

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

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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.

KEYWORDS: seedlings, traits, Relative Growth Rate, Specific Leaf Area, alien, trees

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. 2009, Essl et al. 2010). They are also planted on large scale, which increases propagule pressure, with silvicultural methods enhancing survival rates (Mack 2005, Krivánek 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. 2021, 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. 2015).

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.

MATERIAL AND METHODS

Species selection and invasiveness

Fifteen conifer species non-natives in Europe were selected (Table 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 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. 1). Five species showed no regeneration on the studied sites; they were all assigned the same value of local invasiveness.

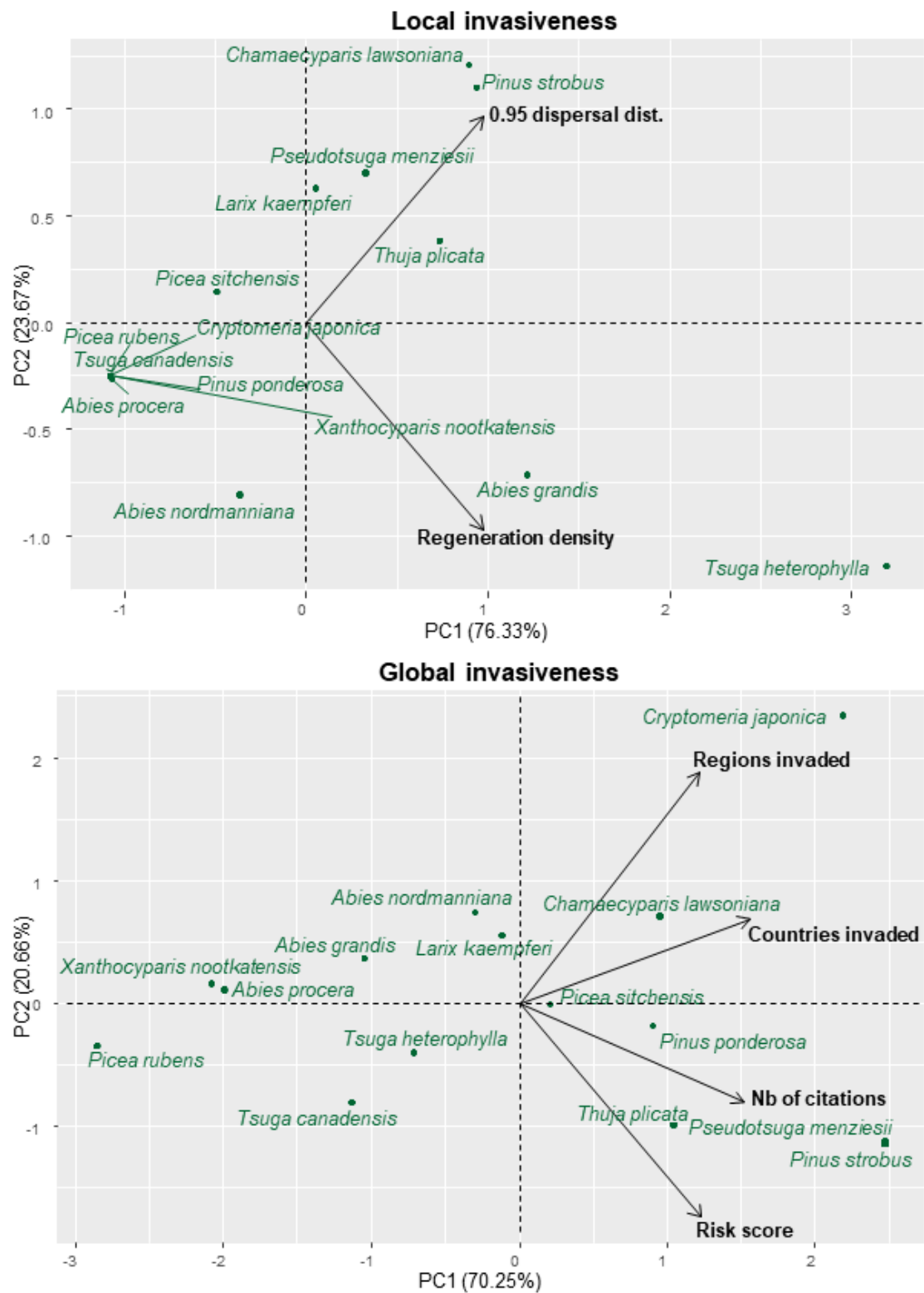


Figure 1: Biplots of the PCA's performed on the 2 proxies of local invasiveness and the 4 proxies of global invasiveness for the 15 studied conifer species.

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

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. 2).

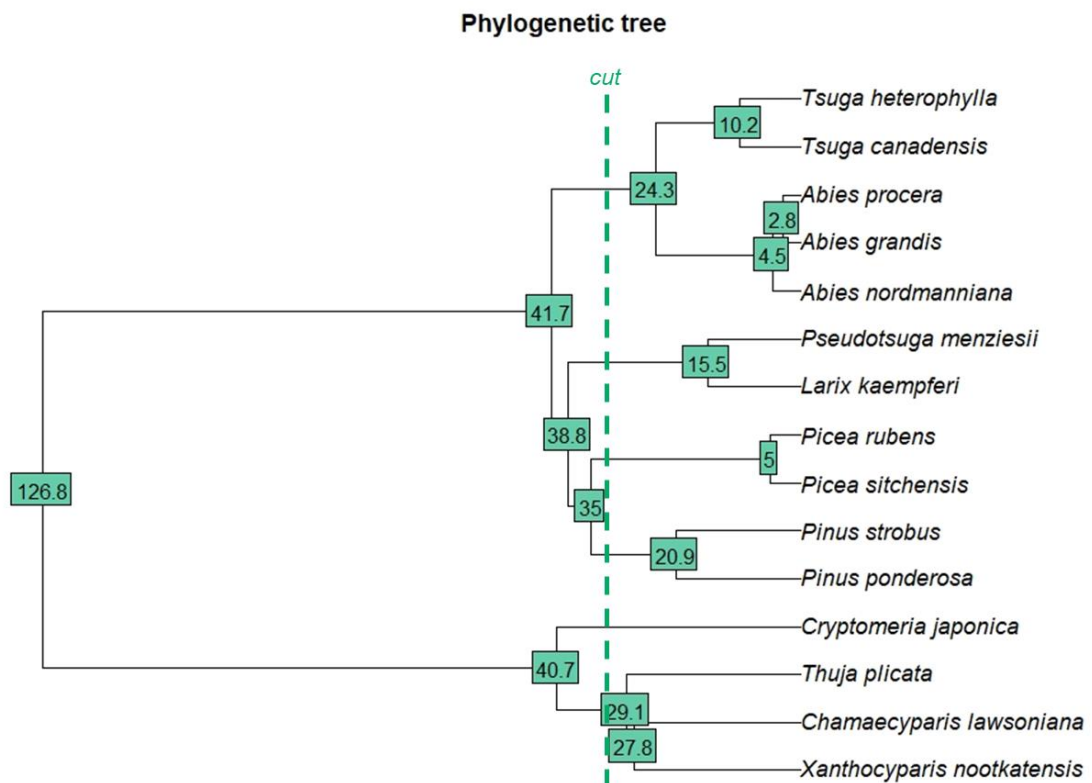


Figure 2: Phylogenetic tree constructed for the 15 studied conifer species with the “V.PhyloMaker2” package (Jin and Qian 2022) and the cutting line defining phylogenetic groups.

Seeds collection, planting and harvests

Seeds of the 15 species were collected in >80 years old forest plantations in good health conditions, in the public arboreta of Seraing, Spa, Gedinne and Saint-Michel, Southern Belgium (Fig. 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 forests. The public Walloon Counter selects several plantations with good silvicultural potential, but the seeds are not sorted except for the removal of empty ones.

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. 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. 2011, 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).

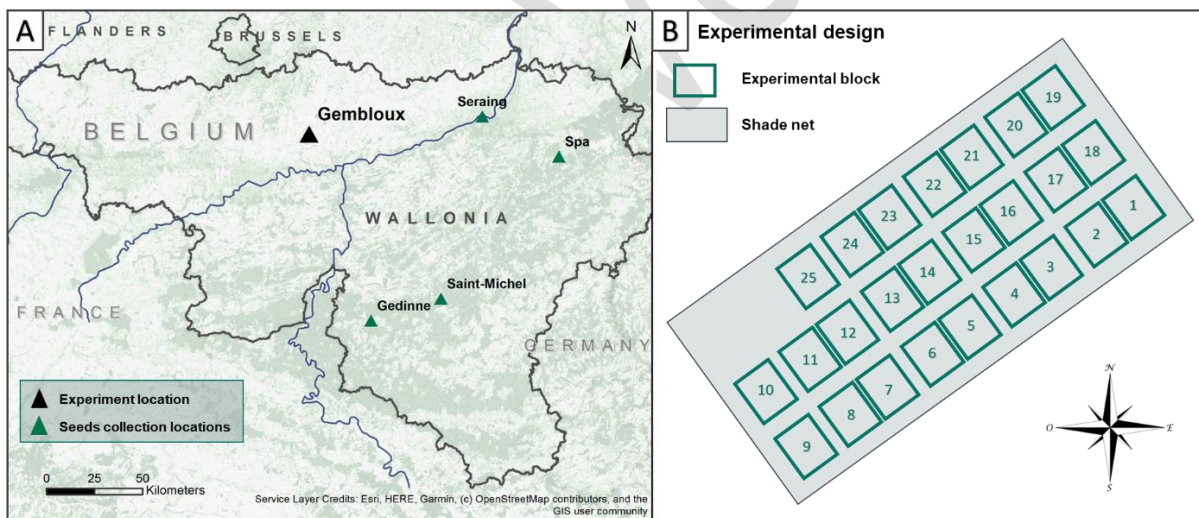


Figure 3: (A) Location of the experiment field and the arboreta where seeds were collected. Background on the map is the tree cover in 2000 (Hansen et al. 2013). (B) Experimental design with 25 blocks, each one containing 2 pots of each species.

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 2019b).

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 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 (cm²) to the total needle dry biomass (g) 10 weeks after germination.

Table 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	$\frac{W_{shoot}}{W_{roots}}$	-

Statistical analyses

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 R^2 . Analyses were performed in RStudio (R Core Team 2022).

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 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 1.

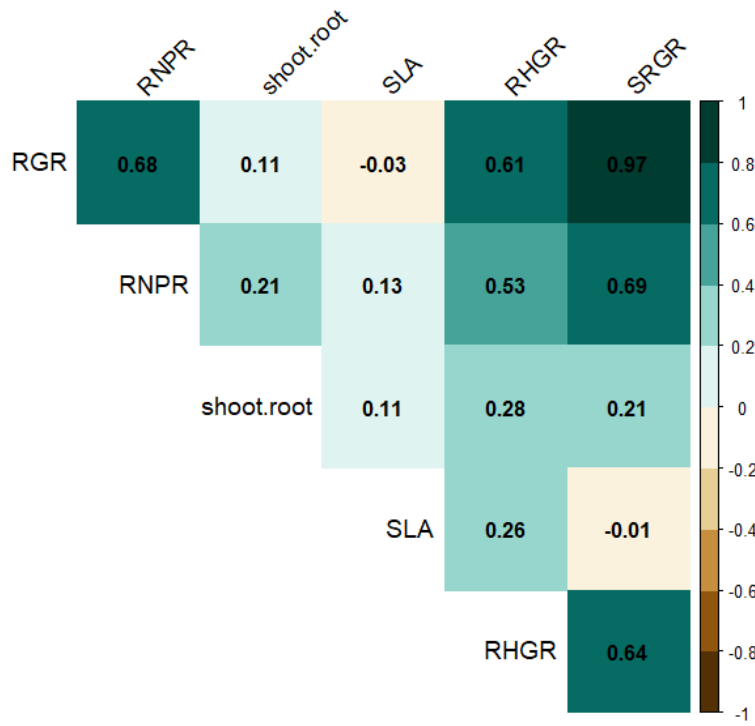


Figure 4: correlation plot of the six studied traits with Spearman coefficient values.

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Species	N	RGR	RHGR	SRGR	RNPR	SLA	Shoot/root
<i>Abies grandis</i>	18	0.026 ± 0.003 ab	0.009 ± 0.002 ab	0.027 ± 0.003 ab	0.026 ± 0.003 a	169.4 ± 6.6 ab	6.69 ± 0.75 a
<i>Abies nordmanniana</i>	21	0.016 ± 0.002 ab	0.001 ± 0.001 b	0.015 ± 0.002 b	0.011 ± 0.003 b	104.78 ± 3.9 c	4.77 ± 0.53 a
<i>Abies procera</i>	17	0.029 ± 0.003 ab	0.007 ± 0.002 bcd	0.028 ± 0.003 ab	0.025 ± 0.005 a	150.4 ± 6.5 b	4.64 ± 0.33 a
<i>Chamaecyparis lawsoniana</i>	13	0.018 ± 0.005 ab	0.008 ± 0.002 ab	0.018 ± 0.005 ab	0.017 ± 0.003 ab	243.4 ± 19.4 ad	4.42 ± 0.59 a
<i>Cryptomeria japonica</i>	15	0.022 ± 0.003 ab	0.012 ± 0.002 ad	0.022 ± 0.003 ab	0.022 ± 0.002 ab	202.3 ± 8.1 bd	6.56 ± 0.88 a
<i>Larix kaempferi</i>	22	0.029 ± 0.004 ab	0.010 ± 0.002 ad	0.029 ± 0.005 ab	0.022 ± 0.003 ab	222.0 ± 7.9 bd	5.94 ± 0.53 a
<i>Picea rubens</i>	17	0.022 ± 0.003 ab	0.005 ± 0.002 bcd	0.020 ± 0.003 ab	0.018 ± 0.001 ab	162.4 ± 7.7 bcd	5.12 ± 0.50 a
<i>Picea sitchensis</i>	14	0.025 ± 0.003 ab	0.010 ± 0.002 ab	0.025 ± 0.003 ab	0.020 ± 0.003 ab	191.0 ± 10.9 bcd	6.76 ± 1.30 a
<i>Pinus ponderosa</i>	12	0.021 ± 0.004 ab	0.005 ± 0.002 bcd	0.020 ± 0.004 ab	0.013 ± 0.002 ab	185.5 ± 4.9 bcd	5.73 ± 0.87 a
<i>Pinus strobus</i>	19	0.022 ± 0.003 ab	0.007 ± 0.002 bcd	0.020 ± 0.003 ab	0.021 ± 0.002 ab	186.5 ± 5.4 bcd	4.05 ± 0.24 a
<i>Pseudotsuga menziesii</i>	15	0.028 ± 0.004 ab	0.014 ± 0.002 ac	0.028 ± 0.004 ab	0.021 ± 0.004 ab	182.1 ± 11.0 bcd	5.98 ± 0.79 a
<i>Thuja plicata</i>	18	0.031 ± 0.004 a	0.017 ± 0.003 a	0.031 ± 0.005 a	0.018 ± 0.002 ab	210.9 ± 9.5 bd	5.71 ± 0.57 a
<i>Tsuga canadensis</i>	17	0.014 ± 0.003 b	0.004 ± 0.002 bd	0.013 ± 0.004 b	0.011 ± 0.003 b	214.6 ± 13.2 d	3.99 ± 0.38 a
<i>Tsuga heterophylla</i>	17	0.024 ± 0.003 ab	0.010 ± 0.002 ab	0.024 ± 0.003 ab	0.020 ± 0.003 ab	223.0 ± 14.5 d	4.50 ± 0.42 a
<i>Xanthocyparis nootkatensis</i>	10	0.020 ± 0.003 ab	0.009 ± 0.002 ab	0.020 ± 0.003 ab	0.019 ± 0.003 ab	209.5 ± 10.1 bd	4.21 ± 0.45 a

Table 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 cm².g⁻¹ for SLA.

Results from the linear mixed effects models are given in Table 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 2). 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. 5).

Table 4: 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 r^2 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

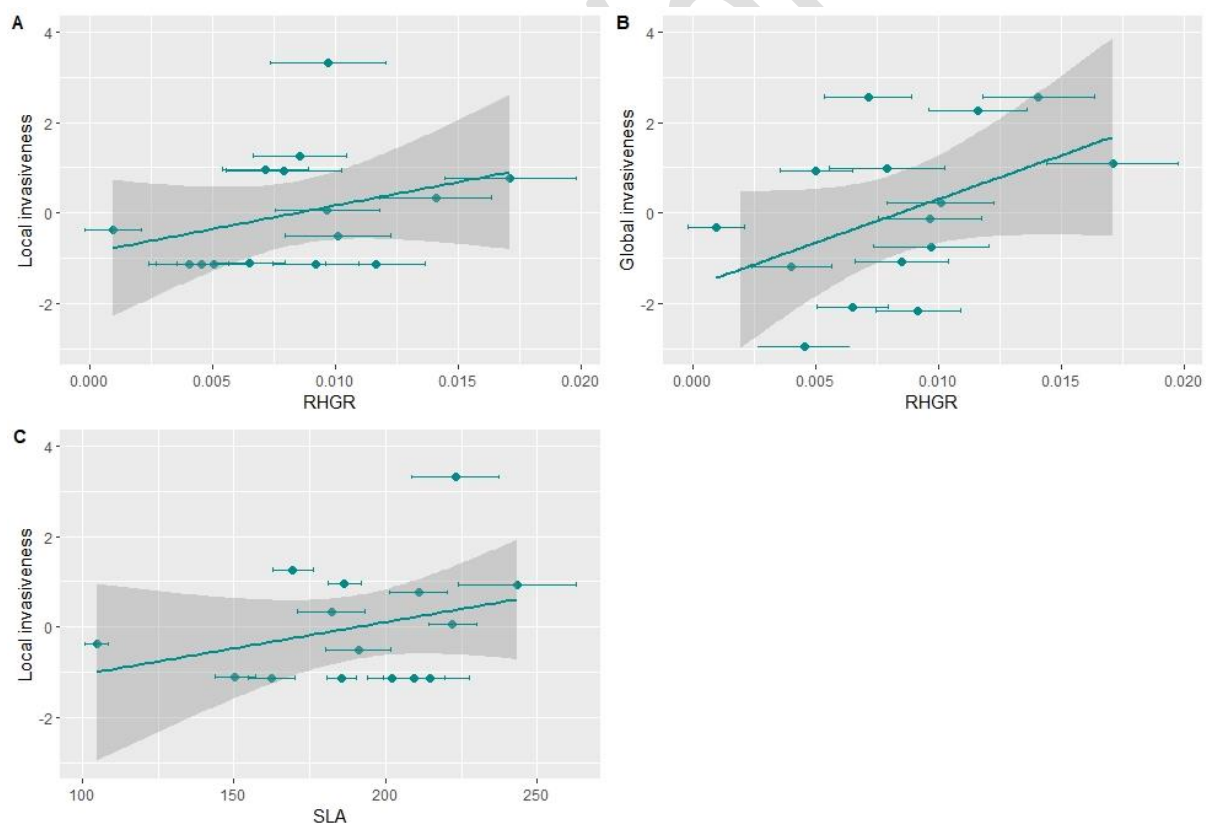


Figure 5: Predicted values for growth traits significantly related to invasiveness for both local and global invasiveness: (A) for RHGR and local invasiveness, (B) for RHGR and global invasiveness, (C) for SLA and local invasiveness. Mean values and standard errors of traits values are represented for each species. Units are $\text{cm}\cdot\text{cm}^{-1}\cdot\text{d}^{-1}$ for RHGR and $\text{cm}^2\cdot\text{g}^{-1}$ for SLA.

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 understory 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. 2010).

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 3). 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, silvicultural 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 adaptive 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).

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.

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STATEMENTS & DECLARATIONS

Author contribution

All authors contributed to the study conception. Material preparation, data collection, analyses and redaction of the drafts were performed by Aurore Fanal. All authors read, modified and commented previous versions of the manuscript. All authors approved the final manuscript.

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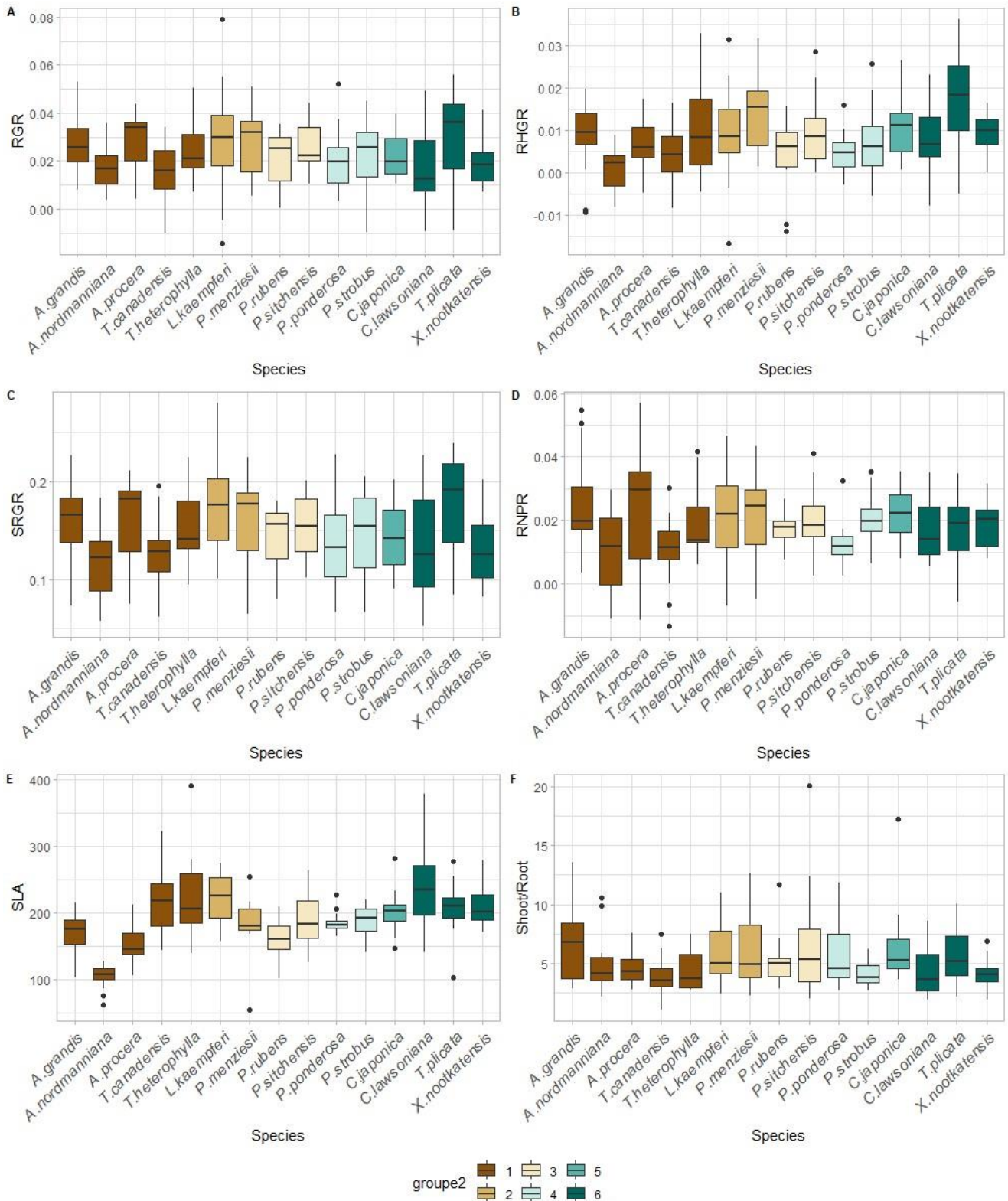
Competing interests

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

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

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



Appendix 2: 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 r^2 are given for each trait.

	Significant predictors	P value	Estimate	t value	Std. error	Adjusted 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 3: 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
<i>Chamaecyparis lawsoniana</i>	9.90	0.98	0.92
<i>Xanthocyparis nootkatensis</i>	8.50	-2.15	-1.12
<i>Pseudotsuga menziesii</i>	5.60	2.56	0.34
<i>Cryptomeria japonica</i>	4.60	2.26	-1.12
<i>Thuja plicata</i>	4.40	1.08	0.76
<i>Larix kaempferi</i>	3.80	-0.12	0.05
<i>Pinus strobus</i>	3.46	2.56	0.96
<i>Tsuga canadensis</i>	2.30	-1.17	-1.12
<i>Picea sitchensis</i>	1.80	0.22	-0.50
<i>Abies procera</i>	1.50	-2.06	-1.10
<i>Tsuga heterophylla</i>	1.40	-0.73	3.30
<i>Pinus ponderosa</i>	0.29	0.93	-1.12
<i>Abies grandis</i>	-0.10	-1.08	1.26
<i>Abies nordmanniana</i>	-5.60	-0.31	-0.38
<i>Picea rubens</i>	NA	-2.95	-1.12