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Research Article

Keywords: Alien invasive plant, Gymnosperm, Seed dispersal, Exotic trees, Escape effect

Posted Date: April 24th, 2024

DOI: https://doi.org/10.21203/rs.3.rs-4218372/v1

Version of Record: A version of this preprint was published at Biological Invasions on September 10th, 2024. See the published version at https://doi.org/10.1007/s10530-024-03438-8.

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

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Abstract

Few conifers are considered invasive in Europe, yet recent studies indicate that several species used for forestry display abundant regeneration and spread into surrounding natural habitats. Three species were identified as being particularly at risk in Belgium, but data is lacking regarding their dispersal. We characterized the recruitment curves of *Tsuga heterophylla*, *Abies grandis* and *Thuja plicata*. Isolated plantations were monitored and realized dispersal (*i.e.* seedlings and recruited regeneration) was exhaustively recorded and measured over 750 meters in 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 above 1.5 m), and the recruitment distances were analyzed for each size class. The effect of the forest type (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 appear to spread beyond documented threshold rate of invasiveness. Regeneration density was higher in coniferous forest type, as well as open areas for *Tsuga heterophylla*. An escape effect was noticed as mean and maximal dispersal distances of saplings and taller trees were greater than those of seedlings. Our study indicates that *Tsuga heterophylla* displays the highest risk of rapid spread into adjacent natural habitats, followed by *Abies grandis*. *Thuja plicata* faces more recruitment limitations.

Keywords: Alien invasive plant; Gymnosperm; Seed dispersal; Exotic trees; Escape effect

Acknowledgments

We are grateful to Louis Abandonné, Guillaume Baralle, Pauline Crasson, Adrien Delforge, Maïké Dellicour, Emilie Guilmin, Vladimir Joassin, Marie Patinet, Thomas Pollet, Lise Pouilloux and Eric Rathle for their help in the field. We also thank the “Département de la Nature et des Forêts” for providing information on stand locations and granting access to study sites.

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 et al. 2004; Richardson and Rejmánek 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 (Kowarik 1995; 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 as 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. 2021).

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. While dispersal curves are built to model seed dispersal over the distance from a seed source, recruitment curves describe the distribution of actual descendants at increasing distance from the parent trees. The former corresponds 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 seed dispersal capacities, such as the propagule size and mass and its terminal velocity and plant height (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). 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 or diseases, 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 and pathogens 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).

Richardson et al. (2000) suggested the threshold of 100 meters in 50 years for seed-dispersed alien 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* (Raf.) Sarg., *Abies grandis* (Douglas ex D.Don) Lindl. and *Thuja plicata* Donn ex D.Don. 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 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.

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 illustrated in Fig. 1. 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 clear-cuts or grasslands.

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. 2). 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.

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 as fixed factor and the site as grouping variable, 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 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.

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 Fig. 3A, Fig. 4A and Fig. 5A.

When we consider the regeneration outside plantings (after distance 0), the number of individuals in each site ranged from 55 to 3593 for *Tsuga heterophylla*, 6 to 33 for *Thuja plicata* and 213 to 12485 for *Abies grandis* (Table 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 50.0 m for *Tsuga heterophylla*, 22.5 m for *Thuja plicata* and 15 m for *Abies grandis*. Maximum distances were 565 m for *T. heterophylla*, 265 m for *T. plicata* and 355 m for *A. grandis*. When comparing maximum dispersal distances across sectors, the three species differed significantly (ANOVA, p= 0.029).

Among sites, WER ranged from 0.14 to 6.21 m.year^{-1} for *Tsuga heterophylla*, with an average of 1.41 m.year^{-1}. It ranged from 0.11 to 1.22 m.year^{-1} for *Thuja plicata*, with an average of 0.63 m.year^{-1} and from 0.17 to 1 m.year^{-1} for *Abies grandis*, with an average of 0.44 m.year^{-1}. FER varied from 0.38 to 17.12 m.year^{-1} for *Tsuga heterophylla*, with an average of 8.20 m.year^{-1}. It ranged from 1.49 to 6.02 m.year^{-1} for *Thuja plicata,* with an average of 3.56 m.year^{-1} and from 2.93 to 10.14 m.year^{-1} for *Abies grandis,* with an average of 7.04 m.year^{-1}.

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 S1, supplementary material). 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* (Fig. 3). 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 S2 (supplementary material), 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 *Tsuga heterophylla*, 85.9 (B) and 82.7 m (C) against 55 m for seedlings of *Abies grandis* and 89.3 (B) and 71.5 m (C) against 48.3 m for seedlings of *Thuja plicata*.

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 S3, supplementary material). 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. 3C). *Abies grandis* clearly favors coniferous covers (Fig 4 C).

Discussion

For an exotic tree species to be considered as invasive according to the widely accepted definition by Richardson et al. (2000), offspring must be generated further than 100 m from parent trees in less than

50 years, which corresponds to a spread of 2 m.year^{-1}. It must also be abundant in the established regeneration (Nygaard and Øyen 2017). Also, 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 2 m.year^{-1} benchmark is only crossed once, for *Tsuga heterophylla* in one site. However, the Frontier Expansion Rate can be considered a more reliable estimate of species actual spread (Skarpaas and Shea 2007). Considering FER, the three species cross the invasive threshold in at least three sites. On average, *Tsuga heterophylla* FER is 8.20 m.year^{-1} but it even reaches 17 m.year^{-1} in the most invaded site of Mirwart. *Abies grandis* FER hits 10 m.year^{-1}, against 6 m.year^{-1} for *Thuja plicata*. As the maximum distance used for the calculation of FER may represent a rare LDD event, we also calculated a similar estimate with values of the 95th percentile; yet again, the three species cross the threshold of 2 m.year^{-1} at least once. 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 *Thuja plicata*, 300 m for *Abies grandis* and even 500 m for *Tsuga heterophylla.*

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). *Tsuga heterophylla* displayed the most important dispersal distances with one site 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. As our three species are wind-dispersed, wind and topography likely affect the maximum dispersal distance, and therefore our observations may 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. Though, 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.

High densities of regeneration were observed for the three conifer species, especially for *Abies 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 *Tsuga 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 *Tsuga heterophylla* and *Abies grandis* were found in our sampling sectors (11077 and 26435 respectively), only 1070 stems of *Thuja plicata* were identified across the four sites. For *Tsuga 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. This clearly shows that not only do the seeds germinate, but the development of the descendants is common. 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 *Abies grandis* and *Thuja plicata* than for *Tsuga heterophylla*.

Not only are recruited trees present for *Tsuga heterophylla* and *Abies grandis*, but taller trees are found further from plantings. The probability of seedlings recruitment is therefore higher with increased distance from parent trees, which validates the escape hypothesis for these studied species. This suggests that the shape of the recruitment curves is dissimilar to the seed shadow, both because of varying favorable micro-sites availability and distance-dependent survival rates. However, we do not have the necessary data to clarify the process under this escape effect, *i.e.* if it is due to competition or herbivory and pest pressures. Though, regeneration was also dense inside the plantations, under the parent trees, but most of this regeneration was under 0.3 m high: dense planting densities and lack of light reaching the understory likely induce competition that hinders seedling development.

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 (Norghauer et al. 2011; Caplat et al. 2012) . 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 in general 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 *Abies grandis* is facilitated by conifer plantations, while *Tsuga 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. *Thuja 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).

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. Still, this method is particularly time-consuming. Almost 100 man.day 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 could 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. 2010; Fanal et al. 2022, 2023). In 2014, Tamme et al. (2014) 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 *Tsuga heterophylla*, 325 m (CI = 189 – 558 m) for *Abies grandis* and 274 m (CI = 150 – 502 m) for *Thuja 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.

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^{-1}, 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.

Declarations

Funding

This work was supported by the University of Liege.

Competing interests

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

Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Aurore Fanal and Arnaud Monty. The first draft of the manuscript was written by Aurore Fanal and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data vailability

The datasets generated during this study are available on reasonable request.

338 **References**

339

340 Amm A, Pichot C, Dreyfus P, et al (2012) Improving the estimation of landscape scale seed dispersal
341 by integrating seedling recruitment. Annals of Forest Science 69:845–856.
342 https://doi.org/10.1007/S13595-012-0208-1/FIGURES/3

343 Beckman NG, Aslan CE, Rogers HS (2020) Introduction to the special issue: The role of seed dispersal
344 in plant populations: Perspectives and advances in a changing world. AoB PLANTS 12:.
345 https://doi.org/10.1093/AOBPLA/PLAA010

346 Bindewald A, Miocic S, Wedler A, Bauhus J (2021) Forest inventory-based assessments of the
347 invasion risk of Pseudotsuga menziesii (Mirb.) Franco and Quercus rubra L. in Germany.
348 European Journal of Forest Research 140:883–899. https://doi.org/10.1007/S10342-021-
349 01373-0/FIGURES/5

350 Brooks M, Kristensen K, van Benthem K, et al (2017) glmmTMB Balances Speed and Flexibility Among
351 Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.
352 https://doi.org/doi:10.32614/RJ-2017-066

353 Bullock JM, Clarke RT (2000) Long distance seed dispersal by wind: Measuring and modelling the tail
354 of the curve. Oecologia 124:506–521. https://doi.org/10.1007/PL00008876/METRICS

355 Bullock JM, Mallada González L, Tamme R, et al (2017) A synthesis of empirical plant dispersal
356 kernels. Journal of Ecology 105:6–19. https://doi.org/10.1111/1365-2745.12666

357 Bullock JM, Shea K, Skarpaas O (2006) Measuring plant dispersal: An introduction to field methods
358 and experimental design. Plant Ecology 186:217–234

359 Calviño-Cancela M, Rubido-Bará M (2013) Invasive potential of Eucalyptus globulus: Seed dispersal,
360 seedling recruitment and survival in habitats surrounding plantations. Forest Ecology and
361 Management 305:129–137. https://doi.org/10.1016/J.FORECO.2013.05.037

362 Caplat P, Nathan R, Buckley YM (2012) Seed terminal velocity, wind turbulence, and demography
363 drive the spread of an invasive tree in an analytical model. Ecology 93:368–377.
364 https://doi.org/10.1890/11-0820.1

365 Carrillo-Gavilán MA, Vilà M (2010) Little evidence of invasion by alien conifers in Europe. Diversity
366 and Distributions 16:203–213. https://doi.org/10.1111/j.1472-4642.2010.00648.x

367 Connell JH (1971) On the Role of Natural Enemies in Preventing Competitive Exclusion in Some
368 Marine Animals and in Rain Forest Trees. In: Den Boer PJ, Gradwell GR (eds) Dynamics of
369 Populations. Centre for Agricultural Publishing and Documentation, Wageningen, The
370 Netherlands

371 Edwards P, Sprague R, Stahlmann-Brown P (2021) Removing invasive conifers - considerations,
372 complexity and costs. Environmental Research Communications 3:071004.
373 https://doi.org/10.1088/2515-7620/AC13C7

374 Essl F, Moser D, Dullinger S, et al (2010) Selection for commercial forestry determines global patterns
375 of alien conifer invasions. Diversity and Distributions 16:911–921.
376 https://doi.org/10.1111/J.1472-4642.2010.00705.X

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. https://doi.org/10.3897/NEOBIOTA.64.56027

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. https://doi.org/10.1007/S11258-022-01266-1/FIGURES/4

Fanal A, Porté A, Mahy G, Monty A (2023) Fast height growth is key to non-native conifers invasiveness in temperate forests. Biological Invasions 1–18. https://doi.org/10.1007/S10530-023-03214-0/TABLES/6

Forestry Commission Scotland (2015) Managing invasive and non-native forestry species

Greene DF, Canham CD, Coates KD, Lepage PT (2004) An Evaluation of Alternative Dispersal Functions for Trees. Source: Journal of Ecology 92:758–766

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. The American Naturalist 159:396–419. https://doi.org/10.1086/338995

Hansen M, Potapov P, Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853. https://doi.org/10.1126/science.1244693

Horn HS, Nathan R, Kaplan SR (2001) Long-distance dispersal of tree seeds by wind. Ecological Research 16:877–885. https://doi.org/10.1046/J.1440-1703.2001.00456.X

Howe F, Smallwood J (1982) Ecology of seed dispersal. Annual review of ecology and systematics Volume 13 201–228. https://doi.org/10.1146/ANNUREV.ES.13.110182.001221

Hubbell SP (1980) Seed predation and the coexistence of tree species in tropical forests. Oikos 35:214. https://doi.org/10.2307/3544429

Janzen DH (1970) Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104:501–528. https://doi.org/10.1086/282687

Johnson JS, Cantrell RS, Cosner C, et al (2019) Rapid changes in seed dispersal traits may modify plant responses to global change. AoB PLANTS 11:1–20. https://doi.org/10.1093/AOBPLA/PLZ020

Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) Plant Invasions - General Aspects and Special Problems. SPB Academic Publishing, pp 15–38

Kuznetsova A, Brockhoff P, Christensen R (2017) lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26. https://doi.org/doi:10.18637/jss.v082.i13

Loebach CA, Anderson RC (2018) Measuring short distance dispersal of Alliaria petiolata and determining potential long distance dispersal mechanisms. PeerJ 2018:. https://doi.org/10.7717/PEERJ.4477/FIG-3

Lüdecke D (2018) ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Open Source Software 3:772. https://doi.org/doi:10.21105/joss.00772

Martin PH, Canham CD (2010) Dispersal and recruitment limitation in native versus exotic tree species: Life-history strategies and Janzen-Connell effects. Oikos 119:807–824. https://doi.org/10.1111/J.1600-0706.2009.17941.X

Martin PH, Canham CD, Kobe RK (2010) Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. Journal of Ecology 98:778–789. https://doi.org/10.1111/j.1365-2745.2010.01666.x

Moravcová L, Pyšek P, Jarošík V, Pergl J (2015) Getting the Right Traits: Reproductive and Dispersal Characteristics Predict the Invasiveness of Herbaceous Plant Species. PloS one 10:. https://doi.org/10.1371/journal.pone.0123634

Nathan R, Klein E, Robledo-Arnuncio JJ, Revilla E (2012) Dispersal kernels: review. . In: Clobert J, Baguette M, Benton TG, Bullock JM (eds) Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK, pp 187–210

Nathan R, Safriel UN, Noy-Meir I, Schiller G (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from Pinus halepensis trees. Ecology 81:2156–2169. https://doi.org/10.1890/0012-9658

Norghauer JM, Nock CA, Grogan J (2011) The Importance of Tree Size and Fecundity for Wind Dispersal of Big-Leaf Mahogany. PLOS ONE 6:e17488. https://doi.org/10.1371/JOURNAL.PONE.0017488

Nygaard PH, Øyen B-H (2017) Spread of the Introduced Sitka Spruce (Picea sitchensis) in Coastal Norway. Forests 8:. https://doi.org/10.3390/f8010024

Petit S, Cordier S, Claessens H, et al (2017) Fichier écologique des essences. Forêt.Nature, UCLouvain-ELIe, ULiège-GxABT, SPWARNE-DNF. https://www.fichierecologique.be/#!/. Accessed 6 May 2020

Proença-Ferreira A, Borda-de-Água L, Porto M, et al (2023) dispfit: An R package to estimate species dispersal kernels. Ecological Informatics 75:102018. https://doi.org/10.1016/j.ecoinf.2023.102018

Pyšek P (2016) What determines the invasiveness of tree species in central Europe? In: Krumm F, Vítková L (eds) Introduced tree species in European forests: opportunities and challenges. European Forest Institute, pp 68–77

R Core Team (2022) R: A Language and Environment for Statistical Computing

Richardson DM, Pysek P, Rejmanek M, et al (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Richardson DM, Rejmánek M (2004) Conifers as invasive aliens: a global survey and predictive framework. Diversity and Distributions 10:321–331. https://doi.org/10.1111/j.1366-9516.2004.00096.x

Richardson DM, Rouget M, Rejmánek M (2004) Using Natural Experiments in the Study of Alien Tree Invasions: Opportunities and Limitations. In: Gordon MS, Bartol SM (eds) Experimental Approaches to Conservation Biology. Univerity of California Press, Ltd., Los Angeles, California, pp 180–201

Sagnard F, Pichot C, Dreyfus P, et al (2007) Modelling seed dispersal to predict seedling recruitment: Recolonization dynamics in a plantation forest. Ecological Modelling 203:464–474. https://doi.org/10.1016/J.ECOLMODEL.2006.12.008

Skarpaas O, Shea K (2007) Dispersal Patterns, Dispersal Mechanisms, and Invasion Wave Speeds for Invasive Thistles. The American Naturalist. https://doi.org/10.1086/519854

Tamme R, Götzenberger L, Zobel M, et al (2014) Predicting species' maximum dispersal distances from simple plant traits. Ecology 95:505–513. https://doi.org/10.1890/13-1000.1

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235–245. https://doi.org/10.1111/J.1461-0248.2009.01418.X

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis

Wyse S V., Hulme PE (2021) Dispersal potential rather than risk assessment scores predict the spread rate of non-native pines across New Zealand. Journal of Applied Ecology 58:1981–1992. https://doi.org/10.1111/1365-2664.13947

Tables

Table 1: 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

Figures

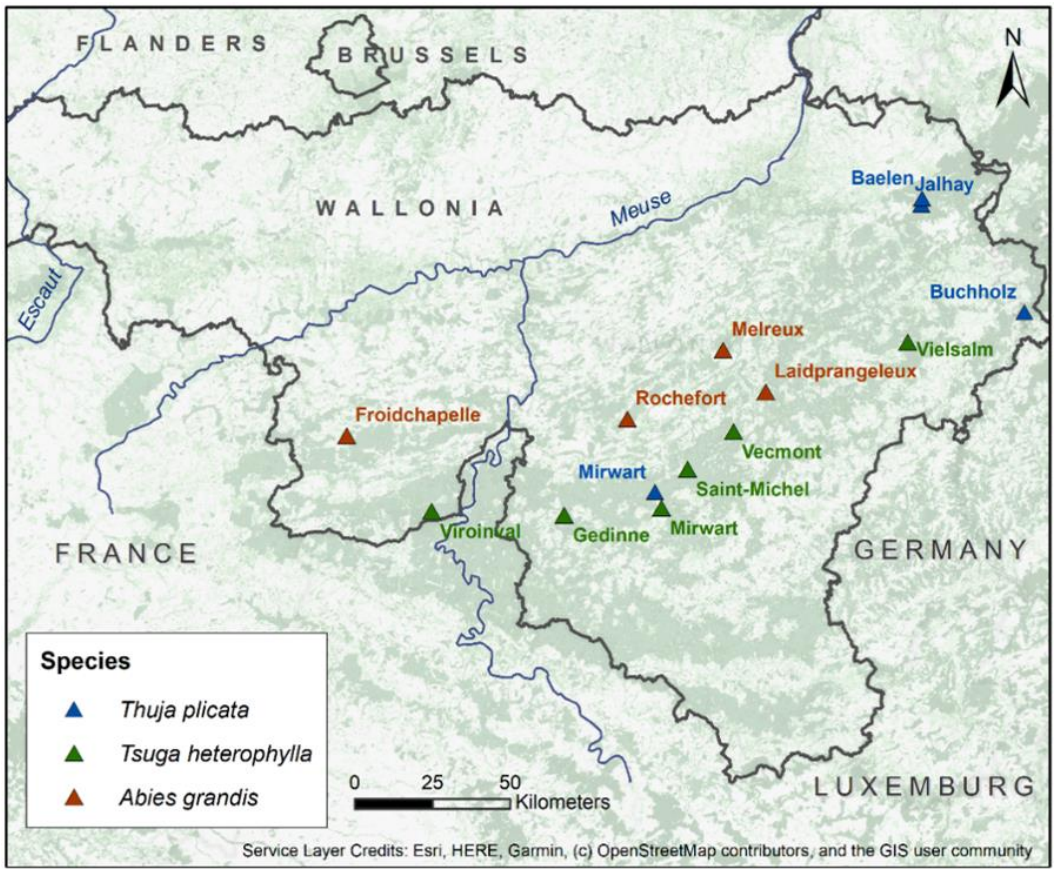

Fig. 1 *Location of the study sites for each species in Wallonia, Belgium. Background on the map is the tree cover in 2000* (Hansen et al. 2013).

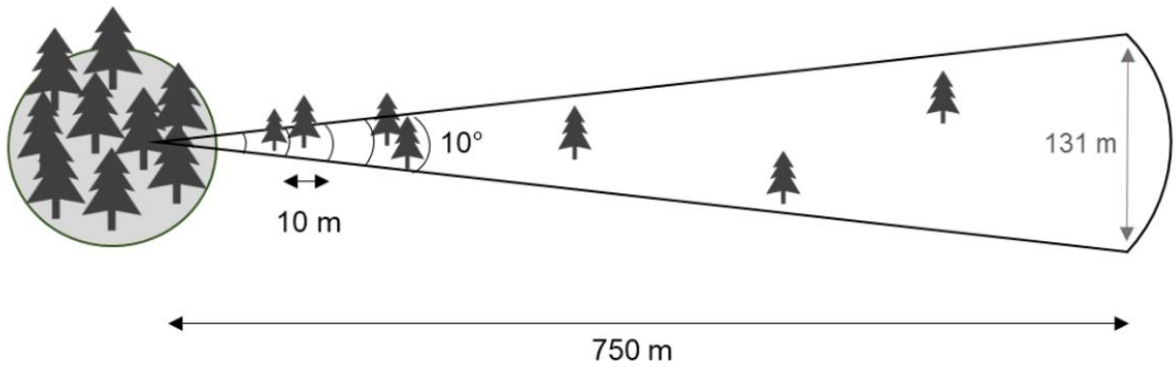

Fig. 2 *Delimitation of a 10° circle sector starting 20 meters inside the planting. The 10-m sections were delimited with stakes and the direction was held with the help of a compass.*

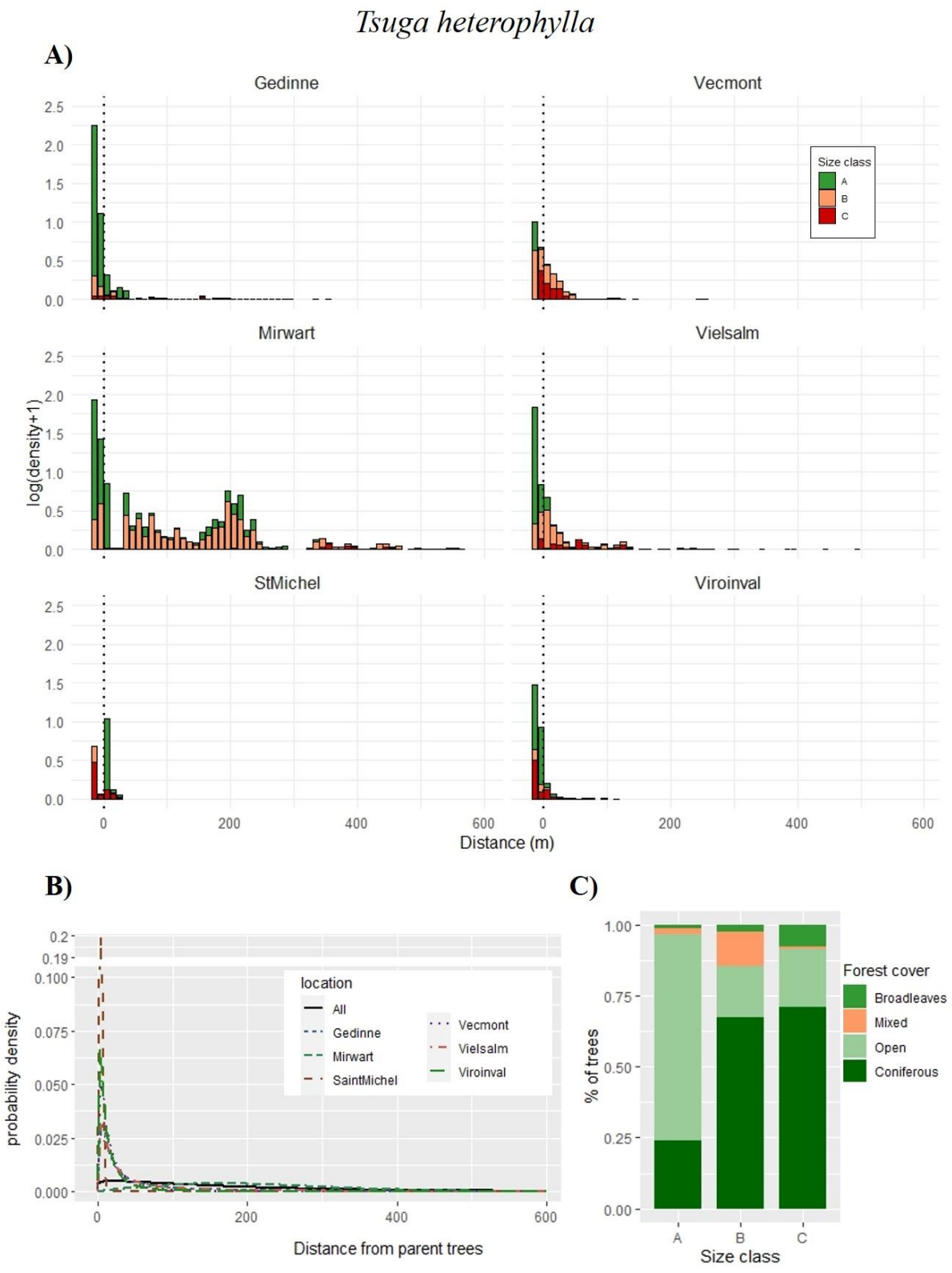

Fig. 3 A) *Raw data of dispersal of Tsuga heterophylla per site. Y axis is the mean of the log of regeneration densities between 3 sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the size classes: A for seedlings < 0.3 m, 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 recruited trees found under each forest cover type.*

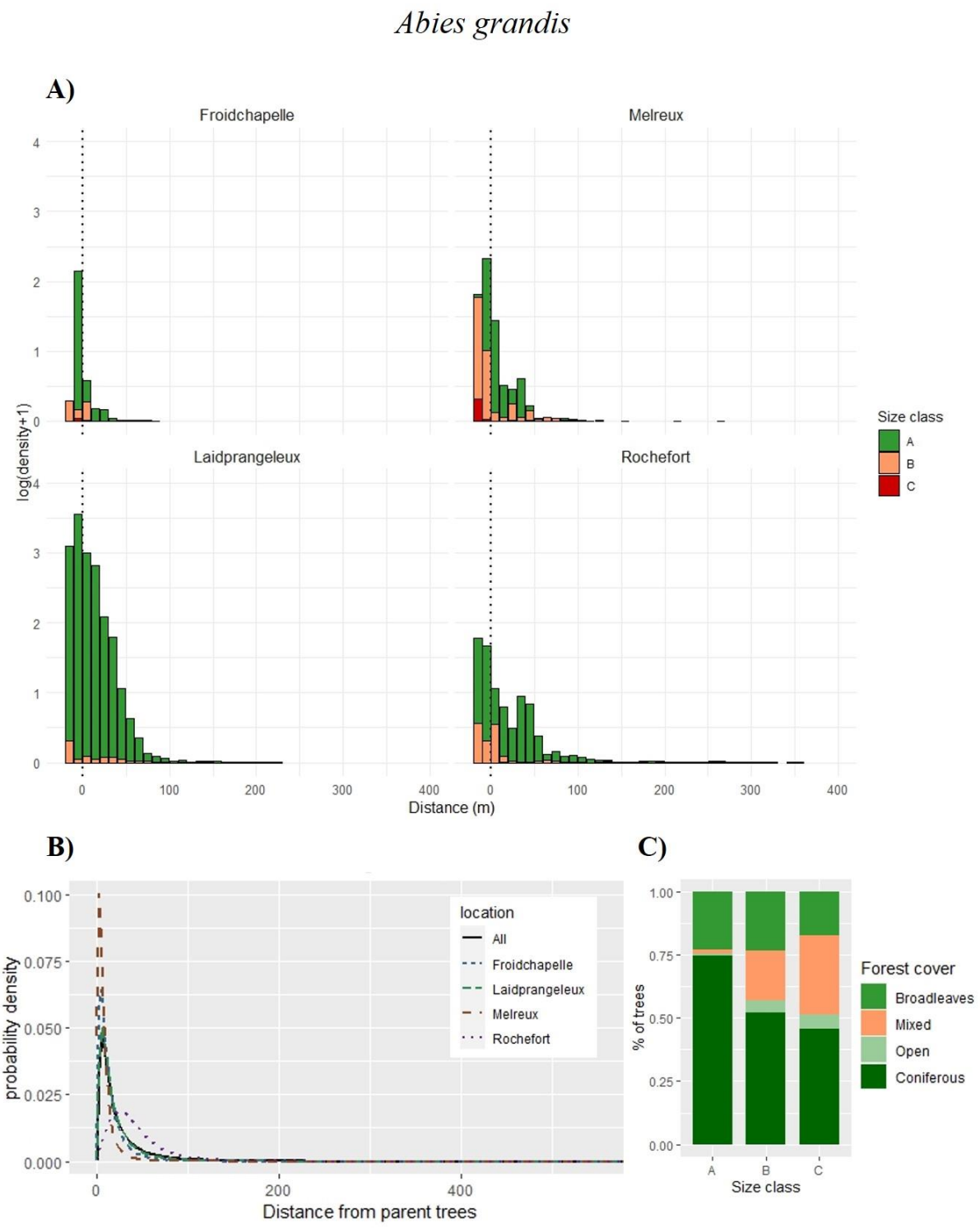

Fig. 4 A) *Raw data of dispersal of Abies grandis per site. Y axis is the mean of the logarithm of regeneration density between three sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the three size classes: A for seedlings 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 recruited trees found under each forest cover type.*

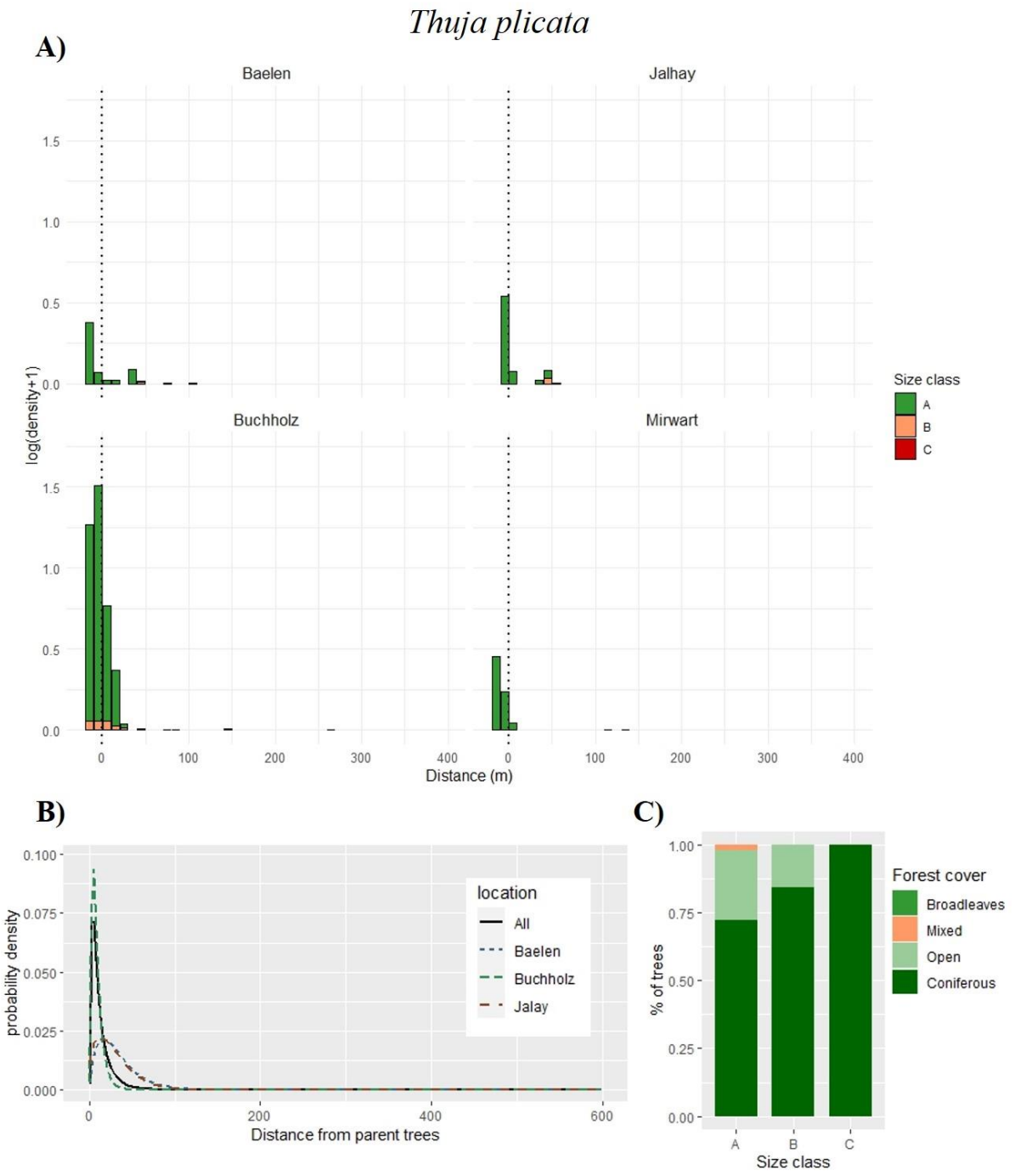

*Figure 5: **A)** Raw data of dispersal of Thuja plicata per site. Y axis is the mean of the logarithm of regeneration density between three sectors in random directions. X axis is the distance from the edge of the plantation. Colors indicate the proportion of trees in the three size classes: A for seedlings 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 recruited trees found under each forest cover type.*

Supplementary material

Table S1: 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 S2: 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 S3: 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				