

Quantile regression for estimating Douglas-fir natural regeneration potential using the R package *quaxnat*: Advanced ecological modeling for the management of nature conservation and silviculture

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ABSTRACT

Recent extreme weather conditions in Europe have led to widespread destruction of Norway spruce by storms and bark beetles, creating large clearings that need replanting. The shortage of planting material has shifted focus to natural regeneration processes, with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) emerging as a potential substitute due to its growth performance and drought tolerance. This study introduces and applies methods for investigating the regeneration ecology of Douglas-fir, focusing on the potential density of established regeneration and its dependence on the distance to the nearest seed source.

This dependence is modelled with various classical spatial dispersal kernels, the parameters of which are estimated with a quantile regression approach implemented in a new R package *quaxnat*. Regeneration data from 44,257 sample plots in the state forest of Lower Saxony, Germany, are combined with remote sensing-based positions of potential seed trees to illustrate these methods. Among the standard dispersal kernels provided by *quaxnat*, the *spatial t distribution* proves to be the most suitable. Here, for the .999th quantile, the estimated potential regeneration density reaches almost 11,000 trees per hectare in the immediate vicinity of the seed trees and decreases sharply with increasing distance.

A simple simulation model that takes dispersal and establishment into account illustrates how these results can be linked to management scenarios. The study provides valuable information for nature conservation and silviculture, suggesting buffer zones around sensitive habitats and guiding forest management decisions regarding natural regeneration options.

1. Introduction

Extreme weather conditions in recent years have resulted in large areas of Norway spruce (*Picea abies* L.) that were destroyed by storm and bark beetles in Europe (Bosela et al., 2021; Krejza et al., 2021; Mezei et al., 2017; Schuldt et al., 2020). This has created huge clearings that need to be replanted in order to restore ecosystem services (Fleischer et al., 2017; Thom et al., 2022). As a result, there is an extreme shortage of planting material, which leads to an increased focus on natural regeneration processes in close-to-nature forestry on non-damaged areas.

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), introduced from

North America to Europe in the end of the 19th century (Lavender and Hermann, 2014), is being discussed as a future tree species to substitute or supplement spruce stands. Due to its growth performance and higher drought tolerance compared to Norway spruce, great importance is attached to it (Nicolescu et al., 2023; Thomas et al., 2022).

Knowledge about the regeneration ecology of Douglas-fir and, in particular, its natural regeneration potential is therefore of immense importance for silvicultural objectives. At the same time, it provides information on the ability of a non-native species to assert itself in ecosystems and spread to other areas (Delavaux et al., 2023). This is important for an assessment of invasiveness to prevent significant changes in biodiversity (Frei et al., 2022; Heinrichs et al., 2022;

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Wohlgemuth et al., 2021).

Of particular interest for these objectives is the density of established Douglas-fir regeneration. Here “established” means that the regeneration has successfully passed through the various cascades of the regeneration cycle that affects natural regeneration from flowering and pollination to seedling establishment (Fischer et al., 2016; Harper, 2010).

Let us summarise the relevant factors in that cycle. Flowering and the total number of seeds depend on the physiological age of the trees and the onset of maturity (Owens and Blake, 1985). Douglas-fir begins to flower at the age of 15 to 40 years (Allen, 1942; Malcolm et al., 2001; Savill, 2019; Silen, 1978; Vor et al., 2015). It is a monoecious tree species and the flowers are wind-pollinated (Pakull et al., 2023; Wojacki et al., 2019). Douglas-fir has varying fruiting intensity and masts irregularly, at intervals of 3 to 7 years (Roy, 1960; Silen, 1978; Spellmann et al., 2015). After successful pollination and fruiting, the cone ripens at the end of September and the winged seeds are gradually anemochorously dispersed (Jones, 1945; Lavender and Hermann, 2014; Owens and Molder, 1973). The majority of the seeds are dispersed at distances shorter than 100 m (Dick, 1955; Lavender and Hermann, 2014; Roy, 1960; Sharpe and Fields, 1982). The seeds lie on the forest floor during the subsequent storage phase and can be predated by mice or voles (Caccia and Ballaré, 1998; Strothmann and Roy, 1984). Douglas-fir seeds require preferably moist mineral soil for successful germination (Huth et al., 2011; Lange et al., 2022). Herbaceous layers or thick grass cover prevent successful germination and establishment (Barnhart et al., 1996; Broncano et al., 2005; Caccia and Ballaré, 1998; Frei et al., 2022; Knoerzer, 1999). Furthermore, a thick litter layer can inhibit the germination and establishment of Douglas-fir, if the radicle does not penetrate it (Caccia and Ballaré, 1998; Frei et al., 2022). After germination, radiation availability affects the establishment of Douglas-fir regeneration. Douglas-fir is classified as an intermediate tree species in terms of shade tolerance (Carter and Klinka, 1992; Mason et al., 2004; Niinemets and Valladares, 2006). According to its radiation ecology, many relationships between regeneration density and radiation availability have been demonstrated (Bindewald et al., 2021; Eberhard and Hasenauer, 2018; Frei et al., 2022; Lange et al., 2022).

Given a large number of seed sources with different seed yields and a variety of ecological conditions affecting regeneration density, it is difficult to quantify the effective dispersal resulting from seed dispersal and establishment (Bindewald et al., 2021; Thomas et al., 2022). There are several studies that have investigated correlations between distance to seed trees and established Douglas-fir regeneration (Barnhart et al., 1996; Bindewald et al., 2021; Eggert, 2014; Lange et al., 2022; Nuñez and Paritsis, 2018; Sankey, 2007). The observed dispersal distances of established regeneration were mostly less than 85 to 100 m (Lange et al., 2022; Sankey, 2007; van Loo et al., 2019), although maximum distances of 200 to 350 m have been observed (Eggert, 2014; Sankey, 2007). But there is still no general dispersal curve quantifying the influence of the distance from the seed source on the regeneration density of Douglas-fir (Wohlgemuth et al., 2019).

Therefore, the present study introduces methods for estimating the functional dependence of the potential density of established Douglas-fir regeneration on the distance to the seed source. This is based on various classical spatial dispersal kernels, and, as in Axer et al. (2021), considers the nearest potential seed source, which can be determined from remote-sensing data. A quantile regression approach (Koenker, 2005; Koenker and Bassett, 1978) is used to account for ecological conditions that reduce the regeneration density. All procedures are implemented in an R package *quaxnat* that has been developed in conjunction with this article and is provided on the CRAN repository <https://cran.r-project.org/web/packages/quaxnat/index.html>.

The methods are applied to inventory data from the state forest of Lower Saxony. Based on the results, the potential of natural Douglas-fir regeneration density can be spatially estimated. These regeneration density estimates can be used for spatial simulation of regeneration

numbers under different silvicultural scenarios. The resulting predictions can guide spatial decisions on forest conversion activities at the forest management level. At the same time, buffers can be identified around sensitive habitats where the dispersal of Douglas-fir should be prevented for nature conservation reasons.

The specific goals the study are the following:

- To develop a method for estimating the potential density of Douglas-fir natural regeneration as a function of distance to the seed source, based on classical spatial dispersal kernels.
- To implement this method in an accessible R package (*quaxnat*) that allows forest managers and ecologists to estimate Douglas-fir regeneration potential.
- To apply the developed method to inventory data from the state forest of Lower Saxony, generating spatially explicit estimates of the Douglas-fir regeneration potential that can guide forest management and conservation activities.

2. Material and methods

2.1. Study area & forest inventory

The study area consists of the federal state of Lower Saxony, Germany. For the state-owned forest in this area, a sample-based forest inventory was available (Fig. 1) (Niedersächsisches Forstplanungsamt, 2023). The inventory employs a two-phase sampling procedure. The sample plots are positioned in the rectangular grid. In the first phase, plots are allocated to different strata according to age and tree species. Based on this, an optimization procedure selects a subset of the sample, which will be visited during the second phase and recorded terrestrially (Böckmann et al., 1998; Saborowski et al., 2010). A total of 44,257 sample plots were selected for the terrestrial survey. The terrestrial recording was carried out in the period between 2009 and 2019. The sample plots cover a wide range of sites from the North Sea coast to the low mountain ranges in the Harz and Solling, reaching up to 971 m above sea level. The mean annual temperature varies between 5 and 9.2 °C while mean annual precipitation ranges between 546 and 1,343 mm (Gauer and Kroiher, 2012).

On the sample plots, the characteristics of the overstorey including trees ≥ 7 cm diameter at breast height (dbh) were recorded in concentric sampling plots with 6 and 13 m radius. The regeneration is recorded in the centre of the sample plot on a regeneration sampling plot with 3 m radius. The number of trees is recorded separately according to artificial (i.e. sowing or planting) and natural regeneration, tree species and size class. Size class *B0* comprises regeneration up to 50 cm in height. Height class *B1* ranges from 50 to 130 cm, while size class *B2* includes regeneration up to 7 cm dbh. The maximum number that was counted per tree species and size class is 30, i.e. the data was truncated at 30.

For the present study the density of established Douglas-fir natural regeneration of size class *B0* was used as an independent variable and is varying across the study area (Fig. 1). Douglas-fir regeneration of size class *B0* was observed on a total of 1,546 sample plots.

2.2. Distance to the nearest potential seed source

A remote sensing-based data-set was used to determine the position of possible Douglas-fir seed trees (Fig. 1). The tree species detection was based on the spectral-temporal reflectance signature in the Sentinel satellite imagery (Blickensdörfer et al., 2024, 2022).

The resulting map provides information on the canopy dominating tree species at a spatial resolution of 10 m for the stocked forest area as defined by Langner et al. (2022). The mapped tree species distribution refers to the years 2017/2018, as satellite imagery of this time period was used for the analysis.

To map the dominant tree species throughout Germany, Blickensdörfer et al. (2022) derived cloud free time series data with 5-day

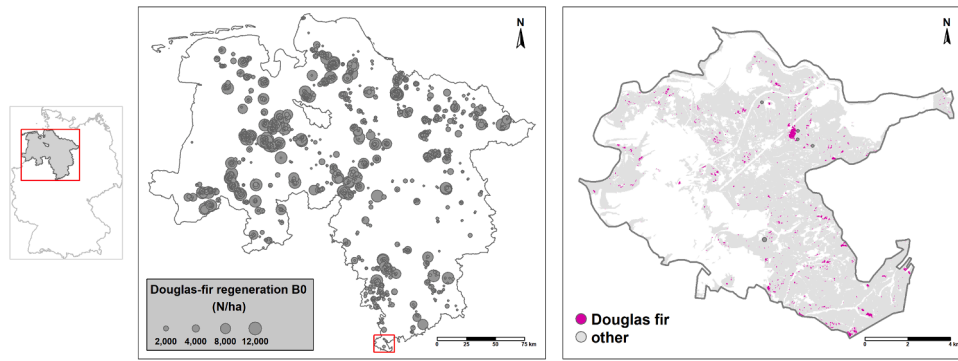


Fig. 1. Study area with the location of sample plots with existing Douglas-fir regeneration in size class B0 (< 50 cm height) (left). The size of the circle reflects the regeneration density. Inventory plots without Douglas-fir regeneration are not shown. The inset map shows remote sensing-based tree species detection for the southernmost area of the study area with the detection of Douglas-fir (right). Forest area with other tree species is shown in grey.

intervals from optical Sentinel-2 imagery and combined those with monthly Sentinel-1 radar backscatter composites. This time series captures species specific spectral signatures and phenology and is used as input to a machine learning classifier to predict the species distribution. As the mapping was performed over a larger area, information on topography, meteorology, and climate was included to account for environmental gradients in Germany. National forest inventory data was used to train the classification model and to estimate the map accuracy at the national level. For a comprehensive description of the methods and data we refer to [Blickensdörfer et al. \(2024\)](#).

The overall accuracy of the map with a total of eleven species groups is estimated at 75.53 ± 0.07 %. Producer's and user's accuracy were used to estimate the accuracy of the map with regard to specific tree species classes. The producer's accuracy is the number of correctly classified samples of class x divided by the number of samples of class x , and user's accuracy is number of correctly classified samples of class x divided by the number of samples classified as class x ([Congalton, 1991](#)). The producer's and user's accuracy of Douglas-fir is estimated at 86.10 ± 2.63 % and 37.07 ± 1.33 % for homogeneous single species forest stands, and at 63.21 ± 0.57 % and 39.46 ± 0.35 % for heterogeneous mixed species forest stands. As locations for potential seed trees, pixels were considered for which Douglas-fir was classified as dominant species.

The distance to the nearest Douglas-fir in the overstorey was determined for all 44,257 inventory sample plots. The geographic distance was computed using the coordinates of both the position of potential seed trees and the sample plots. For this purpose, the function *distance* from the R package *terra* was used ([Hijmans, 2022](#)). By using the distance to the nearest Douglas-fir, no overlapping effects of neighbouring Douglas-firs were taken into account.

2.3. Statistical analysis with the R package *quaxnat*

Regeneration datasets, especially of rare tree species, often contain a large number of zeros ([Welsh et al., 1996](#)). In our case, only 3.5 % of the sample plots (1546) include Douglas-fir regeneration with the height ≤ 50 cm. As the variety of factors which influence or prevent regeneration is not quantifiable, a quantile regression approach was performed following Axer et al. (2021). By this method, the effect of the distance to the nearest seed source on Douglas-fir regeneration density is quantified. The procedures were implemented, with a vastly improved algorithm, in the R package *quaxnat* that has been made available in the CRAN repository (<https://doi.org/10.32614/CRAN.package.quaxnat>). The theoretical details are as follows. Using the *quax* function from *quaxnat*, the parameters N and θ of a spatial dispersal kernel Nk_θ describing regeneration potential as the τ th quantile of regeneration density are estimated. For interpretation, note that this represents the median regeneration potential if the regeneration at a given site realizes its

potential with probability $\alpha = 2(1 - \tau)$ and is otherwise below the median. Here N is the total number of seeds of a tree available for reproduction and k_θ , with a parameter vector θ , is the spatial probability density of the offset of the location of a seed from its source. Let y_1, \dots, y_n be the densities observed at locations x_1, \dots, x_n relative to the seed source. Following the standard approach in quantile regression ([Koenker, 2005](#); [Koenker and Bassett, 1978](#)), we then estimate the parameters by minimizing the expression

$$\sum_{i=1}^n w_i \times (y_i - Nk_\theta(x_i)) \times \begin{cases} \tau & \text{if } y_i > Nk_\theta(x_i) \\ \tau - 1 & \text{if not} \end{cases}$$

in N and θ , where the numbers w_i are optional weights. In our application we choose $w_i = \frac{1}{100 + \|x_i\|}$, which means the weight assigned to observation y_i decreases with the distance $\|x_i\|$ from the seed source, reaching half its maximum value at a distance of 100 m, which is of order of ecologically relevant dispersal distances for Douglas firs (cf. discussion in [Section 4.1](#) below). This weighting is done in order to reduce the influence of unrealistically large distances, which can otherwise cause problems in the analysis. For k_θ we consider various isotropic kernels as defined in [Table 1](#).

A quality criterion for the goodness of fit to the data and for comparing different spatial kernels is the value obtained for the weighted sum of residuals that is minimised in the quantile regression. This can be retrieved with the *summary.quax* function. A description of the complete R code of the computations underlying [Fig. 3](#) is included and explained in [Appendix A](#).

2.4. Predicting established regeneration

Planning and assessing silvicultural responses to transformation would greatly benefit from predictions of future established regeneration for relevant scenarios. Applying the function derived in [Section 2.3](#) to spatial data on the distance to the nearest seed source provides a map of the estimated regeneration density that can, in principle, be used for simulating established regeneration numbers.

As such predictions are not the focus of the present study and would deserve their own investigation, we here only include a very simple illustration of such a simulation model. The model assumes independent regeneration numbers with negative binomial distributions in the $10 \text{ m} \times 10 \text{ m}$ cells. The negative binomial distribution is a standard model for count data and can be thought of as a Poisson distribution whose parameter is itself drawn from a gamma distribution.

The precise mathematical specification of the model, a Cox process directed by a locally scaled stationary gamma random measure ([Daley and Vere-Jones, 2003](#), Ch. 6), is as follows. We consider a stationary gamma random measure with a per hectare shape parameter fixed throughout the model and a scale parameter, the value of which is not

Table 1

Spatial dispersal kernels and corresponding probability density functions of the distance of a seed from its source. Here $\|x\|$ denotes the Euclidean norm and the normalizing constants involve the beta and gamma functions. The parameters a and b are positive numbers. In the present study the spatial dimension d always equals 2.

	Spatial kernel	Probability density of distance
Spatial t distribution Clark et al. (1999), Austerlitz et al. (2004)	$k(x) = \frac{\Gamma((b+d)/2)}{\pi^{d/2} a^d \Gamma(b/2)} \left(1 + \frac{\ x\ ^2}{a^2}\right)^{-(b+d)/2}$	$p(r) = \frac{2}{a^d \text{B}(d/2, b/2)} r^{d-1} \left(1 + \frac{r^2}{a^2}\right)^{-(b+d)/2}$
Weibull distance Tufto et al. (1997)	$k(x) = \frac{b\Gamma(d/2)}{2\pi^{d/2} a^d} \ x\ ^{b-d} e^{-(\ x\ /a)^b}$	$p(r) = \frac{b}{a^d} r^{b-1} e^{-(r/a)^b}$
Lognormal distance Greene and Johnson (1989) Stoyan and Wagner (2001)	$k(x) = \frac{\Gamma(d/2)}{2\pi^{d/2}} e^{-\frac{1}{2b}(\log(\ x\ /a))^2} \ x\ ^{d-2}$	$p(r) = \frac{1}{r\sqrt{2\pi b}} e^{-\frac{1}{2b}(\log(r/a))^2}$
Power Nathan et al. (2012)	$k(x) = \frac{\Gamma(d/2)}{2\pi^{d/2} a^d \text{B}(d, b)} \left(1 + \frac{\ x\ }{a}\right)^{-(b+d)}$	$p(r) = \frac{1}{a^d \text{B}(d, b)} r^{d-1} \left(1 + \frac{r}{a}\right)^{-(b+d)}$
Exponential power Bateman (1947), Clark et al. (1998), Austerlitz et al. (2004), Nathan et al. (2012)	$k(x) = \frac{b\Gamma(d/2)}{2\pi^{d/2} a^d \Gamma(d/b)} e^{-(\ x\ /a)^b}$	$p(r) = \frac{b}{a^d \Gamma(d/b)} r^{d-1} e^{-(r/a)^b}$

essential. Thus, for all measurable subsets of the two-dimensional plane we have gamma distributed random variables, independent for disjoint subsets, with shape parameters proportional to the area of the subset and the same scale parameter. By multiplying the random measure by a factor, which can be seen as a change of the scale parameter, we can arrange that the r th quantile of the gamma distribution in subsets of the same area as the original sampling plots ($= 28.27 \text{ m}^2$) reproduces any desired value. Now, here we apply this scaling only locally within each $10 \text{ m} \times 10 \text{ m}$ cell so as to fit the r th quantiles obtained in the estimation. The resulting locally scaled random measure defines the intensity measure of a Poisson point process that represents the regeneration.

The regeneration numbers in the cells, which are then independent and have negative binomial distributions with parameters determined by those of the respective gamma distributions, are those that we realize in the simulation. Note that the choice of local scaling, or a variable scale parameter, instead of an inhomogeneous shape parameter implies that the regeneration numbers in several cells combined do not typically have negative binomial distributions. This is better suited to the quantile fitting. It means that the negative binomial distributions in all cells belong to the same exponential family, which is also a common choice in negative binomial regression (i.e. with the variance increasing as a quadratic function of the mean). Different scenarios can then be simulated by adjusting the per hectare shape parameter. If set to ∞ , the model is just a Poisson process, with variances equal to the expectations, whereas smaller parameter values imply variances larger than the expectation and, in this respect, more heterogeneity.

3. Results

3.1. Distance to the nearest Douglas-fir

According to the distribution of Douglas-firs in the study area, the mean distance between the 42,711 sample plots and the nearest potential seed trees is 230.67 m. The maximum distance is 3,183 m.

The distances to the nearest seed trees on the 1546 sample plots with existing Douglas-fir regeneration differ from the overall distribution. The mean distance to the nearest Douglas-fir is 51.6 m. There are 775 of the 1,546 sample plots with established Douglas-fir regeneration at distances of up to 20 m to the nearest Douglas-fir. Around 1,451 sample plots are located in distances of up to 300 m to the nearest seed source. However, there were also 55 observed dispersal events in Douglas-fir farther than 300 m in distance. This is shown in Fig. 2, which, for comparison, also includes the corresponding distances for larch regeneration (see also Section 4.1).

3.2. Modelling potential Douglas-fir regeneration density

The highest observed regeneration densities are found at distances

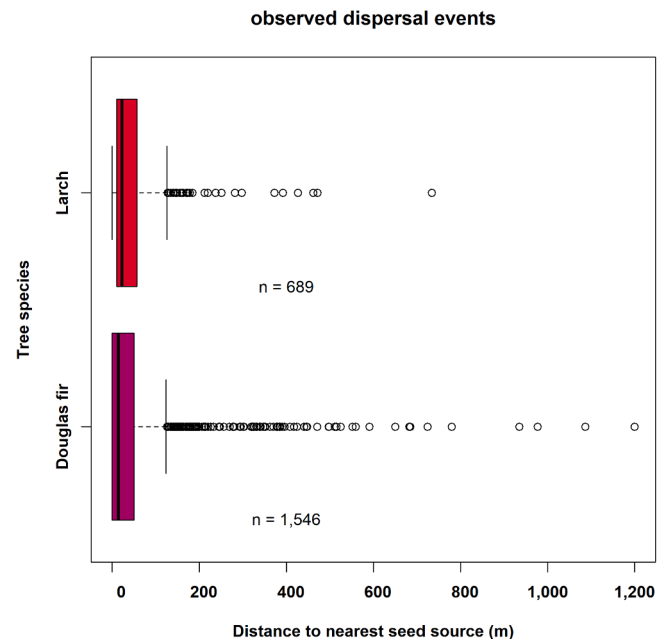


Fig. 2. Observed regeneration occurrence of Larch and Douglas fir according to the distance to the nearest species-specific seed source.

between 0 and 50 m to the nearest Douglas fir seed tree (Fig. 3). With increasing distance, the observed regeneration densities decrease. Especially at long distances $> 500 \text{ m}$, only very low regeneration densities are observed.

The quantile regression by the *quax* function reflects the highly nonlinear relationships between potential Douglas-fir regeneration density and distance to the nearest seed source. A comparison of different dispersal functions makes sense only for a given quantile, the choice of which depends on the particular application and on the interpretation with regard to the regeneration potential (see Section 2.3). The following results are based on the .999th quantile regression, which in our judgement showed the most appropriate visual fit to the data estimating potential Douglas-fir regeneration density.

The comparison of different dispersal functions for calculating the Douglas-fir regeneration potential shows that the spatial t distribution achieves the best fit (Fig. 3). The quality criterion introduced above (see Section 2.3), i.e. the value that is minimised in the quantile regression, is lowest for the t distribution function (Table 2). Along with the t distribution function, the power function and also the exponential power function show a reasonable fit of the regeneration potential, but

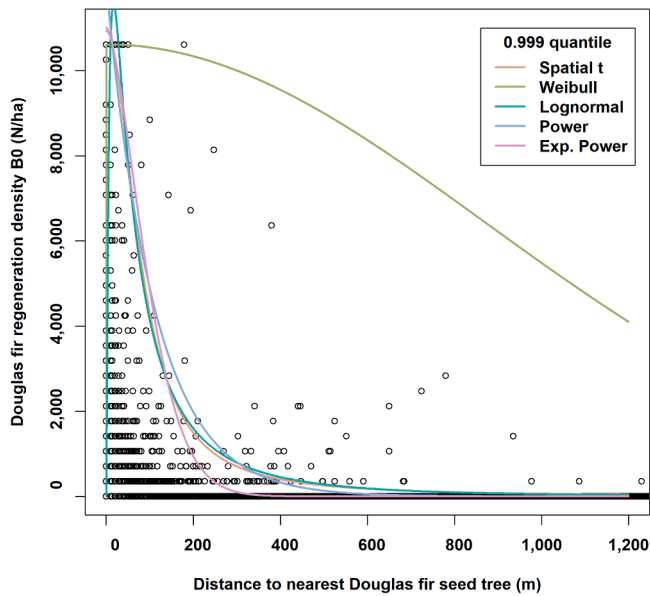


Fig. 3. Potential Douglas-fir regeneration density depending on the distance to the nearest Douglas-fir seed tree. Quantile regression estimates for the .999th quantile are shown for different dispersal functions implemented in *quaxnat*.

Table 2

Regression coefficients of non-linear quantile regression for the .999th quantile. Different probability density functions implemented in the *quaxnat* package were tested.

Function	a	b	quality criterion
Spatial t distribution	83.33	0.083	1760.66
Weibull	1230.42	2	14,952.43
Lognormal	371.50	1.548	14,476.35
Power	3455,255.68	31,184.84	1822.54
Exponential power	113.38	1.586	1801.10

especially at short distances, both of these do not perform as well as the *t distribution* function (Fig. 3). The *Weibull* and *lognormal* functions demonstrate the lowest goodness of fit (Table 2).

The spatial *t distribution* function is therefore used for further calculations. The highest Douglas-fir regeneration density is predicted in immediate proximity to the nearest seed tree (Fig. 3). The predicted regeneration density here is almost 11,000 plants per hectare. After that

point, the potential regeneration density decreases sharply with increasing distance. At a distance of 100 m, 4,300 Douglas-firs per hectare are predicted. At a distance of 250 m, the regeneration density is only approximately 1,000 per hectare. At 450 m, only 314 plants per hectare are predicted, then approaching a density of 0 at further distances.

3.3. Prediction of established regeneration

Based on calculated distance maps to nearest seed trees, the *predict-quax* function provides spatial estimates of the regeneration potential (Fig. 4). Especially in the proximity of seed trees and areas with a high number of Douglas-firs, high potential regeneration densities are predicted. At the same time, there are areas where no Douglas-fir regeneration is predicted due to too high dispersal distances.

Fig. 5 presents simulation results for the expository model introduced in Section 2.4, providing a simple illustration of how silvicultural responses to transformation can be assessed. At each point, the number of individuals follows a negative binomial distribution determined by the estimated regeneration density and a parameter representing the specific scenario in this simplified model. A high parameter value means the regeneration is close to the full regeneration potential, while lower values imply more heterogeneous patterns with less regeneration.

4. Discussion

4.1. Distance to the nearest potential seed tree

We first discuss the issues arising from the use of remote sensing data. When interpreting the observed dispersal distances, the temporal congruence and the classification accuracy of tree species detection must be taken into account. In terms of temporal congruence between the terrestrial surveys on the sample points and the remote sensing data, there is a good match as remote sensing data (2017/2018) refers to the last years of potential terrestrial data acquisition (2019). However, it must be noted that the terrestrial data and the remote sensing data always have a reporting date that represents a specific situation. With regard to the classification quality, a distinction must be made between producer's and user's accuracy as defined in Section 2.2 (Congalton, 1991). A high producer's accuracy of 86 % for the tree species Douglas-fir means that in 86 % of the cases an existing Douglas-fir is also classified as Douglas-fir within the map. This means that existing seed trees were recorded with a high probability and are included for the analysis.

A low user's accuracy means that there is only a probability of 37 %

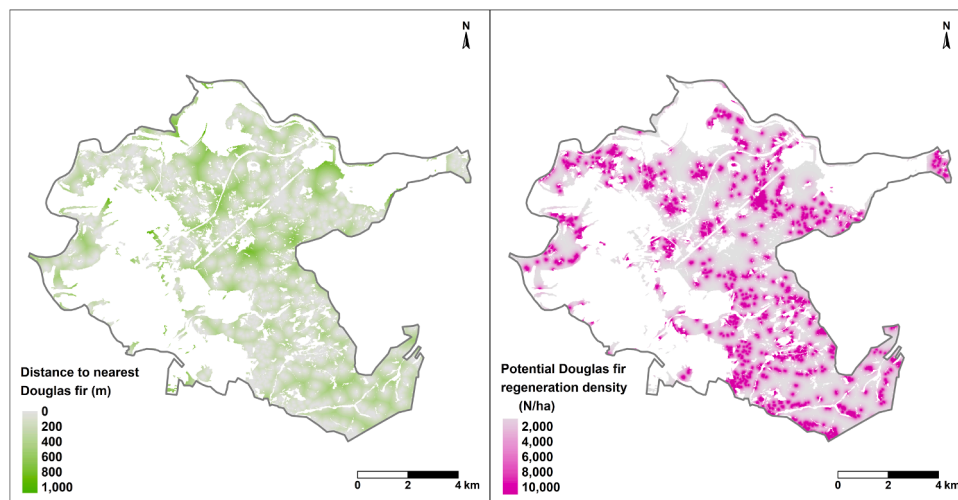


Fig. 4. Distance to the nearest Douglas fir and spatial prediction for a part of the study area using the results of the quantile regression for the spatial *t distribution*.

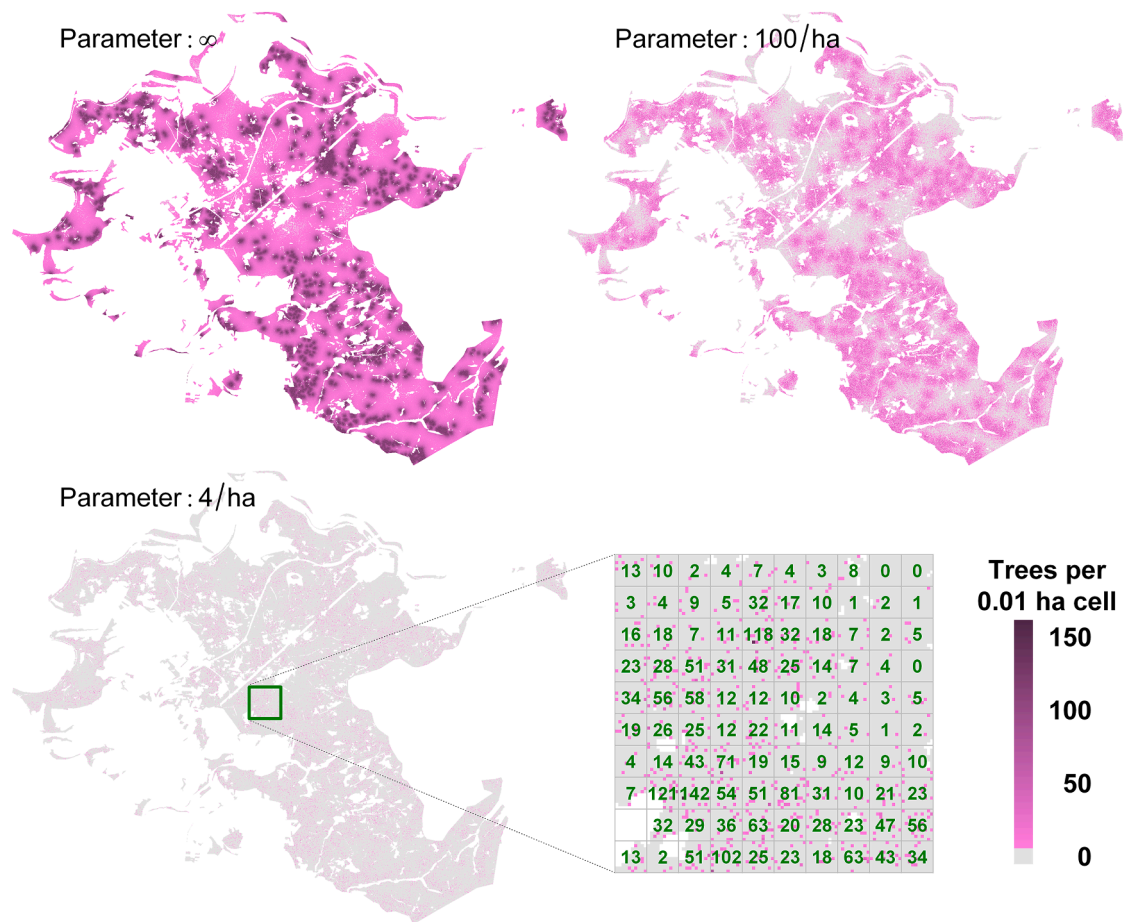


Fig. 5. Simulated Douglas-fir regeneration patterns for three hypothetical scenarios. In the first pattern the regeneration numbers follow Poisson distributions while the other two patterns represent more heterogeneity and smaller regeneration numbers. Regeneration numbers in 10-by-10-cell hectare squares are shown for a detail of the last pattern.

that pixels classified as Douglas-fir in the map are actually Douglas-fir. This means that Douglas-fir proportions in the study area are over-estimated, since some spruces and pines were classified as Douglas-fir. In general, this means that estimated dispersal distances to the nearest seed trees within the study area are lower. It is to be expected, however, that the user’s accuracy is higher at locations in the sampling plot where Douglas fir natural regeneration occurs, and that the dispersal distances are not strongly underestimated due to misclassification.

The observed dispersal distances are in accordance with the findings in literature. Our results are derived from the forest inventory in Lower Saxony with 44,257 plots. Notably, 50 % of plots with Douglas-fir regeneration are found within 14 m of the nearest seed tree. (Fig. 2), which is related to a low seed dispersal distance. This result is in accordance with Gashwiler (1969), who estimate that 61 % of the seeds are deposited within 15 to 30 m to the Douglas-fir. Furthermore, about 39 % of the seeds are transported 60 to 121 m. Similar results were observed by Boe (1953), who observed a sharp decrease in seed density up to 80 m distance. According to the anemochorous dispersal of Douglas-fir seeds, this can be explained by seed weight and average wind speeds (Siggins, 1933). Simulations by Sharpe and Fields (1982) confirm this relationship for Douglas-fir seed dispersal and also consider tree height, which has a decisive effect on dispersal distance. The results for seed dispersal of 30.5 m tall Douglas-fir at different wind speeds are consistent with the above mentioned observed dispersal distances (Sharpe and Fields, 1982).

Besides the mean dispersal distances of Douglas fir, the maximum distances are of particular ecological interest. The maximum dispersal distance of seeds was observed by Boe (1953) at 241 m. Maximum seed

dispersal events are simulated at 200 m (Sharpe and Fields, 1982), which is in line with the observed distances of Douglas-fir seedlings within the study area (Fig. 2). Compared to other native coniferous species such as Scots pine, Norway spruce and European larch, Douglas-fir has a thousand grain weight that is 2 to 4 g higher (Burkart, 2018; Rohmeder, 1972). The comparison of observed dispersal distances of European larch indicates the described effect of different seed weights (Fig. 2).

We conclude that the remote sensing data provide spatially explicit information on the dispersal distances of Douglas-fir regeneration that is in line with previous studies. Despite uncertainties in tree species classification, the existing dataset can be used to identify areas where Douglas-fir cannot establish itself due to lack of seed trees. In the future, the incorporation of recent advances in remote sensing or modelling techniques may contribute to a more refined analysis. Previous studies showed similar accuracies for Douglas-fir (Hologu et al., 2021; Karasiak et al., 2017; Welle et al., 2022). They attribute the low sample size to this accuracy. The aim should be to achieve the same accuracy for Douglas-fir as for the main tree species (Blickensdörfer et al., 2022). Studies from the Netherlands showed higher accuracies and are promising (Plakman et al., 2020).

4.2. Douglas-fir regeneration potential

From the previous discussion on seed dispersal, it is difficult to accurately predict the distribution of seeds from a given seed tree in a given year due to the varying seed fall velocities and the varying heights at which seeds are produced, as well as the direction and speed of the

wind that disperses those seeds. With 3.5 % of the plots showing Douglas-fir regeneration, it appears that Douglas-fir is regenerating naturally. However, the proportion of Douglas-fir regeneration appears to be very low and there are many plots without Douglas-fir regeneration (Axer et al., 2021).

Within the same dispersal distances there is a large variation in regeneration densities (Fig. 3). This suggests that there are other influencing factors that reduce or even prevent Douglas-fir regeneration density. According to Caccia and Ballaré (1998), losses of 70–96 % can occur during seed storage on the forest floor by seed predation. Furthermore, it is known that soil moisture affects germination (Huth et al., 2011). In addition, former studies have shown that a humus layer affects seedling emergence (Caccia and Ballaré, 1998) and thus also has a negative effect on the density of established regeneration (Frei et al., 2022). As an additional factor influencing the regeneration density of Douglas-fir, radiation availability has been identified (Bindewald et al., 2021; Carter and Klinka, 1992; Frei et al., 2022; Lange et al., 2022; Mason et al., 2004; Petritan et al., 2010). Because of their low light availability and leaf litter, beech stands in particular seem less suitable for the establishment of Douglas-fir regeneration (Bindewald et al., 2021; Frei et al., 2022; Lange et al., 2022). However, browsing appears to have only a minor impact on the regeneration density of Douglas-fir (Frei et al., 2022).

Because of these numerous influencing factors, in this study a quantile regression approach for the dispersal of established Douglas-fir regeneration was applied for the first time, i.e., effective dispersal was quantified. The density of established regeneration is the result of several dispersal events as well as further ecological processes such as seed storage, germination, and establishment (Fischer et al., 2016). We interpret the highest seedling densities as a proxy for the potential of the species in the given environment. Due to the numerous influencing factors that reduce or even prevent regeneration density, a high quantile seems justified to elucidate the impact of the distance to the nearest seed source on regeneration density (Axer et al., 2021). The use of the .999th quantile avoids a possible underestimation of the realised dispersal distances. In addition, the use of the .999th quantile also counteracts potential underestimation of the realised dispersal distances estimated from the remote sensing data.

As previous studies have also shown, there is a relationship to existing seed trees for Douglas-fir regeneration (Barnhart et al., 1996; Frei et al., 2022; Knoerzer, 1999; Lange et al., 2022; Nuñez and Paritsis, 2018; Simard et al., 2021). For the regeneration potential of Douglas-fir, this study also demonstrated a strong influence of distance on regeneration density (Fig. 3). The dispersal kernels that resulted in the best fit in the quantile regression (Table 2: spatial *t* distribution, power, exponential-power) have in common that they reach their maximum at zero (Clark et al., 1999; Nathan et al., 2012; Ribbens et al., 1994). Furthermore, these functions show a fat-tailed distribution and are therefore suitable for modelling Douglas-fir dispersal (Bullock et al., 2017; Kot et al., 1996). Previous investigations by Clark et al. (2005) confirm our finding that especially the spatial *t* distribution best describe the anemochorous species. The Weibull and lognormal function show the worst fit for the data (Table 2). This can be explained by the fact that these two kernels are not able to adequately describe densities at distance 0 m that are not zero (Austerlitz et al., 2004; Nathan et al., 2012).

Highest regeneration densities in close proximity to the seed trees can be attributed to high seed densities in close proximity to the seed trees. This is in accordance with Simard et al. (2021) who also observed the highest regeneration densities within 10 m to the nearest Douglas-fir seed trees. Regeneration densities of 15,000 N/ha in direct seed tree proximity were observed by Nuñez and Paritsis (2018), which are close to the maximum regeneration densities of our study. The influence of seed quantity on the regeneration density of Douglas-fir regeneration was also demonstrated in seeding field observations (von Lüpke and Sennhenn-Reulen, 2023). In addition to the seed density-distance relationship the effect of seed quality may also influence the density of

established Douglas-fir regeneration. There are contradictory findings in literature as to whether non-viable seeds are more widely dispersed than viable seeds (Roy, 1960; Siggins, 1933).

From inventory studies, Bindewald et al. (2021) was able to determine that lower regeneration densities can be observed on sampling plots without Douglas-fir seed trees than on sampling plots with seed trees. Without seed trees, densities of up to 5,000 trees per hectare were observed, but the actual distance to neighbouring seed trees is missing here. A strong decrease in regeneration density at approximately 100 m to 2,500 N/ha was observed in recent studies (Lange et al., 2022; Nuñez and Paritsis, 2018). This sharp decrease in regeneration density is in accordance with the findings mentioned above (Fig. 3). Eggert (2014) was able to show that Douglas-fir regeneration above 200 m is rare and at low densities. For their regeneration models, Frei et al. (2022) found that distance from Douglas-fir seed trees had a negative effect on the occurrence of Douglas-fir regeneration, but not on regeneration density, as regeneration density at greater distances is probably very low. Low regeneration densities of 1,000 trees per ha at 250 m in our study's results are in accordance with these previous studies. This result is in line with the observed maximum seed dispersal distances up to 241 m (Boe, 1953).

The uncertainty in the remote sensing-based data set, which provides the information on Douglas-fir seed trees, has also an effect on the spatial prediction of regeneration potential. While the realised dispersal distances in the model are in line with literature and the regeneration density in relation to a seed tree can be expected to be accurate, the number of seed trees is overestimated due to the low producer's accuracy of the Douglas-fir class in the map. This might translate to an overprediction in regeneration potential within the study area (Fig. 4). Such error rates for minor species remains as a challenge in remote sensing tree species mapping approaches and needs further research (Blickensdörfer et al., 2024; Hemmerling et al., 2021; Hermosilla et al., 2022). To date, such data are the only source for wall-to-wall tree species information that enable such analysis.

In the light of the previous discussion and our results, the dispersal potential of Douglas-fir is not considered high, which is also confirmed by the most recent assessments by Vor et al. (2015), Bindewald et al. (2021) and Lange et al. (2022). The maximum regeneration densities estimated by the quantile regression are an indicator of the potential of the Douglas-fir in the given environment.

4.3. Simulation of silvicultural scenarios

The estimated regeneration densities can be combined with models representing the effects of specific silvicultural measures to simulate regeneration patterns at the level of cells or even individual trees. Among the myriad of models that could in principle be feasible, perhaps the simplest one is a model that assumes independent tree numbers following negative binomial distributions, that is, gamma mixtures of Poisson distributions, where the parameters of the gamma mixing distribution can be adjusted to reflect both the estimated density and the scenario. The choice of the shape parameter of the gamma distribution for the scenario can reveal significant differences in the simulated density of established regeneration (Fig. 5). A lower shape parameter might indicate unfavourable conditions affecting the growth and establishment of young Douglas-firs (Heinrichs et al., 2022; Malmqvist et al., 2018). In contrast, a higher parameter might suggest regeneration under more favourable conditions like silvicultural treatments reducing canopy cover or soil preparation measures creating suitable microsites for regeneration establishment (Bindewald et al., 2021; Frei et al., 2022; Nicolescu et al., 2023). The influence of different silvicultural management techniques on established regeneration thus becomes visible. Of course, this is still a very simple model, and silvicultural practice will likely require more advanced models for representing more realistic scenarios.

5. Conclusions for nature conservation & silviculture

The R package *quaxnat* offers the possibility to utilize large-scale remote sensing data and regeneration data from the forest inventory and thus derive management strategies for forestry operations. Furthermore, considering various silvicultural scenarios allows for a practical evaluation of different management approaches. These could include different harvesting intensities, management objectives, or the application of various forestry methods.

From a silvicultural point of view, areas can be identified where natural regeneration potential of Douglas-fir is an option. The natural regeneration potential can be built upon by certain silvicultural measures such as light management or soil cultivation. This means that cost-intensive artificial regeneration can be avoided by utilizing natural regeneration.

Based on the results, it is also possible to derive recommendations regarding a buffer zone around sensitive habitats, such as particularly endangered forest communities. The limited dispersal potential over long distances and the difficulty of successful establishment in different environments act as natural barriers to Douglas fir invasiveness. This means that Douglas-fir is not necessarily considered an invasive species, at least in most of the habitats into which it has been introduced.

Future research should focus on understanding in more detail the complex interactions between Douglas-fir dispersal and various environmental factors influencing its establishment to make more accurate predictions about successful Douglas-fir regeneration.

Appendix A. Estimating the regeneration potential with the R package *quaxnat*

The methods developed in Axer et al. (2021) were significantly enhanced and implemented in the R package *quaxnat*, available at <https://doi.org/10.32614/CRAN.package.quaxnat>. The function *quax* we provide in that R package is a simple implementation of the quantile estimation described in Section 2.3. It presents a straightforward approach to quantile regression and, while likely outperformed by more sophisticated procedures such as those in the R package *quantreg* (Koenker, 2024) in general quantile regression problems, appears to work reasonably well for scaled dispersal kernels such as those considered in this study (see Appendix A in Axer et al., 2021). This Appendix illustrates the use of the *quax* function with step-by-step explanations of the computation underlying the results in Section 3.

```
# Load and check data (requires R package sf) :
#filename <- file.choose() # Get file path of VJ_pot.gpkg.
VJ_pot <- sf::st_read(filename)
str(VJ_pot)
```

This loads the data from the GeoPackage file *VJ_pot.gpkg* using the function *st_read* from the R package *sf* (Pebesma and Bivand, 2023). The function *file.choose* can be of help to find the file path.

```
# Transform Douglas-fir regeneration density in the B0 layer
# to numbers per ha:
VJ_pot$Dgl_B0_ha <- VJ_pot$Dgl_B0 * 10000 / (3^2*pi)
```

This converts the regeneration densities, which *VJ_pot.gpkg* provides as numbers recorded in the circular regeneration sampling plots with a radius of 3 m (see Section 2.1), to numbers per hectare.

```
# Load quaxnat package:
library(quaxnat)
```

After loading the *quaxnat* package, we are now ready to apply the *quax* function, which we do for the .999th quantile, five dispersal kernels implemented in *quaxnat* and the weights defined in Section 2.1.

```
# Estimate regeneration potential based on various dispersal kernels:
tau <- 0.999
f1 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau,
fun=k_t, weights=1/(100+distance_dgl))
f2 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau,
fun=k_weibull, weights=1/(100+distance_dgl))
f3 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau,
fun=k_lognormal, weights=1/(100+distance_dgl))
f4 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau,
fun=k_power, weights=1/(100+distance_dgl))
f5 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau,
fun=k_exponential_power, weights=1/(100+distance_dgl))
f <- list(`Spatial t`=f1, Weibull=f2, Lognormal=f3, Power=f4,
```

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CRediT authorship contribution statement

Maximilian Axer: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robert Schlicht:** Writing – review & editing, Validation, Software, Methodology, Formal analysis, Conceptualization. **Lukas Blickensdörfer:** Writing – review & editing, Methodology, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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```
`Exp. Power`=f5)
```

Note that we here see a large number of warning messages for `k_weibull`. These are due to the fact that the given data contains distance values `distance_dgl` equal to 0, where all Weibull kernels with a parameter $b < d$ provide a fit for which the criterion to be minimized (see Section 2.3) is infinite.

```
# Plot regeneration density as a function of the distance to
# the nearest seed tree:
plot(Dgl_B0_ha ~ distance_dgl, VJ_pot, xlim=c(0,1200), cex=.8)
```

This generates a simple scatter plot of the regeneration densities as a function of the distance.

```
# Pick some colors:
col <- hcl.colors(length(f), palette="Dynamic")
```

We are now ready to add the estimated functions to the plot. Since `quax` directly returns those functions, this is conveniently done with the `curve` function.

```
# Add estimated functions to diagram:
for (i in seq_along(f))
  curve(f[[i]](x), add=TRUE, n=10000, col=col[i], lwd=2)
```

We increased the number of sample points to 10000 in order to obtain a more accurate representation of the curve, especially at distances close to 0.

```
# Add legend:
legend("topright", title=paste0(tau, " quantile"),
  legend=names(f), lty=1, lwd=2, col=col)
```

For the `quax` objects returned by the `quax` function, `summary` outputs the estimated coefficients and the attained value of the objective function. The latter can be used to compare fits of different dispersal kernels for the same quantile to the same data.

```
# Compare quality of fits:
sapply(f, summary)
```

We see that `k_weibull` provides the worst fit for our data, closely followed `k_lognormal`. This can be explained by the inability of these two kernels to adequately describe nonzero densities at distance 0 (except in the case $b = d$ for `k_weibull`).

```
# Try computation for k_t without weights:
f1_w1 <- quax(Dgl_B0_ha ~ distance_dgl, VJ_pot, tau=tau, fun=k_t)
coef(summary(f1_w1))
```

Without the weighting, `k_t` fails to describe the data, as the degrees of freedom parameter b approaches 0. In fact, b would here become negative if we were to modify the kernel so as to admit such values, but such a kernel would no longer present a probability density and hence be ecologically meaningless.

```
# Simulate regeneration numbers for scenario with parameter 5/ha:
plotsize <- (3^2*pi)/10000
shape <- plotsize * 5
mu <- plotsize * f1(VJ_pot$distance_dgl) *
  shape / qgamma(tau, shape=shape)
sim <- rnbinom(length(mu), mu=mu, size=shape)
plot(sim ~ distance_dgl, VJ_pot, cex=.8)
```

This simulation, which presents the model underlying Figure 5, generates regeneration numbers in individual sampling plots from distance information. We here used the fact that the τ th quantile of the gamma distribution with mean μ and shape parameter s equals μ/s times the τ th quantile of the gamma distribution with shape parameter s and scale parameter 1.

Data availability

The authors do not have permission to share data.

References

- Allen, G.S., 1942. Douglas fir seed from young trees. *J. For.* 40, 722–723. <https://doi.org/10.1093/jof/40.9.722>.
- Austerlitz, F., Dick, C.W., Dutech, C., Klein, E.K., Oddou-Muratorio, S., Smouse, P.E., Sork, V.L., 2004. Using genetic markers to estimate the pollen dispersal curve. *Mol. Ecol.* 13, 937–954. <https://doi.org/10.1111/j.1365-294X.2004.02100.x>.
- Axer, M., Schlicht, R., Wagner, S., 2021. Modelling potential density of natural regeneration of European oak species (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) depending on the distance to the potential seed source: methodological approach for modelling dispersal from inventory data at forest enterprise level. *For. Ecol. Manag.* 482, 118802. <https://doi.org/10.1016/j.foreco.2020.118802>.
- Barnhart, S.J., McBride, J.R., Warner, P., 1996. Invasion of northern oak woodlands by *Pseudotsuga menziesii* (Mirb.) Franco in the Sonoma Mountains of California. *Madroño* 28–45.
- Bateman, A.J., 1947. Contamination in seed crops: III. Relation with isolation distance. *Heredity* 1, 303–336. <https://doi.org/10.1038/hdy.1947.20>.
- Bindewald, A., Miocic, S., Wedler, A., Bauhus, J., 2021. Forest inventory-based assessments of the invasion risk of *Pseudotsuga menziesii* (Mirb.) Franco and *Quercus rubra* L. in Germany. *Eur. J. For. Res.* 140, 883–899. <https://doi.org/10.1007/s10342-021-01373-0>.
- Blickensdörfer, L., Oehmichen, K., Pflugmacher, D., Kleinschmit, B., Hostert, P., 2024. National tree species mapping using Sentinel-1/2 time series and German National Forest Inventory data. *Remote Sens. Environ.* 304, 114069. <https://doi.org/10.1016/j.rse.2024.114069>.
- Blickensdörfer, L., Oehmichen, K., Pflugmacher, D., Kleinschmit, B., Hostert, P., 2022. Large-area Tree Species Mapping Across Environmental gradients: Combining Sentinel-2 and Sentinel-1 Time Series With German National Forest Inventory data, Project brief /Thünen Institute. Thünen-Institut, Bundesforschungsinstitut für Ländliche Räume, Wald und Fischerei, Braunschweig. <https://doi.org/10.3220/DATA20221214084846>.
- Böckmann, T., Saborowski, J., Dahm, S., Nagel, J., Spellmann, H., 1998. Die Weiterentwicklung der betriebsinventur in niedersachsen. *Forst Holz* 53, 219–226.
- Boe, K.N., 1953. Western larch and Douglas-fir seed dispersal into clearcuttings Research Note-Northern Rocky Mountain Forest and Range Experiment Station (Missoula, Mont).
- Bosela, M., Tumajer, J., Cienciala, E., Dobor, L., Kulla, L., Marčíš, P., Popa, I., Sedmák, R., Sedmáková, D., Sitko, R., Šeběn, V., Štěpánek, P., Büntgen, U., 2021. Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. *Sci. Total Environ.* 752, 141794. <https://doi.org/10.1016/j.scitotenv.2020.141794>.
- Broncano, M.J., Vilà, M., Boada, M., 2005. Evidence of *Pseudotsuga menziesii* naturalization in montane Mediterranean forests. *For. Ecol. Manag.* 211, 257–263. <https://doi.org/10.1016/j.foreco.2005.02.055>.
- Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., Hooftman, D.A., 2017. A synthesis of empirical plant dispersal kernels. *J. Ecol.* 105, 6–19. <https://doi.org/10.1111/1365-2745.12666>.
- Burkart, A., 2018. Kulturanleitungen für Waldbäume und Wildsträucher: anleitungen zur Samenernte, Klengung, Samenlagerung und Samenausbeute sowie zur Anzucht von

- Baum-und Straucharten. Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL.
- Caccia, F.D., Ballaré, C.L., 1998. Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. *Can. J. For. Res.* 28, 683–692. <https://doi.org/10.1139/x98-036>.
- Carter, R.E., Klinka, K., 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. *For. Ecol. Manag.* 55, 87–105. [https://doi.org/10.1016/0378-1127\(92\)90094-P](https://doi.org/10.1016/0378-1127(92)90094-P).
- Clark, C., Poulsen, J., Bolker, B., Connor, E., Parker, V., 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* 86, 2684–2694. <https://doi.org/10.1890/04-1325>.
- Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J., 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475–1494. [https://doi.org/10.1890/0012-9658\(1999\)080\[1475:SDNAFP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1475:SDNAFP]2.0.CO;2).
- Congalton, R.G., 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sens. Environ.* 37, 35–46. [https://doi.org/10.1016/0034-4257\(91\)90048-B](https://doi.org/10.1016/0034-4257(91)90048-B).
- Daley, D.J., Vere-Jones, D., 2003. *An introduction to the theory of point processes. In: Elementary Theory and Methods*. I. Springer, New York.
- Delavaux, C.S., Crowther, T.W., Zohner, C.M., Robmann, N.M., Lauber, T., van den Hoogen, J., Kuebbing, S., Liang, J., De-Miguel, S., Nabuurs, G.-J., others, 2023. Native diversity buffers against severity of non-native tree invasions. *Nature* 1–9. <https://doi.org/10.1038/s41586-023-06440-7>.
- Dick, J., 1955. *Studies of Douglas fir Seed Flight in South Western Washington*. Tacoma Weyerhaeuser Timber Co.
- Eberhard, B., Hasenauer, H., 2018. Modeling Regeneration of Douglas fir forests in Central Europe. *Austrian J Sci* 135, 33–51.
- Eggert, M., 2014. Verjüngungspotenzial der Douglasie in Bayern. Keine Einstufung als invasive Art gemäß BNatSchG. *Naturschutz Landschaftsplanung* 46, 345–352.
- Fischer, H., Huth, F., Hagemann, U., Wagner, S., 2016. Developing restoration strategies for temperate forests using natural regeneration processes. In: Stanturf, J.A. (Ed.), *Restor. Boreal Temp. For.* CRC Press, Boca Raton USA, pp. 103–164.
- Fleischer, P., Pichler, V., Fleischer Jr, P., Holko, L., ek Máli, F., Gömöröyvá, E., Cudlín, P., Hokeš, J., Michalová, Z., Homolová, Z., others, 2017. Forest ecosystem services affected by natural disturbances, climate and land-use changes in the Tatra Mountains. *Clim. Res.* 73, 57–71.
- Frei, E.R., Moser, B., Wohlgenuth, T., 2022. Competitive ability of natural Douglas fir regeneration in central European close-to-nature forests. *For. Ecol. Manag.* 503, 119767. <https://doi.org/10.1016/j.foreco.2021.119767>.
- Gashwiler, J.S., 1969. Seed fall of three conifers in west-central Oregon. *For. Sci.* 15, 290–295. <https://doi.org/10.1093/forests/15.3.290>.
- Gauer, J., Kroiher, F., 2012. *Waldökologische Naturräume Deutschlands, Sonderheft 359*. Johann Heinrich von Thünen-Institut.
- Greene, D., Johnson, E., 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70, 339–347. <https://doi.org/10.2307/1937538>.
- Harper, J.L., 2010. *Population Biology of Plants*. The Blackburn Press, London [u.a.].
- Heinrichs, S., Dölle, M., Vor, T., Balcar, P., Schmidt, W., 2022. Understorey vegetation dynamics in non-native douglas fir forests after management abandonment—A case study in two strict forest reserves in Southwest Germany. *Diversity* 14, 795. <https://doi.org/10.3390/d14100795>.
- Hemmerling, J., Pflugmacher, D., Hostert, P., 2021. Mapping temperate forest tree species using dense Sentinel-2 time series. *Remote Sens. Environ.* 267, 112743. <https://doi.org/10.1016/j.rse.2021.112743>.
- Hermosilla, T., Bastyr, A., Coops, N.C., White, J.C., Wulder, M.A., 2022. Mapping the presence and distribution of tree species in Canada's forested ecosystems. *Remote Sens. Environ.* 282, 113276. <https://doi.org/10.1016/j.rse.2022.113276>.
- Hijmans, R.J., 2022. terra: spatial Data Analysis.
- Hologa, R., Scheffczyk, K., Dreiser, C., Gärtner, S., 2021. Tree species classification in a temperate mixed mountain forest landscape using random forest and multiple datasets. *Remote Sens.* 13, 4657.
- Huth, F., Korner, A., Lemke, C., Karge, A., Wollmerstädt, J., Wagner, S., Hartig, M., Knoerzer, D., 2011. Untersuchungen zur Keimung und Keimlingsentwicklung der Douglasie (*Pseudotsuga menziesii* Mirb. Franco) in Abhängigkeit von Feuchte und Strahlung-ein Gewächshausversuch. *Forstarchiv* 82, 108–119. <https://doi.org/10.4432/0300-4112-82-108>.
- Jones, E.W., 1945. The regeneration of douglas fir, *pseudotsuga taxifolia* britt., in the new forest. *J. Ecol.* 33, 44. <https://doi.org/10.2307/2256558>.
- Karasiak, N., Sheeren, D., Fauvel, M., Willm, J., Dejoux, J.-F., Monteil, C., 2017. Mapping tree species of forests in southwest France using Sentinel-2 image time series. 2017 9th International Workshop On the Analysis of Multitemporal Remote Sensing Images (MultiTemp). IEEE, pp. 1–4.
- Knoerzer, D., 1999. Zur Naturverjüngung der Douglasie im Schwarzwald: Inventur und Analyse von Umwelt- und Konkurrenzfaktoren sowie Eine Naturschutzfachliche Bewertung, *Dissertationes botanicae*. Cramer, Berlin Stuttgart.
- Koenker, R., 2024. quantreg: Quantile Regression. R package version 5.98, <<https://CRAN.R-project.org/package=quantreg>>.
- Koenker, R., 2005. *Quantile regression, Econometric Society Monographs*. Cambridge Univ. Press, Cambridge, 38[u.a.].
- Koenker, R., Bassett, G., 1978. Asymptotic theory of least absolute error regression. *J. Am. Stat. Assoc.* 73, 618–622.
- Kot, M., Lewis, M.A., van den Driessche, P., 1996. Dispersal data and the spread of invading organisms. *Ecology* 77, 2027–2042. <https://doi.org/10.2307/2265698>.
- Krejza, J., Cienciala, E., Světlík, J., Bellan, M., Noyer, E., Horáček, P., Štěpánek, P., Marek, M.V., 2021. Evidence of climate-induced stress of Norway spruce along elevation gradient preceding the current dieback in Central Europe. *Trees* 35, 103–119. <https://doi.org/10.1007/s00468-020-02022-6>.
- Lange, F., Ammer, C., Leitinger, G., Seliger, A., Zerbe, S., 2022. Is Douglas Fir [*Pseudotsuga menziesii* (Mirbel) franco] invasive in central europe? A case study from South-West Germany. *Front. For. Glob. Change* 5, 844580. <https://doi.org/10.3389/ffgc.2022.844580>.
- Langner, N., Oehmichen, K., Henning, L., Blickensdörfer, L., Riedel, T., 2022. Bestockte Holzbodenkarte 2018. 10.3220/DATA20221205151218.
- Lavender, D.P., Hermann, R.K., 2014. Douglas-fir: the Genus *Pseudotsuga*. Forest Research Laboratory, Oregon.
- Malcolm, D., Mason, W., Clarke, G., 2001. The transformation of conifer forests in Britain—Regeneration, gap size and silvicultural systems. *For. Ecol. Manag.* 151, 7–23. [https://doi.org/10.1016/S0378-1127\(00\)00692-7](https://doi.org/10.1016/S0378-1127(00)00692-7).
- Malmqvist, C., Wallertz, K., Johansson, U., 2018. Survival, early growth and impact of damage by late-spring frost and winter desiccation on Douglas-fir seedlings in southern Sweden. *New For* 49, 723–736. <https://doi.org/10.1007/s11056-018-9635-7>.
- Mason, W.L., Edwards, C., Hale, S.E., 2004. Survival and early seedling growth of conifers with different shade tolerance in a Sitka spruce spacing trial and relationship to understorey light climate. *Silva Fenn* 38, 357–370. <https://doi.org/10.14214/sf.404>.
- Mezei, P., Jakuš, R., Pennerstorfer, J., Havašová, M., Škvarenina, J., Ferencík, J., Slivinský, J., Bičárová, S., Bilčík, D., Blaženec, M., Netherer, S., 2017. Storms, temperature maxima and the Eurasian spruce bark beetle Ips typographus—An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. *Agric. For. Meteorol.* 242, 85–95. <https://doi.org/10.1016/j.agrformet.2017.04.004>.
- Nathan, R., Klein, E., Robledo-Arnuncio, J.J., Revilla, E., 2012. Dispersal kernels: review. *Dispersal Ecology and Evolution*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199608898.003.0015>.
- Nicolescu, V.-N., Mason, W.L., Bastien, J.-C., Vor, T., Petkova, K., Podrázský, V., Dodan, M., Perić, S., La Porta, N., Brus, R., Andrašev, S., Slávik, M., Modranský, J., Pástor, M., Rédei, K., Cvjetkovic, B., Sivacioglu, A., Lavnyy, V., Buzatu-Goață, C., Mihăilescu, G., 2023. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in Europe: an overview of management practices. *J. For. Res.* 34, 871–888. <https://doi.org/10.1007/s11676-023-01607-4>.
- Niedersächsisches Forstplanungsamt, 2023. Lower Saxony Forest Inventory, Unpublished data. Wolfenbüttel.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- Núñez, M.A., Parisits, J., 2018. How are monospecific stands of invasive trees formed? Spatio-temporal evidence from Douglas fir invasions. *AoB PLANTS* 10. <https://doi.org/10.1093/aobpla/ply041>.
- Owens, J.N., Blake, M.D., 1985. *Forest Tree Seed production. A review of the Literature and Recommendations For Future research*. No.PI-X-53. ed. Information Report. Petawawa National Forestry Institute, Canadian Forestry Service. -.
- Owens, J.N., Molder, M., 1973. A study of DNA and mitotic activity in the vegetative apex of Douglas fir during the annual growth cycle. *Can. J. Bot.* 51, 1395–1409. <https://doi.org/10.1139/b73-175>.
- Pakull, B., Wojacki, J., Eusemann, P., Fussi, B., Ahnert, D., Liesebach, H., 2023. Sexual reproduction in two mixed stands of coastal and interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in Germany. *Eur. J. For. Res.* 142, 175–182. <https://doi.org/10.1007/s10342-022-01514-z>.
- Pebesma, E., Bivand, R., 2023. Spatial data science: with applications in R. Chapman and Hall/CRC. <https://doi.org/10.1201/9780429459016>.
- Petrutan, I., Lüpke, B.von, Petritan, A., others, 2010. Influence of different cutting types on growth of planted beech and Douglas fir saplings. *Forstarchiv* 81, 40–52.
- Plakman, V., Janssen, T., Brouwer, N., Veraverbeke, S., 2020. Mapping species at an individual-tree scale in a temperate forest, using sentinel-2 images, airborne laser scanning data, and random forest classification. *Remote Sens.* 12, 3710.
- Ribbens, E., Silander Jr, J.A., Pacala, S.W., 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75, 1794–1806. <https://doi.org/10.2307/1939638>.
- Rohmeder, E., 1972. *Das Saatgut in Der Forstwirtschaft*. Parey, Hamburg, Berlin.
- Roy, D.F., 1960. Douglas-Fir seed production and dispersal in northwestern California. *Douglas-Fir Seed Prod. Dispersal Northwest*. Calif 22.
- Saborowski, J., Marx, A., Nagel, J., Böckmann, T., 2010. Double sampling for stratification in periodic inventories—Infinite population approach. *For. Ecol. Manag.* 260, 1886–1895. <https://doi.org/10.1016/j.foreco.2010.08.035>.
- Sankey, T.T., 2007. Spatial patterns of Douglas-fir and aspen forest expansion. *New For* 35, 45–55. <https://doi.org/10.1007/s11056-007-9062-7>.
- Savill, P.S., 2019. *The Silviculture of Trees Used in British forestry*. CABI, Boston.
- Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübke, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgenuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl. Ecol.* 45, 86–103. <https://doi.org/10.1016/j.baec.2020.04.003>.
- Sharpe, D.M., Fields, D.E., 1982. Integrating the effects of climate and seed fall velocities on seed dispersal by wind: a model and application. *Ecol. Model.* 17, 297–310. [https://doi.org/10.1016/0304-3800\(82\)90036-9](https://doi.org/10.1016/0304-3800(82)90036-9).
- Siggins, H.W., 1933. Distribution and rate of fall of conifer seeds. *J. Agric. Res.* 47, 119–128.
- Silen, R.R., 1978. *Genetics of Douglas-fir*. Department of Agriculture, Forest Service.
- Simard, S.W., Roach, W.J., Beauregard, J., Burkart, J., Cook, D., Law, D., Murphy-Steed, A., Schacter, T., Zickmantel, A., Armstrong, G., others, 2021. Partial retention

- of legacy trees protect mycorrhizal inoculum potential, biodiversity, and soil resources while promoting natural regeneration of interior Douglas-fir. *Front. For. Glob. Change* 3, 620436. <https://doi.org/10.3389/ffgc.2020.620436>.
- Spellmann, H., Weller, A., Brang, P., Michiels, H.-G., Bolte, A., 2015. Douglasie (Pseudotsuga menziesii (Mirb.) Franco), in: *potenziale Und Risiken Eingeführter Baumarten: baumartenportraits Mit Naturschutzfachlicher Bewertung*. pp. 187–217.
- Stoyan, D., Wagner, S., 2001. Estimating the fruit dispersion of anemochorous forest trees. *Ecol. Model.* 145, 35–47. [https://doi.org/10.1016/S0304-3800\(01\)00385-4](https://doi.org/10.1016/S0304-3800(01)00385-4).
- Strothmann, R.O., Roy, D.F., 1984. Regeneration of Douglas-fir in the Klamath Mountains Region. California and Oregon. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. <https://doi.org/10.2737/PSW-GTR-81>.
- Thom, D., Jentsch, A., Seidl, R., Jentsch, A., 2022. Disturbances and Ecosystem Services. *Disturbance Ecology*. Springer, pp. 413–434.
- Thomas, F.M., Rzepecki, A., Werner, W., 2022. Non-native Douglas fir (Pseudotsuga menziesii) in Central Europe: ecology, performance and nature conservation. *For. Ecol. Manag.* 506, 119956. <https://doi.org/10.1016/j.foreco.2021.119956>.
- Tufto, J., Engen, S., Hindar, K., 1997. Stochastic dispersal processes in plant populations. *Theor. Popul. Biol.* 52, 16–26. <https://doi.org/10.1006/tpbi.1997.1306>.
- van Loo, M., Lazić, D., Chakraborty, D., Hasenauer, H., Schüler, S., 2019. North American Douglas-fir (*P. menziesii*) in Europe: establishment and reproduction within new geographic space without consequences for its genetic diversity. *Biol. Invasions* 21, 3249–3267. <https://doi.org/10.1007/s10530-019-02045-2>.
- von Lüpke, N., Sennhenn-Reulen, H., 2023. Quantifying success share and plant density of direct seeding of Douglas fir using a hurdle negative binomial regression model. *New For* 54, 399–419. <https://doi.org/10.1007/s11056-022-09927-9>.
- Vor, T., Spellmann, H., Bolte, A., Ammer, C. (Eds.), 2015. *Potenziale Und Risiken eingeführter Baumarten: Baumartenportraits mit Naturschutzfachlicher Bewertung*, Göttinger Forstwissenschaften. Göttingen University Press, Göttingen. <https://doi.org/10.17875/gup2015-843>.
- Welle, T., Aschenbrenner, L., Kuonath, K., Kirmaier, S., Franke, J., 2022. Mapping dominant tree species of German forests. *Remote Sens* 14, 3330.
- Welsh, A.H., Cunningham, R.B., Donnelly, C.F., Lindenmayer, D.B., 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecol. Model.* 88, 297–308. [https://doi.org/10.1016/0304-3800\(95\)00113-1](https://doi.org/10.1016/0304-3800(95)00113-1).
- Wohlgemuth, T., Hafner, J., Höltermann, A., Moser, B., Nehring, S., Rigling, A., 2019. Impact of Douglas-fir on Forests and Open Land habitats. *Douglas-Fir—An Option Eur. Spiecker H Lindner M Sch*, pp. 57–62. J Eds.
- Wohlgemuth, T., Moser, B., Pötzelsberger, E., Rigling, A., Gossner, M.M., 2021. Über die Invasivität der Douglasie und ihre Auswirkungen auf Boden und Biodiversität. *Schweiz. Z. Forstwes.* 172, 118–127. <https://doi.org/10.3188/szf.2021.0118>.
- Wojacki, J., Eusemann, P., Ahnert, D., Pakull, B., Liesebach, H., 2019. Genetic diversity in seeds produced in artificial Douglas-fir (*Pseudotsuga menziesii*) stands of different size. *For. Ecol. Manag.* 438, 18–24. <https://doi.org/10.1016/j.foreco.2019.02.012>.