



Quantifying success share and plant density of direct seeding of Douglas fir using a hurdle negative binomial regression model

Nikolas von Lüpke¹ · Holger Sennhenn-Reulen¹ 

Received: 1 October 2021 / Accepted: 20 May 2022 / Published online: 28 June 2022
© The Author(s) 2022

Abstract

In recent years, direct seeding as a means of stand establishment has experienced a revival. Among other things it allows for an undisturbed root development and is assumed to be cost-efficient. While success factors have been worked out through numerous experiments, sound overviews of success and failure in practice are scarce. With the goals of (i) quantifying the success proportion and (ii) extracting the associated influencing factors, we conducted an inventory of direct seedings of Douglas fir in Northern Germany and fitted a hurdle negative binomial regression model to the data. The results reveal a high variability of plant density within, as well as between stands. We could attribute these differences, and thus the success, to stocking degree of the shelter, seed amount and age. The model shows both, a high precision and accuracy, and respects previous physical and biological knowledge of the data-generating mechanisms.

Keywords Direct seeding · Douglas fir · Bayesian inference · Count data regression · Hurdle model · Negative binomial regression · Informative prior

Introduction

According to current climate projections (IPCC 2015), the growth conditions for forests will change markedly in the future, while Pretzsch et al. (2014) showed that stand growth dynamics of forests in Central Europe already have changed since 1960 in comparison to the period 1870–1960. The years 2018 and 2019 might be seen as heralds of a changed climate. In order to cope with this, Bolte et al. (2009) distinguish between (i) conservation of forest structures, (ii) active adaptation and (iii) passive adaptation as management strategies. Among other things, the extended use of non-native tree species is discussed as a measure of active adaptation (Brang et al. 2008; Bolte et al. 2009; von Lüpke 2009).

Nikolas von Lüpke and Holger Sennhenn-Reulen have been equally contributed to this work.

✉ Nikolas von Lüpke
nikolas.von-luepke@nw-fva.de

¹ Northwest German Forest Research Institute, Grätzelstraße 2, 37079 Göttingen, Germany

A species, on which practitioners pin great hope, is Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), since it is more tolerant to extreme drought than e.g. Norway spruce (*Picea abies* [L.] Karst) (Vitali et al. 2017). Introduced by Booth in 1831 (Lavender and Hermann 2014; van Loo and Dobrowolska 2019b) and cultivated in forestry since 1850 (Spellmann et al. 2015), it currently covers 2 % of the forested area in Germany (217,604 ha). This corresponds to a standing volume of 72,731,000 m³ and 26.4 % of the Douglas fir area in Europe (Thünen-Institut 2014; van Loo and Dobrowolska 2019a). The proportion of Douglas fir in parts of Germany is planned to increase in the future (Möges et al. 2008; Böckmann et al. 2019). However, there is an ongoing debate about the risk of cultivating this species, since negative ecological impacts are feared (Bindewald et al. 2019).

Even though Douglas fir is valued for its high productivity, favourable wood properties and mild impact on soil (Spellmann et al. 2015), it is known to be very vulnerable in young stands. Heavy losses of planted Douglas firs are common, which has long been known (e.g. Hesmer 1952; Larsen 1976; Röhrig 1976; Kohnle et al. 2019). This vulnerability is mainly attributed to low resistance to late as well as to early frost events (Röhrig 1976), incorrect plant handling and planting, large differences between provenances (Dong 1973; Larsen 1976; Braun and Wolf 2001), and the influence of game (e.g. browsing).

In order to reduce the risk in stand establishment, direct seeding and the use of containerised seedlings have gained more attention in recent years (Ruppert and Rothkegel 2018). Regarding direct seeding, Grossnickle and Ivetić (2017) distinguish between (i) ecological, (ii) biological, (iii) economic and (iv) operational benefits of this stand establishment method for reforestation and Huth et al. (2017) list, for example, an undisturbed root development, high numbers of plants, an avoidance of the transplant shock, and comparably low costs as advantages of direct seeding of shade tolerant tree species under shelter. These benefits also apply to Douglas fir, even though it is considered moderately shade-tolerant in Europe (Nicolescu 2019).

Although there are successful direct seedings of Douglas fir (Petersen 2019), this method is seldom used for Douglas fir in comparison to other species. Successful stand establishment cannot be guaranteed, and for this reason plantin2020g has superseded direct seeding as the most common regeneration technique in Germany (Burschel and Huss 1997; Bartsch et al.). According to Huth et al. (2017), the disadvantages of direct seeding are, among others, the strong dependence on climatic conditions and canopy cover, lower germination rates in comparison to nursery plants and a limited time window for successful establishment. The latter clearly distinguishes direct seeding from natural regeneration, which ensures its success through a constant seed production (Ruppert and Rothkegel 2018).

Since successes are often reported, but not failures, we aimed at gaining a sound overview of the success share of direct seeding in Northern Germany. For the assessment of success, it is important to consider not only the number of plants, but also their distribution within the stand. Even though the distribution does not necessarily have to be completely even to achieve silvicultural goals, it is important to pay attention to this feature. If the distribution is too patchy, interspecific competition might play a decisive role and lead to unsatisfactory results. Thus, we aimed at finding a method, which allows us to quantify both key figures. To do so, we conducted an inventory of stands cultivated between 2015 and 2019 and used a hurdle negative binomial model to analyse the data. This model allows us to simultaneously draw conclusions about the probability for cultivation success as well as how the number of plants per ha is distributed in the case of success.

Field study

Preliminary considerations and work

Because we aimed at drawing inferences about both plant number and density, it was essential to design the study in an appropriate manner. In order to draw conclusions about the distribution of plants, it is important to gather data from the whole stand and hence we decided on a systematic sampling design with relatively small sampling units. All seedlings were executed row-wise and preliminary studies of cultures of seedling origin showed that sampling along the seed-rows is feasible (Rumpf 2007; Petersen 2019). We therefore established the *number of seedlings per seed-row segment* ('counting strip') as our primary outcome. In order to set up an efficient sampling scheme, we conducted a simulation study with count-data from three previous investigations of seeded Douglas fir cultures in Northern Germany. Different lengths of counting-strips as well as different sample sizes were compared, assuming a Poisson distribution of the seedling counts. Based on the results of this simulation study and practical considerations, we decided to count the seedlings on 50 systematically placed strips of 4 m length per ha. Assuming a distance of 2 m between the seed-rows, each strip represents an area of 8 m². By this, our sampling effort covers 400 m² per ha, which is 4 % area share.

In addition to the data on the Douglas firs, we intended to gather data on factors that might affect the development of the cultures. Since the timespan between seeding and inventory was variable and up to seven years long, time-varying factors of influence like e.g. soil moisture content, were not integrated in the non-recurring inventory. Moreover, we orientated the inventory towards variables that could be (i) controlled by silvicultural measures and (ii) collected in an adequate time. Hence, we focussed on stand-wise variables.

Study sites and data collection

In summer 2019 and in cooperation with the main producer of forest seeds in Northern Germany, the fsb Oerrel, we contacted all of their customers who had purchased seeds of Douglas fir within the last five years. The provenances were chosen based on valid local recommendations and might differ from stand to stand. A total of 74 stands from 12 enterprises was reported and we decided to sample 50 % of the reported stands with a minimum size of 0.5 ha (in total 28), mostly located in the Federal State of Lower Saxony (Fig. 1). Data acquisition was carried out between October 2019 and March 2020. Counting-strips of 4 m length were placed systematically along the seed-rows and all plants on the respective segments were counted. Due to deviations between reported and assessed size, the smallest stand had an area of 0.36 ha (Table 1). The number of counting-strips per stand ranged from 18 to 136 (in total 1,807). In addition, several variables were collected at the stand-level (Table 1). Nutrient and water supply were assessed and classified through forest site mapping according to the instructions for Lower Saxony (NFP and LLUR 2009a, b). The shelter was characterised through species, stocking degree and age class. Whereas the latter was gathered from the forest management plans, the stocking degree was assessed as a relative value in relation to the yield table for pine of Wiedemann (1943). Information on the implementation of the seedlings were provided by the respective forest practitioners. Different soil preparation methods were applied before seeding started, in most of the cases a TTS-device

Table 1 Overview of the study sites

		n	Mean	SD	Range
<i>Site</i>					
Nutrient supply class	Eutrophic	1			
	Mesotrophic	17			
	Oligotrophic	10			
Water supply class	Stagnic	2			
	Bottom moist/fresh	12			
	Neither stagnic nor bottom moist	14			
<i>Regeneration</i>					
Area (ha)			1.19	0.7	0.36-2.74
Age (yrs)			4.53	1.21	1-7
Mean height (m)			0.54	0.29	0.2-1.6
Fenced	Yes	2			
	No	26			
Browsing	Yes	9			
	No	19			
<i>Shelter</i>					
Existing shelter	Yes	27			
	No	1			
Stocking degree			0.39	0.17	0.0-0.7
Age class					40-140
Species		27			
<i>Seeding</i>					
Amount (kg ha ⁻¹)			0.83	0.22	0.47-1.34
Stratification of seeds	Yes	16			
	No	12			
Season	Spring	17			
	Winter	9			
Soil preparation method	TTS	17			
	Plow	5			
	Misc.	6			
Seeding method	Bottle	21			
	Misc.	7			

n denotes the number per class, *Mean* the arithmetic mean value, *SD* the standard deviation and *Range* the range

(two-trench scarification). For more than half of the direct seedings, the seeds were stratified beforehand and the seed amounts used varied considerably. Seeding was carried out during both, spring and winter, mainly manually. In these cases, the seeds were brought out by persons using plastic bottles as seeding devices. During the inventory, additional data on the regeneration were collected. Even though most of the cultures were not fenced, browsing was an apparent problem only in one third of them.



Fig. 1 Location of the sampled cultures

Statistical analysis

At the heart of a statistical model for our unknown data-generating process, we need to formulate a likelihood function that satisfies our (domain) expertise about the system under examination. The likelihood is a probabilistic statement about the data at given parameter values. Appropriateness of the likelihood is one of the most important decisions in statistical modelling and, therefore, several important features of collected data enter our likelihood formulation.

First, we gathered *count data* and therefore need to build the likelihood upon a distribution for non-negative and integer scaled random variables.

Second, there is higher variability than allowed for by the familiar Poisson distribution. This increased variability is usually an inherent property of count data generating processes and is referred to as *over-dispersion*: “The negative binomial regression model can account for over-dispersion and can nest the Poisson, it is commonly used for truncated and censored count data and hurdle or two-part models.” (Shonkwiler 2016).

Third, for given estimated distributional parameters, count data distributions have a fixed (conditional) probability mass for $Y = 0$: in application, this probability mass is often too small in comparison to the empirical (conditional) mass on 0. For regeneration data, such a *zero-inflated* data generating process is frequently reported and in Forest Science several approaches to cope with it have been applied.

Zhang et al. (2012) compared different methodological approaches for modelling tree recruitment and recommend the use of negative binomial mixture models, in particular zero-inflated (ZINB) or hurdle negative binomial models (HNB), for this purpose. To

account for the high proportion of zero counts, Fortin and DeBlois (2007) presented zero-inflated models. Crotteau et al. (2014) showed that the negative binomial distribution is well-suited for modelling natural postfire regeneration, especially when the overdispersion is heterogeneous. Li et al. (2011) tested different modelling approaches and recommend ZINB for modelling ingrowth, while Rathbun and Fei (2006) used a Bayesian approach to model oak regeneration by means of a spatial zero-inflated Poisson Regression (ZIP). In order to model seedling abundance of non-native tree species, Terwei et al. (2013) applied a HNB.

Beyond these experiences with regeneration modelling, one further theoretical consideration makes the case for applying HNB: Zeileis et al. (2008) point out that it facilitates interpretation, since two components are modelled that can be separated for interpretation; one that controls the binary process of a complete loss of the seeding investment, and a second one that determines the quantity if still existing. Therefore, we decided to apply a HNB.

Hurdle negative binomial regression model

The *hurdle negative binomial* (HNB) distribution has a probability mass function (Bhaktha 2018, p. 22):

$$p_{\text{HNB}}(y | \pi, \mu, \theta) = \begin{cases} \pi, & y = 0 \\ (1 - \pi) \cdot p_{\text{ZTNB}}(y | \mu, \theta), & y > 0 \end{cases} \quad (1)$$

where π is the probability mass for $y = 0$, and $p_{\text{ZTNB}}(y | \mu, \theta)$ is the probability mass function of a zero-truncated negative binomial (ZTNB) distribution. μ denotes the mean and θ the shape parameter. The HNB has the expectation (Bhaktha 2018, p. 23):

$$\mathbb{E}_{\text{HNB}}(Y) = (1 - \pi) \cdot \mathbb{E}_{\text{ZTNB}}(Y), \quad (2)$$

where $\mathbb{E}_{\text{ZTNB}}(Y)$ is the expectation of the ZTNB.

For a random variable Y distributed according to the HNB, we write:

$$Y_i \sim \text{Hurdle-NegBin}(\pi_i, \mu_i, \theta_i). \quad (3)$$

For more mathematical details regarding the HNB, we refer to Bhaktha (2018).

The *hurdle component* is based on a Bernoulli distribution for $Y_i = 0$ vs. $Y_i \geq 1$, with the single parameter $\pi_i \in (0, 1)$ modelled using the *Logit link-function*:

$$\pi_i = \frac{\exp(\eta_{\pi,i})}{1 + \exp(\eta_{\pi,i})}, \quad (4)$$

where $\eta_{\pi,i}$ is the linear predictor incorporating the respective covariate-values for an individual i with attached parameters quantifying their influences.

The *positive count component* is based on a ZTNB distribution for a zero-truncated random variable, denoted $Z_i := Y_i | Y_i > 0$, with non-negative integers $z_i \in \mathbb{Z}^+$. We write:

$$Z_i \sim \text{ZeroTrunc-NegBin}(\mu_i, \theta_i). \quad (5)$$

Non-negative distributional parameters μ_i and θ_i are modelled using the *logarithmic link-function*:

$$\mu_i = \exp(\eta_{\mu,i}), \quad (6)$$

$$\theta_i = \exp(\eta_{\theta,i}), \quad (7)$$

where $\eta_{\mu,i}$ and $\eta_{\theta,i}$ are parameter-specific linear predictors, again incorporating the respective covariates with attached parameters modelling their influences.

Bayesian inference

For the analysis, we applied the Bayesian method of statistical inference, which is based on updating current, *prior*, evidence about a model's parameters, ξ , in light of the information contained in newly generated data/measurements, denoted by $\mathbf{y}$, of the *response* random variable, denoted by Y . This updating is a direct application of *Bayes' theorem*:

$$p(\xi | \mathbf{y}) = \frac{p(\mathbf{y} | \xi) \cdot p(\xi)}{p(\mathbf{y})} \propto p(\mathbf{y} | \xi) \cdot p(\xi)$$

The prior, $p(\xi)$, is formulated as a probability distribution for each parameter involved in the *likelihood* component, $p(\mathbf{y} | \xi)$, of the statistical model. Using priors, we can introduce any information — present before seeing any newly collected data — about the parameters of a statistical model. In this study, some of this prior knowledge is very strong, as some parts of the data-generating mechanism are clearly of a monotonic nature, such as the influence of time on seedling survival. Exploitation of this improves the consistency of a statistical model with inductive logic (Jaynes 1976, p. 190). By formulation of probabilistic statements of our prior knowledge about the data-generating mechanism, we further rule out implausible areas of the parameter space and consequently increase the precision of causal statements derived from our statistical model (see e.g. Morris et al. (2015)).

Jaynes (2003) and Gelman et al. (2014) are highly recommended for a thorough introduction to Bayesian thinking and statistical inference. See also Mohamedou et al. (2022) for a very recent review about usage of and reasons for Bayesian methods in forestry research.

Modelling covariate influences

Our aim is to quantify how the distributional model parameters, (π_i, μ_i, θ_i) , change when the influencing variables $x_{1,i}, x_{2,i}, \dots$ take on different values. Preferably, this is simultaneously and equivalently done for each of these distributional model parameters (*fully distributional regression approach*). In our case, this approach would have led to strictly *progressing* or *regressing dispersion* (Supplementary Material, Section 'Roles of Parameters on Expectation of the ZTNB'), which seems a rather strict approach that is not backed up by adequate prior knowledge. We have therefore stepped back from the fully distributional regression approach and introduced covariate effects only on μ , and π . To account for varying dispersion in different stands, we introduced respective grouping terms, called *random effect/random intercept* in the frequentist statistical regression modelling (see Fig. 2).

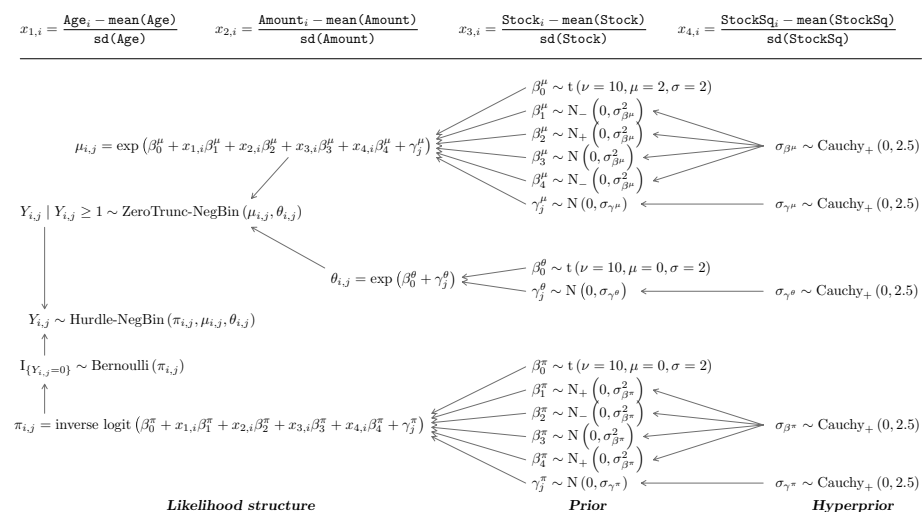


Fig. 2 Model scheme, i : counting strip, j : stand

Covariate terms part

We include three covariates into our analysis: (i) seeding age (at the year of inventory, in years), (ii) amount of seeds (in kg ha⁻¹), and (iii) stocking degree (at the year of inventory). These variables were constant per stand, centred according to their empirical mean, and scaled by their respective standard deviation (Fig. 2) — values given in Table 1. The inclusion of further covariates was prevented by the unbalanced data structure.

Figure 2 portrays the structure of our model.

Here, β_0^μ and β_0^π are *intercept parameters* specifying distributional parameters π and μ on the link scale, for all scaled covariates equal to 0, i. e. on their empirical mean. We define this first part of the linear predictor for θ as intercept only; the reasoning behind this is given in Section ‘Modelling covariate influences’.

β_p^π and β_p^μ , $p = 1, 2, 3$, is the linear influence of covariate x_p on linear predictors η_π , and $x_{4,i}$ is the scaled square of stocking degree — with respective effects β_4^π and β_4^μ .

Even though a negative interaction of seeding age and seed amount has to be expected from theoretical considerations, we found, however, no possibility to introduce such an interaction effect while maintaining sign restrictions for β_1^μ , β_2^μ , β_1^π , and β_2^π . Further, our experimental design with 1,807 counting-strips in 28 stands was not designed for incorporation of (complex) interactions, as “Estimating interactions is similar to comparing coefficients estimated from subsets of the data [...]” (Gelman and Hill 2006). Further, interactions “[...] typically are smaller and have relatively larger standard errors than main effects [...]” (Gelman and Hill 2006). Both reasons similarly apply for flexible non-linear effects as estimated in additive models. Mild to strong regularisation priors should still be able to make such complex models run, but as we have no clear theoretical framework for presence of interactions, we introduce no interaction terms or further covariate effects.

Grouping terms part

As a last building-block, we need to incorporate the fact that several count segments belong to the same stand, leading to intra-class correlations (Faraway 2016, Chapter 10.1), making measurements from one stand plausibly more similar to each other than to measurements from another stand. Such a dependence structure is taken care of by the use of grouping terms — in non-Bayesian regression modelling referred to as *random intercept* (Faraway 2016, Chapter 10). For counting-strip i belonging to stand j , we therefore add the respective coefficient, γ_j^k , to the distributional parameter, $k \in \{\mu, \theta, \pi\}$, specific linear predictor:

$$\eta_i^k = \beta_0^k + \gamma_j^k + \sum_{l=1}^4 x_{l,i} \beta_l^k, \quad (8)$$

Going back to Stein's paradox (Efron and Morris 1977), we assume — independently for each k — the γ_j^k coefficients to be independent and identically distributed (*i.i.d.*) normal random variables (Fahrmeir et al. 2013, Ch. 7):

$$\gamma_j^k \sim \text{Normal}\left(0, \sigma_{\gamma^k}^2\right),$$

with distributional parameter specific variance $\sigma_{\gamma^k}^2$. For each parameter specific linear predictor, these coefficients model the stand-specific distributional parameters beyond what was considered already by the remaining part, i.e. linear predictors $\eta_i^k - \gamma_j^k = \beta_0^k + \sum_{l=1}^4 x_{l,i} \beta_l^k$.

Choice of priors

We are able to gather prior information on a plausible range of response measurements (Supplementary Material, Section 'Plausible Range of Response Measurements'), guiding us in specifying *weakly informative priors* for the intercept parameters ($\beta_0^\mu, \beta_0^\theta, \beta_0^\pi$) by prior predictive checking (Wesner and Pomeranz 2020). These are set up strong enough such that the model predicts implausible values with only low frequency, but at the same time weak enough — i.e. with a low-enough precision — such that these priors can be overwhelmed by the evidence of the likelihood (Lemoine 2019).

For covariate influences β^μ and β^π , we lack prior information on the scale of effects, but (i) we aim to follow the general statistical principle of regularisation, and (ii) introduce sign-restrictions on these marginal effects. We therefore apply regularised regression by using shrinkage priors (van Erp et al. 2019), a Bayesian strategy for trying to get an insurance against unstable parameter estimation and over-fitted models.

Sign-restrictions were established by half-normal priors — instead of normal priors — for parameters with prior sign knowledge (Gelman et al. 2014, Subsection 'Prior information in the form of inequality constraints on parameters'). These sign-restrictions lead to truncated posteriors, which are in line with our understanding of the underlying process.

To sum up, our prior considerations result in four different classes of prior distributions (see also Fig. 2): (i) distribution-parameter specific intercept parameters are a priori Student-t distributed, (ii) covariate-effect parameters without a priori sign knowledge are a priori Normal distributed, (iii) covariate-effect parameters with a priori sign knowledge are a priori half-Normal distributed, and (iv) standard-deviations for grouping coefficients and standard-deviations for covariate-effect parameters are a priori

half-Cauchy distributed. The latter hyperprior for standard-deviations for covariate-effect parameters then leads to Ridge-type shrinkage (van Erp et al. 2019). See also Supplementary Material, Section ‘Further Considerations for Specifications of Priors’ for further explanations.

Software and posterior sampling details

We used the R (R Core Team 2019) statistical software environment, and especially the R add-on package *brms* (Bürkner 2017, 2018) for modelling. *brms* provides a low-threshold access to the probabilistic programming language *Stan*, which is the actual software in which the models are implemented in. Within *Stan*, we used the Hamiltonian Monte Carlo (HMC) sampler, described in detail in Stan Development Team (2019). HMC is a Markov Chain Monte Carlo (MCMC) method. In general, MCMC algorithms are sampling methods that are used for quantification of not directly analytically quantifiable, high-dimensional probability distributions. As a result of a practical application of HMC/MCMC, one yields samples for the full vector of a high-dimensional probability distribution. By means of — algebraically very simple — post-estimation calculations — that also very flexibly allow for consideration of combinations of parameters — on this sample, one gets to point estimates for parameters or correlations among parameters, one- or multi-dimensional uncertainty estimates, up to illustrations of full one- or multi-dimensional parameter distributions.

For all models — main model, and alternative models for sensitivity checking — we were using 1,000 warmup samples, followed by 1,000 samples from the posterior used for making inference statements. This was done for eight chains, where starting values for all parameters were set to 0. Stan control parameter `adapt_delta` was set to 0.99, `max_treedepth` was set to 20, all other control parameters were kept on their defaults.

Model predictions

In order to translate the modelling results into useful recommendations for forest practitioners, we used the samples from the posterior distribution to calculate conditional probabilities for exceeding a lower performance threshold. For this, we first established several applied covariate scenarios from the observed range of values, where grouping term coefficients were set to the value of 0, corresponding to their assumed population mean. For each of these scenarios, and for every sample of the posterior distribution (in our case 8,000), a pair of values was generated, with the probability for a loss of the culture (hurdle component) as first element, and the expectation for the number of surviving plants if at least one has survived (expectation of the zero-truncated negative binomial distribution) as second element. The resulting bivariate posterior distribution allows to draw simultaneous inferences about the parameter effects on the two components of the HNB distribution. We further scaled these results up to stand-level values to facilitate the interpretation. Thereby, the stand density was estimated as mean of the calculated expectation values per ha and the proportion of counting strips without any plant was used as proxy for the distribution of plants. In a following step, we calculated the proportion of posterior samples that achieved at least the lower performance conditions, defined by a combined threshold for

plant density and hurdle probability. These proportions can be interpreted as conditional probabilities for achieving performance objectives, i.e. silvicultural goals.

Reproducibility

The R code for full reproduction of the analysis is given in the Supplementary Material (Section ‘Reproduction’) and the data is available under von Lüpke et al. (2021).

Results

Empirical results

The counts per 4-m strip varied between 0 and 30 (Fig. 3) and the counts per ha between approx. 200 and 9,200 (Fig. 4). As expected, the distribution of counts contains a considerable number of 0 measurements and is right-skewed (Fig. 5). Within, as well as between the cultures, the differences were remarkable. According to Bartsch et al. (2020) the German Forest Administrations aim at 1,000–3,000 plants ha^{-1} for the establishment of stands of adequate quality (shaded area in Fig. 4), while Klädtke et al. (2012) state that 1,000 plants ha^{-1} are sufficient. Only three stands fell below this minimum number. The proportion of occupied counting-strips varied between 0.16 and 0.97, whereby in 7 cultures (25 %) less than half of the strips were occupied.

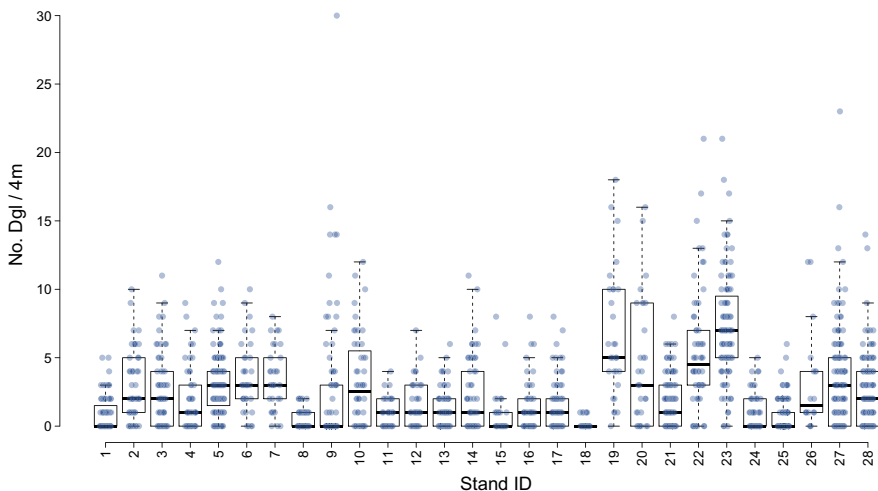


Fig. 3 Number of plants per 4-m counting-strip in the different stands. The black line denotes the median and the hinges denote versions of the first and third quartile. For further details regarding the underlying statistics, we refer to the documentation in R Core Team (2019)

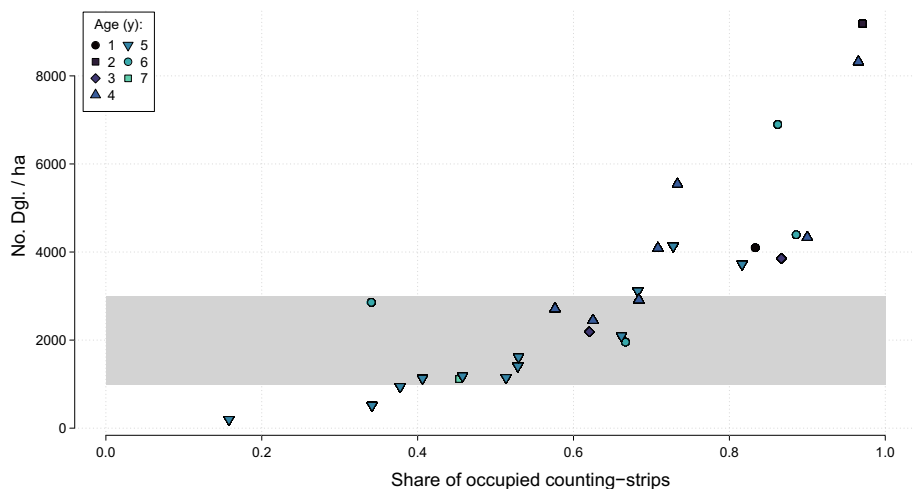


Fig. 4 Estimated mean no. of plants ha^{-1} in dependence on the share of counting-strips occupied with Douglas fir. The shaded area denotes the plant numbers, recommended by the German forest administrations for plantations (Bartsch et al. 2020)

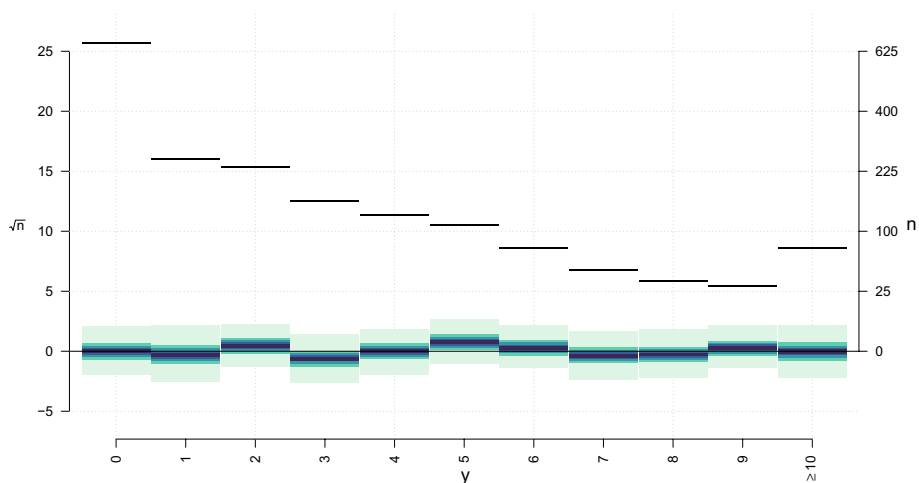


Fig. 5 Hanging rootogram: Black lines illustrate square-root transformed absolute frequencies $\sqrt{n}$ of observed count classes $y \in \{1, 2, \dots, 9, \geq 10\}$, and coloured boxes illustrate differences of these observed frequencies to the predicted frequencies by the model, per posterior sample. Colour coding is from light green to dark blue: posterior range, inner 80%, 60%, 40%, 20% posterior intervals

Modelling results

The probability densities of the posterior parameter estimates are narrower than the prior distributions (Fig. 6), indicating clear signals in the data. Apart from the hurdle-component of β_3 , they are furthermore clear regarding their sign. Even though the latter is no surprise, since bounds were set, the distributions support our approach, as the densities towards the

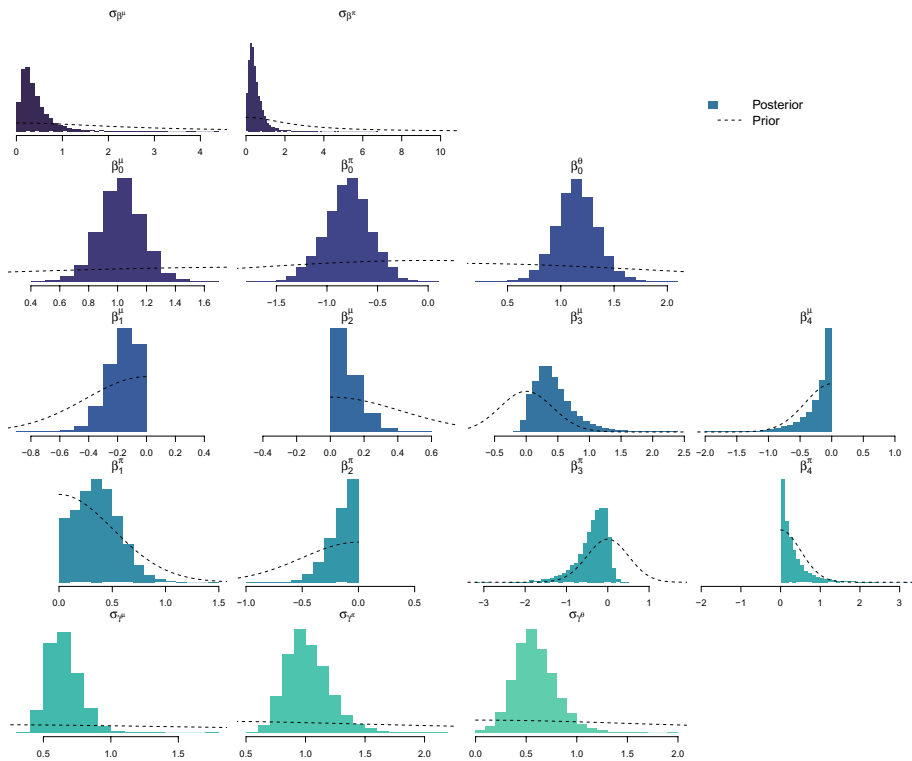


Fig. 6 Density distributions of the posterior parameter estimates

bounds are small (see the Supplementary Material for a sensitivity check of the bounding assumption). Moreover, the distributions highlight the fact that parameters are estimated flexibly with different distributional forms.

For count data regression, it is easier to visually check for the predictive performance of a model based on *rootograms* than on more traditional visualisations (Kleiber and Zeileis 2016). Here, we use a slightly adjusted version of a *hanging rootogram* (Fig. 5), where instead of defining the vertical gap from $\sqrt{E_r}$ to $\sqrt{E_r} - \sqrt{O_r}$ — where E is *expected*, O is *observed*, and index r is for response value (class) $r \in \{1, 2, \dots, 9, \geq 10\}$ —, we define it as from $\sqrt{O_r}$ to $\sqrt{O_r} - \sqrt{E_r}$. This has the benefit that, in our inference statements, which are based on samples from the posterior, we can draw variability of the ‘gap’ along the horizontal line instead of along a curve. We therefore speak of posterior predicted counts P_r instead of expected counts E_r .

Doing so, we see that the model performs highly satisfactorily (Fig. 5); the proportion of $y = 0$ is modelled with particularly high accuracy — coloured boxes are central, with a compact distribution around the x-axis $\sqrt{O_r} - \sqrt{P_r} = 0$. Hence, one of the main requirements for the model is met.

Sensitivity checks for all of our prior and model structure choices are given in Supplementary Material (Section ‘Prior/model-structure sensitivity checks’).

The model predictions for the two parts of the HNB (Fig. 7) show contrasting trends for the covariates seeding age and seed amount. While the probability of detecting no seedlings on a counting strip increases with increasing age, it decreases with increasing seed amount. The estimated plant densities per counting-strip decrease with increasing age and increase with increasing seed amount. The modelled detection-probability is lowest at stocking degrees of approximately 0.4–0.5 and the highest density is calculated for a stocking degree of about 0.7.

To combine these two predictions, we calculated the overall expectation values of our model in dependence on the three covariates (Fig. 8). This way of presentation has the benefit that the results can be interpreted flexibly, conditional on the readers choice. To illustrate this, we exemplarily defined cultures with more than (i) 50 % of the area occupied and (ii) 1,000 plants ha^{-1} as successful. The expectation value met these conditions in almost all cases at an age of three years. At an age of six, success can be expected with probabilities between 63.5 % and 89.1 % (Fig. 8, second row). Obviously, the best results are achieved with high seed amounts.

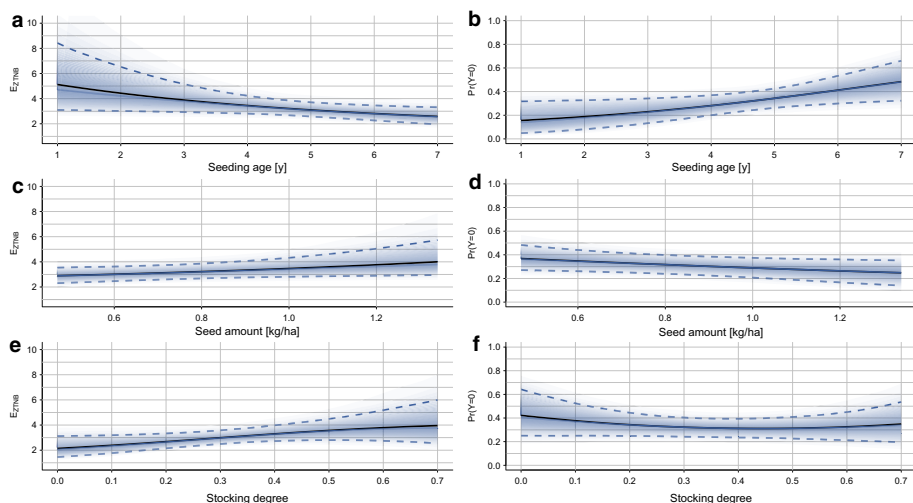


Fig. 7 Conditional predictions for a counting-strip in dependence on the covariates seeding age, seed amount and stocking degree. For each of the subplots, the variable given on the respective x-axis varies in the given range, while all other covariates are held fixed on their respective arithmetic means. The uncertainty of the intercept parameter estimation is included in the uncertainty measures, the grouping term coefficient ("random intercept") for variation between stands is held fixed on 0, corresponding to the assumed population mean. Shaded blue regions give point-wise (symmetric, quantile based) credible intervals, dashed lines are lower and upper limits of point-wise 90 % (symmetric, quantile based) credible intervals. Left column (a, c, e): conditional expectation of plant density (ZTNB model part); right column (b, d, f): conditional probability of detecting no plant (Hurdle model part)

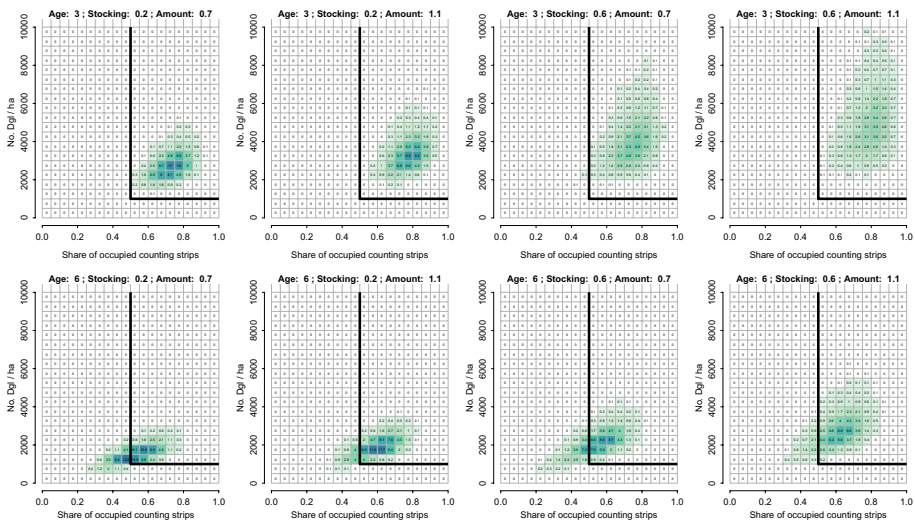


Fig. 8 Proportions of expectation values in dependence on the covariates seeding age, seed amount and stocking degree. The proportions are based on 8,000 simulation runs

Discussion

In this study, we used an integrative approach, which allows us to draw inferences about both; cultivation success probability and plant density in the case of success of directly seeded Douglas fir plants from one analysis. By this means, the results are consistent and methodological breaks are omitted. HNB has been frequently used in regeneration modelling and has proven its suitability for this task (see Sect. [Statistical analysis](#)). Furthermore, we were able to improve our analysis through the inclusion of existing knowledge. As a result, the presented model is stable and sound and leads to reasonable results.

We are aware of the fact, that the success of direct seeding of Douglas fir is affected on the single-plant scale by many more covariates than the ones included in the model. However, the main goal of our inventory was to give a sound overview of the success of direct seedings on a relatively large scale. The relationships between different covariates and the success of direct seeding have been investigated in other experiments (e.g. [Caccia and Ballaré 1998](#); [Huth et al. 2011](#)); the corresponding results might help to understand and interpret our results.

Even though our study could not capture all success-factors of direct seeding, its results are valuable for forest practitioners. They clearly reveal the impact of stocking degree, seed amount and seeding age on both the density and distribution of plants. The results are based on a comparatively broad range of conditions and allow us to draw conclusions with more generality than case studies from single trials. Furthermore, we focussed on stand-wise variables, knowing that these in particular could be controlled in practical forestry. With the help of our model, it can be easily estimated how likely direct seedings are to be successful in dependence on the mentioned factors. By this, the chance of making elementary mistakes and consequent misinvestments can be reduced. Seeds are a precious good and should be used carefully, especially in times with enormous demands, e.g. after large-scale disturbances.

The main success-factors have been known for a long time. Already in [1916](#), [Toumey](#) named (i) the quality of the seed, (ii) the species, (iii) the vegetative cover, (iv) the condition of the surface soil, (v) the freedom of the site from seed-eating birds and rodents,

(vi) the quantity of seed sown per unit of area, (vii) the time of sowing and (viii) the depth of covering as the factors with the greatest influence. From these factors, our study only gives indication of the importance of seed amount. Bearing in mind that, several years after sowing, most of these factors cannot be validated, this is neither surprising nor a disadvantage of our inventory. Further, it is important to note, that not all of them (i) are controllable with the help of silvicultural measures and (ii) become important at the same time. At the main development stages of direct seeding — storage, germination, development of seedlings and saplings, and growth (Huth et al. 2017) — different factors decide on failure or success of the investment.

The phase of storage is known to be the one with the heaviest losses (Lawrence and Rediske 1962) and during this phase the survival probability mainly depends on predation. Caccia and Ballaré (1998) observed risks of postdispersal seed predation between 70 and 96 % and concluded that successful natural regeneration of Douglas fir mainly depends on the presence of seed-eating animals. Also Sullivan and Sullivan (1984) and Grossnickle and Ivetić (2017) point to the central role of predation for the success of direct seeding. Silvicultural measures to reduce this risk, covering of the seeds, provision of alternative foods and the use of chemicals (e.g. repellents or rodenticides), are discussed (Grossnickle and Ivetić 2017). Unfortunately, we were not able to examine the impact of predation on the sites of our study.

Once a seed has overcome the hurdle of predation, germination still cannot be guaranteed. Seeds only germinate under favourable conditions, whereby favourable is mainly associated with soil humidity and not with light availability. In a greenhouse experiment with seeds of Douglas fir, Huth et al. (2011) showed that the surface humidity of the substrate controls the germination. More generally, Grossnickle and Ivetić (2017) state that the success of direct seeding is mainly related to site conditions and the dependent availability of soil water. Relying on this knowledge, forest management may exclude inappropriate sites and use soil scarification to prepare seedbeds. Moreover, the germination can be enhanced through covering of the seeds (Caccia and Ballaré 1998; Huth et al. 2011). Even though information on both, soil type and soil preparation were available, this information could not contribute to improving our analysis due to the unbalanced data structure. Consequently, we did not include them in our model. Reasons for the reduced explanatory power of these variables might be seen in the resolution of the information. Both variables were only available on a categorical scale per stand, whereas the real conditions might vary on a much smaller scale. The high variability of seedling counts within stands (Fig. 3) hints at such a small-scale variation of key-factors. Furthermore, these factors have to be considered in interaction with other explanatory variables such as weather conditions, for example, which were not collected.

After germination, seedling and sapling development depends on light availability (Huth et al. 2011). Whereas an increased extension of the hypocotyl indicates demand for light, a positive correlation between biomass production and light availability could be detected in later developmental stages (Minore 1972; Reed et al. 1983; Huth et al. 2011; Petersen 2019). Petriřan et al. (2010) observed that 6-year-old Douglas firs stopped height-growth at total site factors (TSF, available photosynthetically active radiation in relation to above canopy light) of 11 % and 16 % respectively. The impact of light is not restricted to aboveground biomass, but could also be proven for the root system (Kühne et al. 2011, 2015). Foresters are able to control the light availability via stand density of both the shelter and the culture. Regulating the stand density is not only beneficial for radiation but also diminishes the overstorey root competition, which is known to negatively affect sapling growth (Petriřan et al. 2011). The measure for stand

density in our model — stocking degree — shows a light dependency of plant density. However, this relationship is not continuous, but rather shows an optimum-curve with a maximum around 0.5–0.7 (Fig. 7). This curvature seems reasonable, since on the one hand shelter can reduce the risks of frost and desiccation, but on the other hand should not be so dense as to outcompete the saplings in terms of light, nutrients and water. In Northern Germany, a maximal stocking degree of 0.6 is recommended (Preuß et al. 2017) and the results of our analysis support this advice.

It is apparent, that seedling density is positively related to seed amounts. The observed seed amounts (0.47–1.34 kg ha⁻¹, Table 1) have to be considered as relatively low. Whereas practical recommendations in Germany reach from 0.5 to 2 kg ha⁻¹ (Preuß et al. 2017; Ruppert and Rothkegel 2018), only in 1/3 of the stands ($n = 9$) 1 kg or more was applied per ha. From other studies, it is known that the relationship between seed amount and resulting plant density is not linear, but rather shows a saturation, which originates from the limited number of suitable microhabitats (Grossnickle and Ivetić 2017).

Further tools to enhance the chances of success of direct seeding, are stratification of the seeds as well as an appropriate timing. Despite contrary recommendations (Preuß et al. 2017; Ruppert and Rothkegel 2018), the seeds were often (i) not stratified and (ii) seeded in autumn (Table 1). Again due to the unbalanced structure of the inventory data, we could not assess the effect of these measures.

The impact of ungulates must also be taken into consideration. Even though it is well known that roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*) can cause severe damage in Douglas fir plantations (Spellmann et al. 2015), our inventory could not prove such a relationship, which, among others, might be attributed to the unbalanced data (only 2 of 28 stands were fenced, Table 1).

The chance of successful direct seeding can be raised through the choice of an appropriate provenance. Douglas fir is known for a huge variability between provenances, which i.a. affects the resistance to frost (Dong 1973; Larsen 1976). According to Braun and Wolf (2001) and Konnerth and Bastien (2019), provenances that sprout their leaves late, generally showed a comparably high resistance to late frost. Although, they react sensitively to early and winter frosts, there is evidence that the risk of damage by late-spring frost decreases once the trees have reached heights of 1 – 2 m (Malmqvist et al. 2018).

The outline above makes clear how fragile direct seeding of Douglas fir is. Thus, it is not surprising that we observed a broad range of densities and covering (Fig. 4). In their review, Grossnickle and Ivetić (2017) compared direct seeding programs of different species and observed that less than a half of them can be considered as successful. Success, however, can be defined in different ways and strongly depends on management goals. From a financial point of view, Mitchell et al. (1990) argue that at least 80 % of the site has to be covered by plants, in order that direct seeding becomes more cost-efficient than planting. If we had applied this standard to our results, only 8 cultures (29 %) would have met this requirement. Even under a more generous standard, one has to keep in mind that planted seedlings usually show a quicker growth than seeded ones (Grossnickle and Ivetić 2017), which in turn shortens the critical time frame of stand establishment. Furthermore, additional costs for complementary plantings or competition control might accumulate, if the achieved result is not satisfactory.

Direct seeding is a powerful stand establishment technique with, among others, advantages for root development. Nevertheless it does not fit for all situations. Especially since resources (i.e. labour, finances, seed) are scarce, they should be invested with caution and in the best possible manner.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11056-022-09927-9>.

Acknowledgements We thank the *fsb Oerrel* for help with finding suitable stands, André Olschewski for the field work, Robert Larkin for proofreading, Christoph Fischer and Regina Petersen for comments on a previous version of this manuscript, and Thomas Kneib for giving us advice on specific issues in our analysis. Moreover, we gratefully acknowledge the constructive comments of two reviewers and the Associate Editor, which improved the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Bartsch N, von Lüpke B, Röhrig E (2020) Waldbau auf ökologischer Grundlage, UTB, vol 8310, 8th edn. Ulmer, Stuttgart
- Bhaktha N (2018) Properties of hurdle negative binomial models for zero-inflated and overdispersed count data. Electronic dissertation. Retrieved from <https://etd.ohiolink.edu/>
- Bindewald A, Michiels HG, Bauhus J (2019) Risk is in the eye of the assessor comparing risk assessments of four non-native tree species in Germany. *Forestry Int J Forest Res* 93(4):519–534. <https://doi.org/10.1093/forestry/cpz052>
- Böckmann T, Hansen J, Hauskeller-Bullerjahn K, Jensen T, Nagel J, Nagel RV, Overbeck M, Pampe A, Petereit-Bitter A, Schmidt M, Schröder M, Schulz C, Spellmann H, Stüber V, Suttmöller J, Wolborn P (2019) Klimaangepasste Baumartenwahl in den Niedersächsischen Landesforsten, Aus dem Walde–Schriftenreihe Waldentwicklung in Niedersachsen, vol 61
- Bolte A, Ammer C, Löf M, Madsen P, Nabuurs GJ, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. *Scandinavian J Forest Res* 24(6):473–482, Pii 917227340. <https://doi.org/10.1080/02827580903418224>
- Brang P, Bugmann H, Bürgi A, Mühlethaler U, Rigling A, Schwitter R (2008) Klimawandel als waldbauliche Herausforderung | climate change as a challenge for silviculture. *Schweizerische Zeitschrift für Forstwesen* 159(10):362–373. <https://doi.org/10.3188/szf.2008.0362>
- Braun H, Wolf H (2001) Untersuchungen zum Wachstum und zur Frosthärte von Douglasien-Populationen in Ostdeutschland. *Beiträge für Forstwirtschaft und Landschaftsökologie* 35(4):211–214
- Bürkner PC (2017) brms: An R package for Bayesian multilevel models using Stan. *J Stat Softw* 80(1):1–28. <https://doi.org/10.18637/jss.v080.i01>
- Bürkner PC (2018) Advanced Bayesian multilevel modeling with the R package brms. *R J* 10(1):395–411. <https://doi.org/10.32614/RJ-2018-017>
- Burschel P, Huss J (1997) Grundriß des Waldbaus: ein Leitfaden für Studium und Praxis, 2nd edn. No. 49 in Pareys Studentexte, Parey, Berlin, oCLC: 610707337
- Caccia F, Ballaré C (1998) Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. *Canadian J Forest Res* 28:683–692
- Crotteau JS, Ritchie MW, Varner JM (2014) A mixed-effects heterogeneous negative binomial model for postfire conifer regeneration in Northeastern California, USA. *Forest Sci* 60(2):275–287. <https://doi.org/10.5849/forsci.12-089>, <https://academic.oup.com/forestscience/article/60/2/275-287/4583762>
- Dong PH (1973) Anbau-Folgerungen aus den bisherigen Ergebnissen über Ausfälle bei verschiedenen Douglasien-Herkünften im Aufwuchsstadium. *Allgemeine Forstzeitschrift* 28(48):1056–1058
- Efron B, Morris C (1977) Stein's Paradox in statistics. *Sci Am* 236(5):119–127. <https://doi.org/10.1038/scientificamerican0577-119>, <http://www.nature.com/doifinder/10.1038/scientificamerican0577-119>

- Fahrmeir L, Kneib T, Lang S, Marx B (2013) Regression: models, methods and applications. Springer, Berlin
- Faraway JJ (2016) Extending the linear model with R, 2nd edn. CRC Press
- Fortin M, DeBlois J (2007) Modeling tree recruitment with zero-inflated models: the example of hardwood stands in Southern Québec, Canada. *Forest Sci* 53(4):529–539. <https://doi.org/10.1093/forestscience/53.4.529>
- Gelman A, Hill J (2006) Sample size and power calculations, Cambridge University Press, pp 437–456. Analytical methods for social research. <https://doi.org/10.1017/CBO9780511790942.026>
- Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2014) Bayesian data analysis, 3rd edn. Texts in statistical science series, CRC Press, Boca Raton, FL
- Grossnickle S, Ivetić V (2017) Direct seeding in reforestation—a field performance review. *REFORESTA* (4):94–142. <https://doi.org/10.21750/REFOR.4.07.46>, <http://journal.reforestationchallenges.org/index.php/REFOR/article/view/76>
- Hesmer H (1952) Anzucht und Anbau der Douglasie. *Forstarchiv* 23(1):1–13
- 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(4):108–119. <https://doi.org/10.4432/0300-4112-82-108>
- Huth F, Wehnert A, Tiebel K, Wagner S (2017) Direct seeding of silver fir (*Abies alba* Mill.) to convert Norway spruce (*Picea Abies* L.) forests in Europe: a review. *Forest Ecol Manag* 403:61–78. <https://doi.org/10.1016/j.foreco.2017.08.017>, <http://www.sciencedirect.com/science/article/pii/S0378112717307946>
- IPCC (2015) Climate change 2014: synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland
- Jaynes ET (1976) Confidence intervals vs bayesian intervals. In: Harper WL, Hooker CA (eds) Foundations of probability theory, statistical inference, and statistical theories of science, Springer, Netherlands, Dordrecht
- Jaynes ET (2003) Probability theory: the logic of science. Cambridge University Press
- Kleiber C, Zeileis A (2016) Visualizing count data regressions using rootograms. *Am Statist* 70(3):296–303. <https://doi.org/10.1080/00031305.2016.1173590>
- Klädtké J, Kohnle U, Kublin E, Ehling A, Pretzsch H, Uhl E, Spellmann H, Weller A (2012) Wachstum und Wertleistung der Douglasie in Abhängigkeit von der Standraumgestaltung. *Schweizerische Zeitschrift für Forstwesen* 163(3):96–104. <https://doi.org/10.3188/szf.2012.0096>
- Kohnle U, Klädtké J, Chopard B (2019) Management of Douglas-fir. In: Spiecker H, Lindner M, Schuler JK (eds) Douglas-fir: an option for Europe. What Sci. Can Tell Us, vol 9, pp 73–83
- Konnert M, Bastien JC (2019) Genecology of Douglas-fir and tree improvement strategies. In: Spiecker H, Lindner M, Schuler JK (eds) Douglas-fir: an option for Europe, What Science Can Tell Us, vol 9, pp 46–56
- Kühne C, Bauhus J, Hörnig T, Oh S (2011) Einfluss von Überschirmung, Dichtstand und Pflanzengröße auf die Wurzelentwicklung natürlich verjüngter Douglasien. *Forstarchiv* 82(5):184–194. <https://doi.org/10.4432/0300-4112-82-184>
- Kühne C, Karrié C, Forrester DI, Kohnle U, Bauhus J (2015) Root system development in naturally regenerated Douglas-fir saplings as influenced by canopy closure and crowding. *J Forest Sci* 61(9):406–415. <https://doi.org/10.17221/53/2015-JFS>
- Larsen JB (1976) Untersuchungen über die Frostempfindlichkeit von Douglasienherkünften und über den Einfluß der Nährstoffversorgung auf die Frostresistenz der Douglasie. *Der Forst- und Holzwirt* 31(15):299–302
- Lavender DP, Hermann RK (2014) Douglas-Fir: the Genus *Pseudotsuga*. OSU College of Forestry
- Lawrence WH, Rediske JH (1962) Fate of sown Douglas-Fir seed. *Forest Sci* 8(3):210–218. <https://doi.org/10.1093/forestscience/8.3.210>
- Lemoine NP (2019) Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128(7):912–928. <https://doi.org/10.1111/oik.05985>
- Li R, Weiskittel AR, Kershaw JA (2011) Modeling annualized occurrence, frequency, and composition of ingrowth using mixed-effects zero-inflated models and permanent plots in the Acadian Forest Region of North America. *Canadian J Forest Res* 41(10):2077–2089. <https://doi.org/10.1139/x11-117>
- 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 Forests* 49(6):723–736. <https://doi.org/10.1007/s11056-018-9635-7>
- Minore D (1972) Germination and early growth of coastal tree species on organic seed beds, USDA Forest Service Research Paper, vol pnw 135

- Mitchell W, Dunsworth G, Simpson D, Vyse A (1990) Planting and seeding. In: Lavender DP, Parish R, Johnson C, Montgomery G, Vyse A, Willis R, Winston D (eds) Regenerating British Columbia's forests. University of British Columbia Press, Vancouver, pp 235–253
- Möges M, Ruppert O, Mergner W (2008) Die Douglasie in den Bayerischen Staatsforsten. In: Die Douglasie—Perspektiven im Klimawandel, no 59 in LWF-Wissen, pp 44–48
- Mohamedou C, Kangas A, Hamedianfar A, Vauhkonen J (2022) Potential of bayesian formalism for the fusion and assimilation of sequential forestry data in time and space. *Canadian J Forest Res* -(-):-, <https://doi.org/10.1139/cjfr-2021-0145>
- Morris WK, Vesik PA, McCarthy MA, Bunyavejchewin S, Baker PJ (2015) The neglected tool in the bayesian ecologist's shed: a case study testing informative priors' effect on model accuracy. *Ecol Evol* 5(1):102–108. <https://doi.org/10.1002/ece3.1346>
- NFP, LLUR (2009a) Forstliche Standortsaufnahme. Geländeökologischer Schätzrahmen - Varianten. Anwendungsbereich: pleistozänes (diluviales) Flachland, Mittelgebirge, Berg- und Hügelland. Niedersächsisches Forstplanungsamt & Landesamt für Landwirtschaft, Umwelt und ländliche Räume Schleswig-Holstein
- NFP, LLUR (2009b) Forstliche Standortsaufnahme. Geländeökologischer Schätzrahmen. Anwendungsbereich: pleistozänes (diluviales) Flachland. Niedersächsisches Forstplanungsamt und Landesamt für Landwirtschaft, Umwelt und ländliche Räume Schleswig-Holstein
- Nicolescu VN (2019) Natural range, site requirements and shade tolerance. In: Spiecker H, Lindner M, Schuler JK (eds) Douglas-fir: an option for Europe, What Science Can Tell Us, vol 9, pp 33–39
- Petersen R (2019) Freisaat von Douglasie—eine Alternative zur Pflanzung. *AFZ-DerWald* 74(19):28–31
- Petrişan IC, von Lüpke B, Petrişan AM (2010) Einfluss unterschiedlicher Hiebsformen auf das Wachstum junger Buchen und Douglasien aus Pflanzung. *Forstarchiv* 81(2):40–52. <https://doi.org/10.4432/0300-4112-81-40>
- Petrişan IC, von Lüpke B, Petrişan AM (2011) Effects of root trenching of overstorey Norway spruce (*Picea abies*) on growth and biomass of underplanted beech (*Fagus sylvatica*) and Douglas fir (*Pseudotsuga menziesii*) saplings. *Eur J Forest Res* 130(5):813–828. <https://doi.org/10.1007/s10342-010-0473-1>
- Pretzsch H, Biber P, Schütze G, Uhl E, Rötzer T (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Commun* 5. <https://doi.org/10.1038/ncomms5967>
- Preuß A, Kiefer K, Gille K, Heinrichs D (2017) Praxistipps der fsb Oerrel zur Freisaat im Wald
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rathbun SL, Fei S (2006) A spatial zero-inflated poisson regression model for oak regeneration. *Environ Ecol Statist* 13(4):409–426. <https://doi.org/10.1007/s10651-006-0020-x>
- Reed KL, Shumway JS, Walker RB, Bledsoe CS (1983) Evaluation of the interaction of two environmental factors affecting Douglas-fir seedling growth: light and Nitrogen. *Forest Sci* 29(1):193–203. <https://doi.org/10.1093/forestscience/29.1.193>
- Röhrig E (1976) Anzucht und Pflanzung von Douglasien. *Der Forst- und Holzwirt* 31(15):295–299
- Rumpf H (2007) Erste Ergebnisse eines Freisaatversuches mit Traubeneiche im Nordwestdeutschen Flachland. *Forst und Holz* 62(3):13–18
- Ruppert O, Rothkegel W (2018) Die Saat im Wald - wieder entdeckt. *LWF aktuell* 116(1):37–40
- Shonkwiler J (2016) Variance of the truncated negative binomial distribution. *J Econ* 195(2):209–210. <https://doi.org/10.1016/j.jeconom.2016.09>
- Spellmann H, Weller A, Brang P, Michiels HG, Bolte A (2015) Douglasie. In: Vor T, Spellmann H, Bolte A, Ammer C (eds) Potenziale und Risiken eingeführter Baumarten: Baumartenportraits mit naturschutzfachlicher Bewertung, Göttinger Forstwissenschaften, vol 7. Universitätsverlag Göttingen, Göttingen, pp 187–217
- Stan Development Team (2019) Stan: a C++ library for probability and sampling, version 2.19.2. <http://mc-stan.org/>
- Sullivan TP, Sullivan DS (1984) Operational direct seeding of Douglas-fir and Lodgepole Pine with alternative Foods in British Columbia. Tech. Rep. 97, Applied Mammal Research Institute, Langley, British Columbia
- Terwei A, Zerbe S, Zeileis A, Annighöfer P, Kawaletz H, Mölder I, Ammer C (2013) Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? *Forest Ecol Manag* 304:192–203. <https://doi.org/10.1016/j.foreco.2013.05.003>, <https://linkinghub.elsevier.com/retrieve/pii/S0378112713002934>
- Thünen-Institut (2014) Third National Forest Inventory—results database. <https://bwi.info/>. Accessed 2 Sept 2016
- Toumey JW (1916) Seeding and Planting. A manual for the guidance of forestry students, foresters, nurserymen, forest owners, and farmers., 1st edn. Wiley, New York
- van Erp S, Oberski DL, Mulder J (2019) Shrinkage priors for bayesian penalized regression. *J Math Psychol* 89:31–50. <https://doi.org/10.1016/j.jmp.2018.12.004>

- van Loo M, Dobrowolska D (2019a) Current situation. In: Spiecker H, Lindner M, Schuler JK (eds) Douglas-fir: an option for Europe. What Sci Can Tell Us, vol 9, pp 26–29
- van Loo M, Dobrowolska D (2019b) History of introducing Douglas-fir to Europe. In: Spiecker H, Lindner M, Schuler JK (eds) Douglas-fir: an option for Europe, What Science Can Tell Us, vol 9, pp 21–25
- Vitali V, Büntgen U, Bauhus J (2017) Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. *Glob Chang Biol* 23(12):5108–5119. <https://doi.org/10.1111/gcb.13774>
- von Lüpke B (2009) Überlegungen zu Baumartenwahl und Verjüngungsverfahren bei fortschreitender Klimaänderung in Deutschland. *Forstarchiv* 80(3):67–75
- von Lüpke N, Sennhenn-Reulen H, Olschewski A (2021). Inventory data of directly seeded Douglas fir regeneration in Northwest Germany. <https://doi.org/10.5281/zenodo.5541226>
- Wesner JS, Pomeranz JP (2020) Choosing priors in Bayesian ecological models by simulating from the prior predictive distribution. *bioRxiv*. <https://doi.org/10.1101/2020.12.10.419713>
- Wiedemann E (1943) Ertragstafel für die Baumart Kiefer. Ertragstafeln wichtiger Baumarten bei verschiedener Durchforstung, 4th edn. J.D. Sauerländer's Verlag, Frankfurt a. M., pp 104–121
- Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. *J Statist Softw* 27(8):1–25. <https://doi.org/10.18637/jss.v027.i08>
- Zhang X, Lei Y, Cai D, Liu F (2012) Predicting tree recruitment with negative binomial mixture models. *Forest Ecol Manag* 270:209–215. <https://doi.org/10.1016/j.foreco.2012.01.028>, <https://linkinghub.elsevier.com/retrieve/pii/S0378112712000382>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.