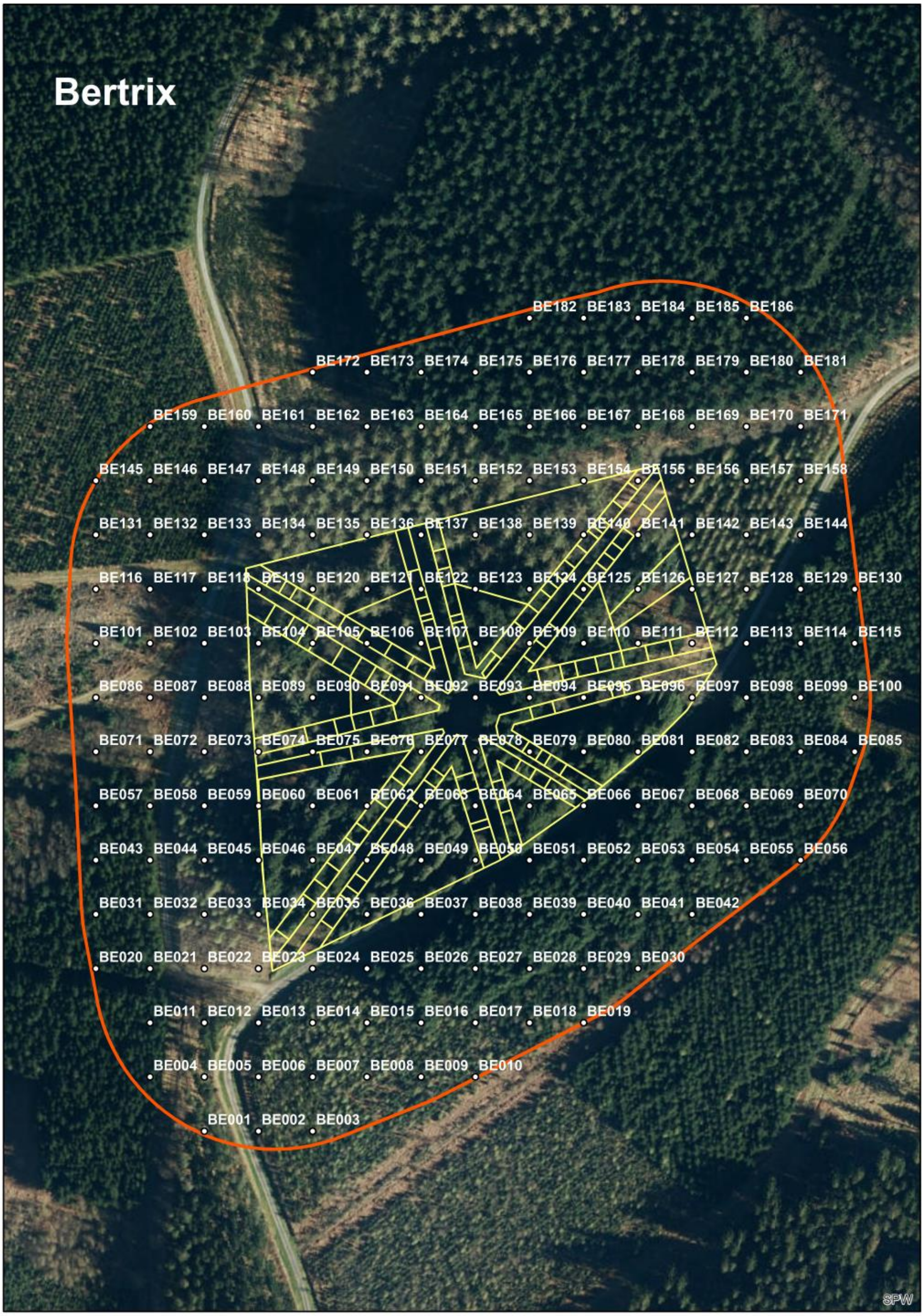
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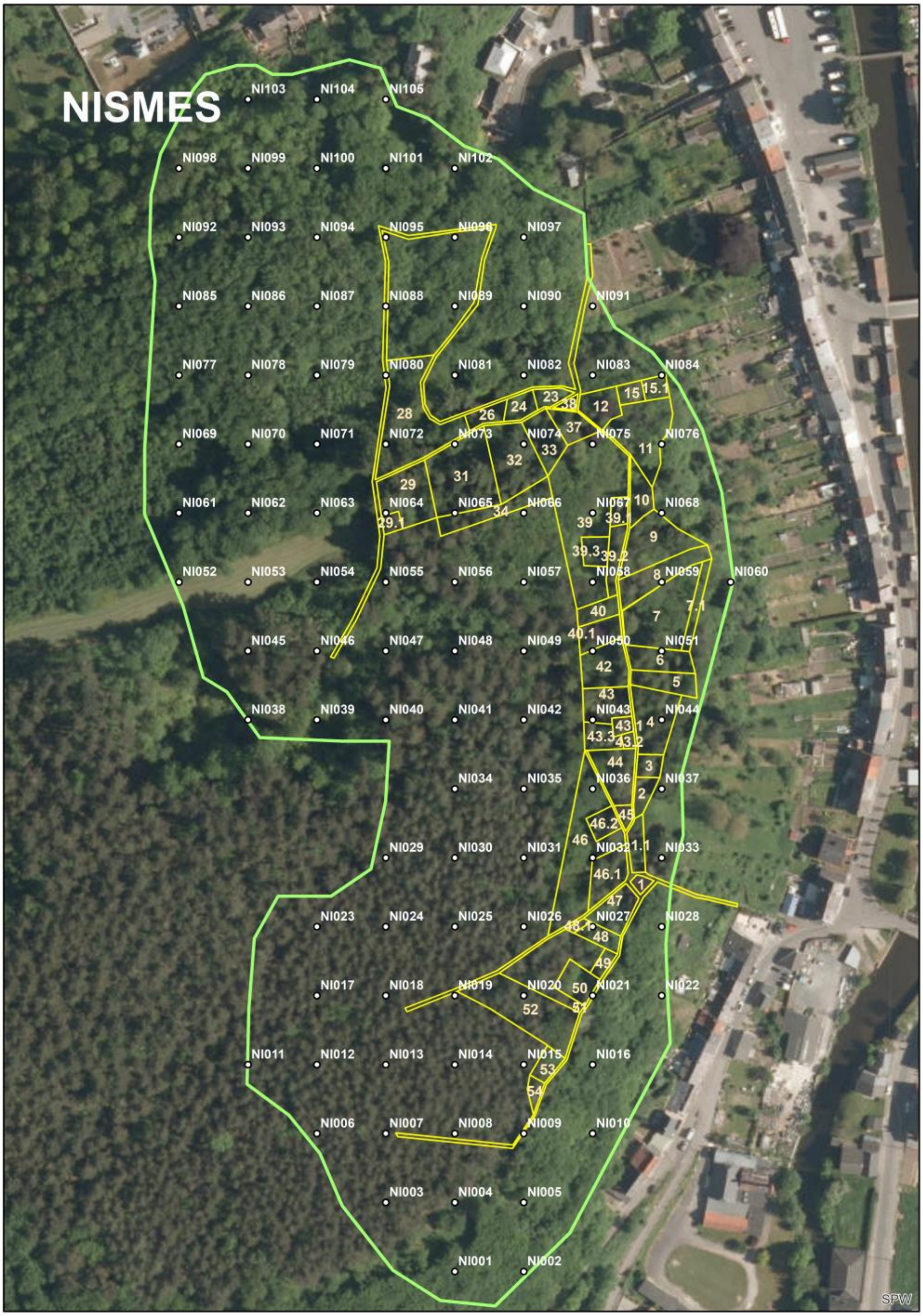
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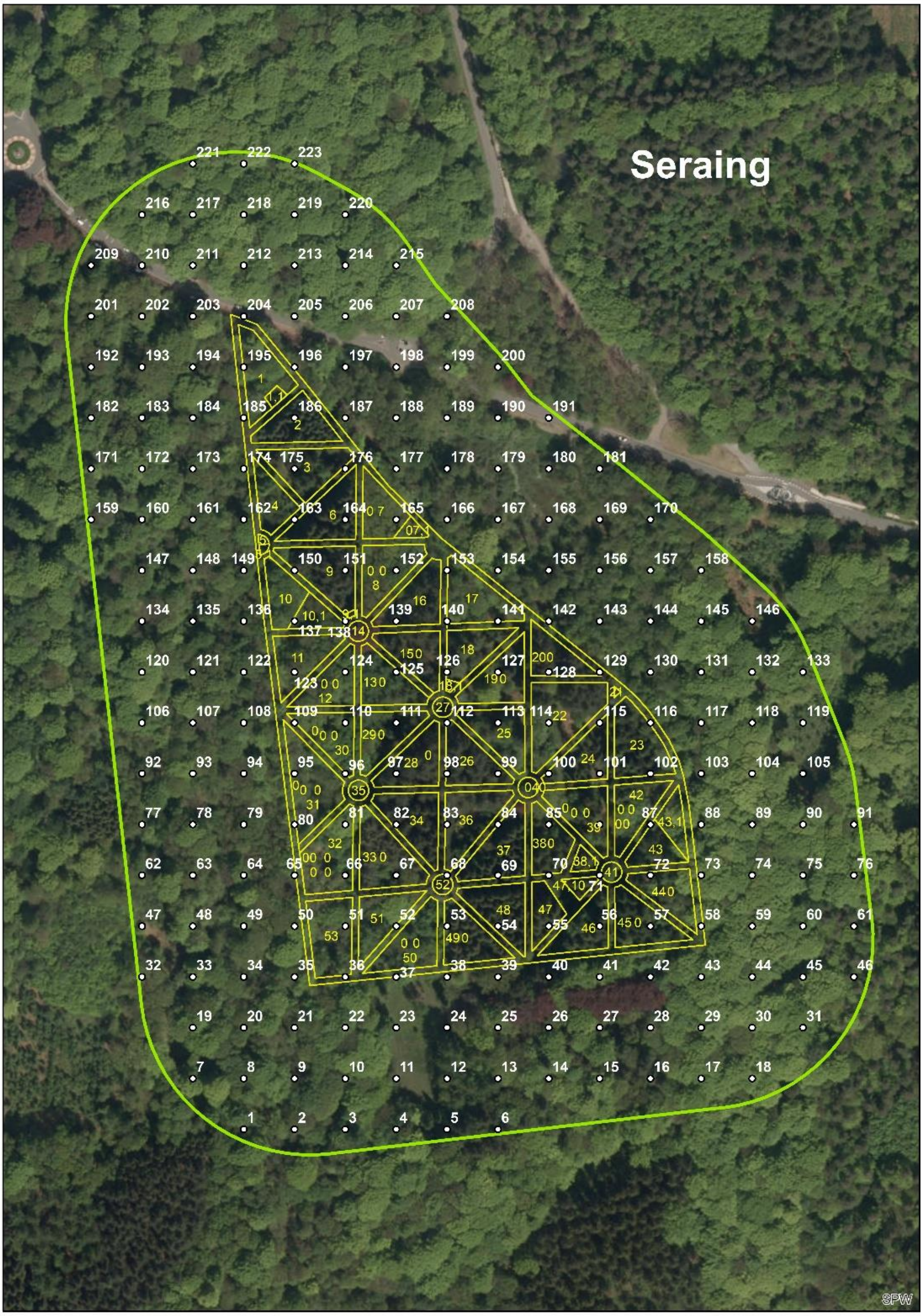
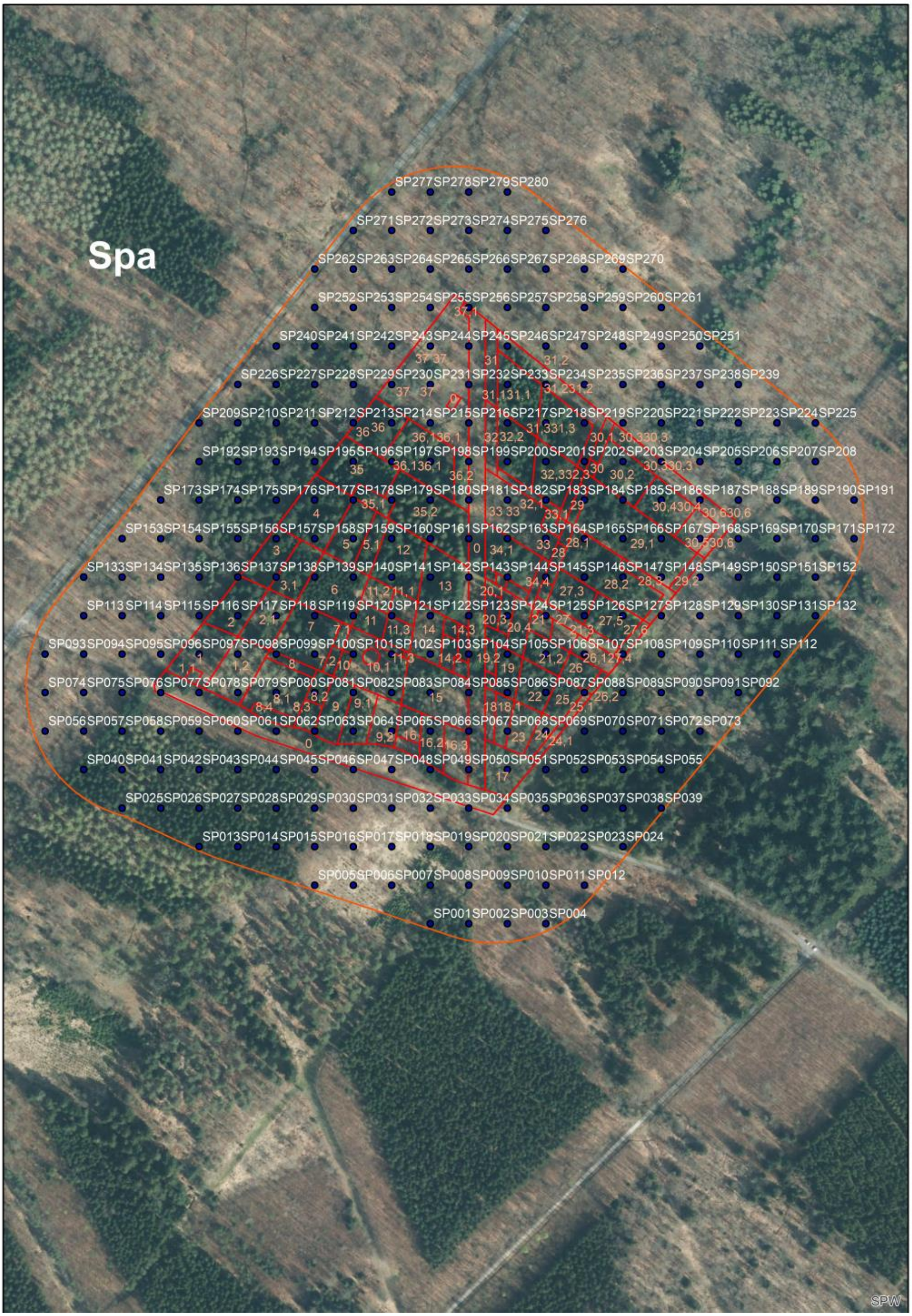

Seraing
SPW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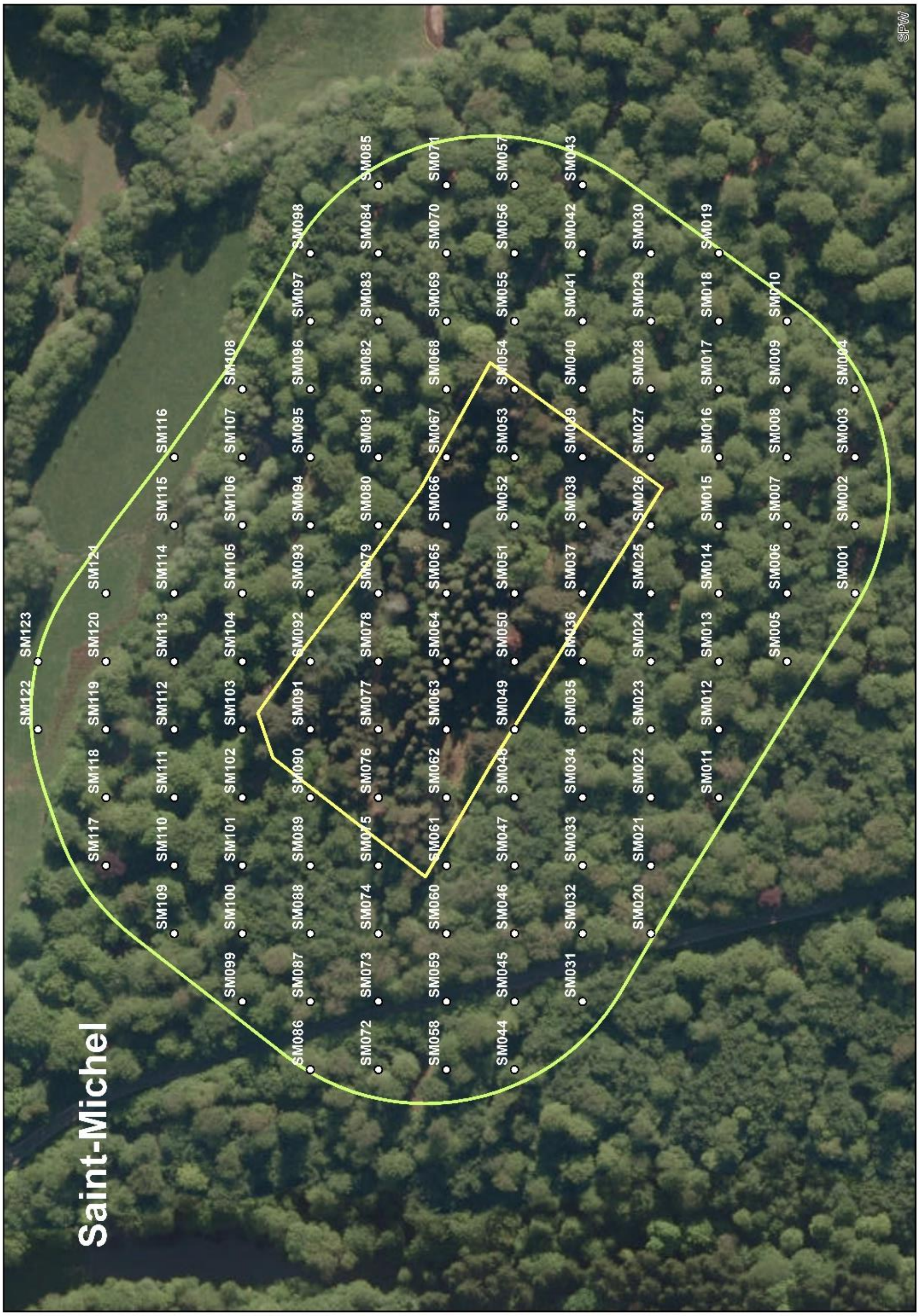
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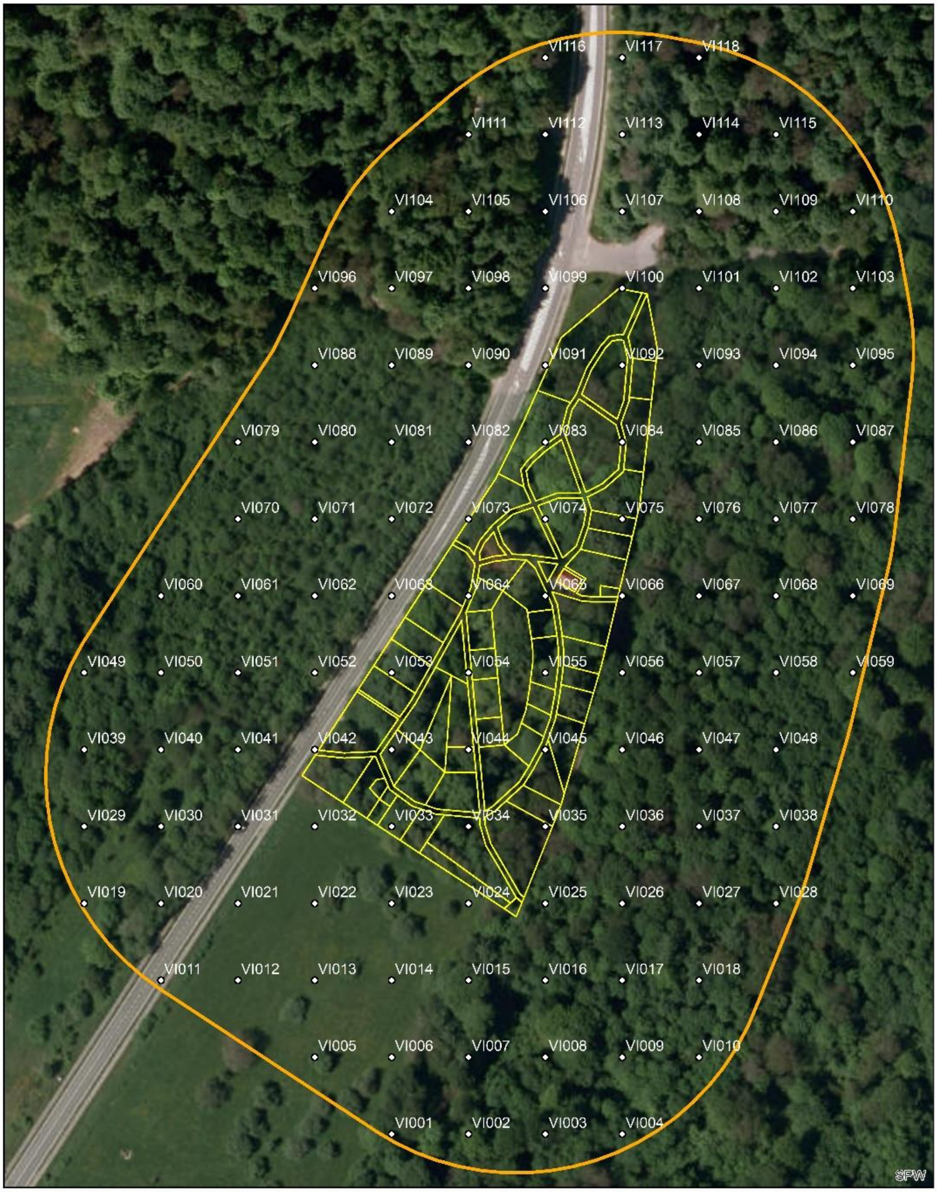
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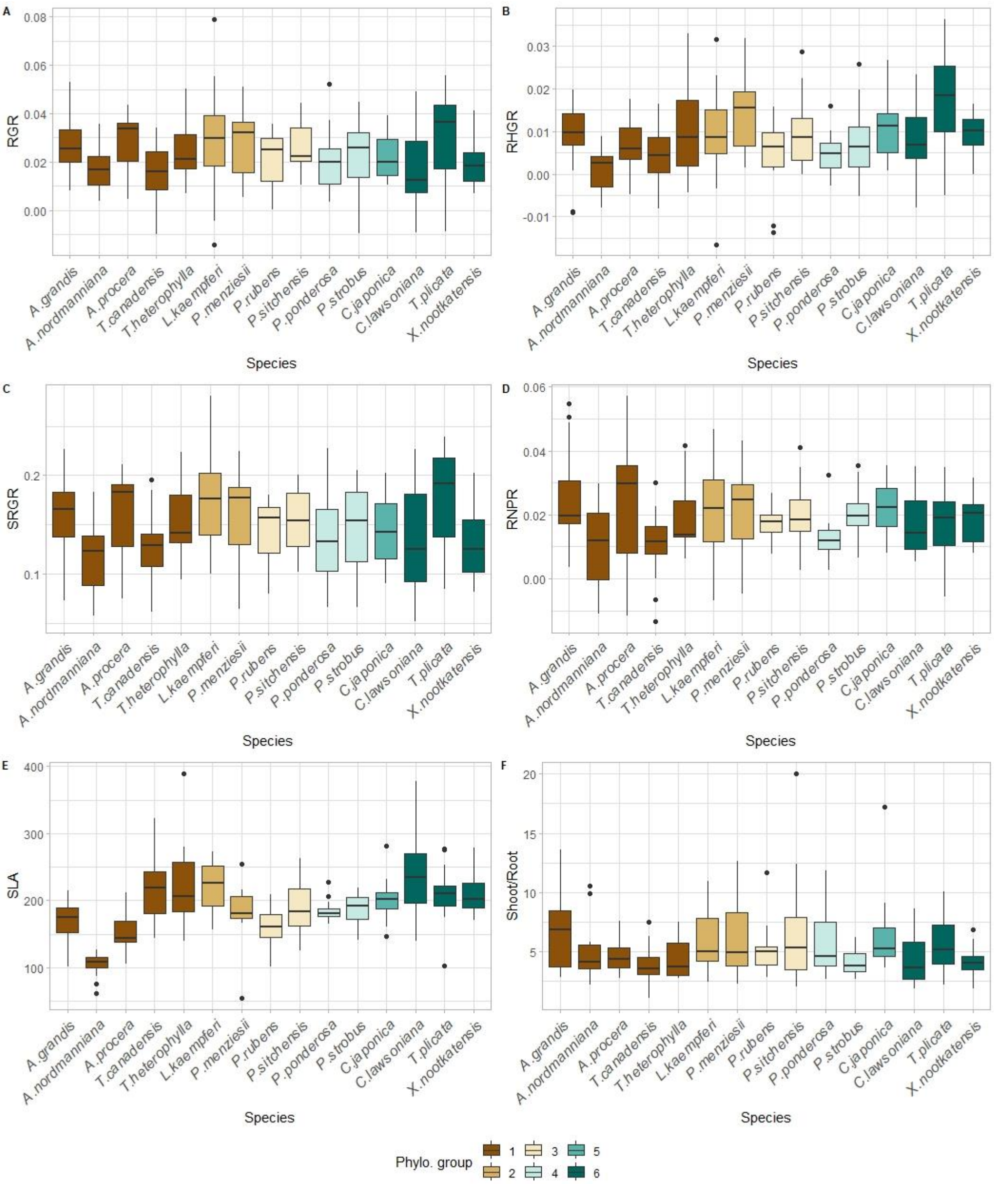
Virton

Appendix 3: Boxplots of traits for each conifer species. Colors correspond to the phylogenetic group. Units are g.g^{-1}.d^{-1} for RGR and SRGR, cm.cm^{-1}.d^{-1} for RHGR, needles.needles^{-1}.d^{-1} for RNPR and cm^{2}.g^{-1} for SLA.



Appendix 4: Regression summary of the two models selected by stepwise regression on growth traits without accounting for the taxonomic group. Response is either local or global invasiveness. P values, estimates, t values, standard errors and conditional r² are given for each trait.

	Significant predictors	P value	Estimate	t value	Std. error	Adjused R²
Local	SLA	<0.001	0.275	3.55	0.078	0.052
	SRGR	0.0829	0.135	1.74	0.078	
Global	RHGR	<0.001	0.522	3.84	0.136	0.059
	SRGR	0.0502	-0.267	-1.97	0.136	

Appendix 5: Z scores, global and local invasiveness for the 15 studied species. Z scores are retrieved from Richardson and Rejmánek (2004) and are built with a model integrating three traits: mean seed mass, minimum juvenile period and time between large seed crops.

Species	**Z score**	**Global**	**Local**
Chamaecyparis lawsoniana	9.90	0.98	0.92
Xanthocyparis nootkatensis	8.50	-2.15	-1.12
Pseudotsuga menziesii	5.60	2.56	0.34
Cryptomeria japonica	4.60	2.26	-1.12
Thuja plicata	4.40	1.08	0.76
Larix kaempferi	3.80	-0.12	0.05
Pinus strobus	3.46	2.56	0.96
Tsuga canadensis	2.30	-1.17	-1.12
Picea sitchensis	1.80	0.22	-0.50
Abies procera	1.50	-2.06	-1.10
Tsuga heterophylla	1.40	-0.73	3.30
Pinus ponderosa	0.29	0.93	-1.12
Abies grandis	-0.10	-1.08	1.26
Abies nordmanniana	-5.60	-0.31	-0.38
Picea rubens	NA	-2.95	-1.12