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Modelling natural regeneration of Oak in Saxony, Germany: identifying factors influencing the occurrence and density of regeneration

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In the course of climate change, natural regeneration of oaks (*Quercus* spp.) is gaining in importance for forest conversion to climate-adapted mixed forests. In order to predict areas in which natural oak regeneration could establish, variables influencing the occurrence and density of oak regeneration were identified using geostatistical zero-altered negative binomial generalized linear models (ZANB). For this purpose, large-scale inventory data from the state forest of Saxony were analysed. The dataset was derived from 6060 permanent plots. The results show that the occurrence of oak regeneration depends on a number of environmental variables. In addition to seed availability, the establishment environment, especially with regard to the light ecology of oak regeneration, was important. High basal area of pine increased the probability for oak regeneration occurrence. The most important variables for the regeneration density of oak have similarly been found to be those describing the seed availability. The highest regeneration densities are predicted within oak stands, with an optimum relationship at 25 m^2 ha^{-1} of oak basal area. The results further show that a high regeneration density was achieved on sites with low fertility and favourable light conditions. Oak regeneration density increased with increasing browsing percent on rowan, indicating that browsing on oak can be reduced if other palatable species are available. Using the identified variables, the occurrence and density of oak regeneration can be predicted in space with high accuracy. The statistical tool developed can be used for planning forest conversion incorporating natural regeneration.

Keywords: Oak, Established Natural Regeneration, INLA, Zero-altered Negative Binomial Model, Spatial Random Effects, Bayesian Inference

Introduction

Pedunculate oak (*Quercus robur* L.) and Sessile oak (*Quercus petraea* [Matt.] Liebl.) are particularly widespread in Central Europe, and are among the ecologically and economically most important deciduous tree species (Löf et al. 2016, Mölder et al. 2019a). In the course of climate change, both European oak species are important tree species that will probably gain in importance as components of mixed species stands due to their drought tolerance (Zimmermann et al. 2015, Arvai et al. 2018, Kunz et al. 2018). Modern silvicultural planning prefers natural oak regeneration to planting in terms of cost reduction (Vrška et al. 2016, Kaliszewski 2017), genetic diversity (Chybicki & Burczyk 2010) and undisturbed root development (González-Rodríguez et al. 2011). However, natural oak regeneration often fails because a number of environmental factors take effect during the regeneration cycle (Watt 1919, Shaw 1968, Mölder et al. 2019b, Kohler et al. 2020).

Regeneration establishment is the result of a cascade of successive processes, which start with flowering and fruiting (Fischer et al. 2016). Studies suggest that the availability of acorns (*i.e.*, masting behavior – Caignard et al. 2017, Hanley et al. 2019), as well as their dispersal potential (Axer et al. 2021b), are not relevant in limiting the occurrence of natural regeneration (Clark et al. 2007). In contrast, during storage, many acorns can be damaged by fungi (Schroder 2002) or destroyed by predation (Crawley & Long 1995, Nilsson et al. 1996, Myczko et al. 2014). During germination and following establishment, abiotic factors such as radiation availability (Ziegenhagen & Kausch 1995, Annighöfer et al. 2015, Modrow et al. 2020) and water availability, but also biotic factors such as competing vegetation (Collet & Frochot 1996, Humphrey & Swaine 1997, Ligot et al. 2013), pathogens (Demeter et al. 2021) and browsing by deer (Bideau et al. 2016) are crucial for successful regeneration.

Combining large-scale inventory data and environmental information (*e.g.*, seed dispersal) factors influencing the success of natural oak regeneration can be identified (Annighöfer et al. 2015, Mölder et al. 2019b). Based on these influencing factors, spatial predictions of natural oak regeneration can be made with geostatistical models and thus be integrated into forest management practice (Brown 2015, Krainski et al. 2019). This leads to the research question of the present work: (i) which are the

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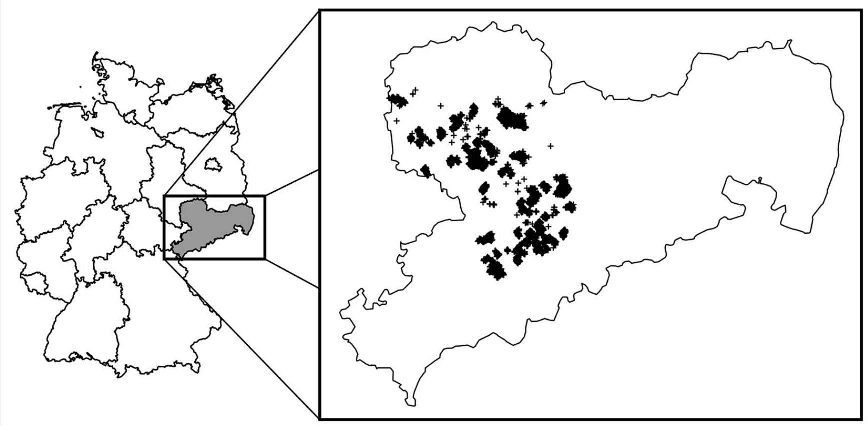

Fig. 1 - Overview of the study area with location of the state forest areas and inventory design.

most relevant factors influencing the presence and absence of natural oak regeneration? And (ii) if oak regeneration is present, which factors influence the density of oak regeneration?

Material and methods

Study area and inventory design

The study was conducted in the state forest of Saxony, Germany. The data used for the study were compiled as part of a forest inventory and provided by Sachsenforst, *i.e.*, the administration that manages the state forest of Saxony. The data was collected in the period from 2018 to 2020. As part of the forest inventory, 6060 plots were surveyed on a square grid with a side length of 200 metres.

The plots are located in the two altitudinal zones "hill terrain" and "lower mountain terrain" of the Ore mountains (Fig. 1). An altitudinal gradient of 94 to 592 m a.s.l. is covered. The hill terrain is dominated by a strong loess-loam influence. In the hill terrain, temporally waterlogged sites are particularly frequent.

The presence and density of naturally regenerated oaks were recorded within a subplot with a radius of 2 m (≈ 12.57 m^2) located 5 m north of the plot centre. Within each subplot, regeneration with a height ≥ 20 cm and < 50 cm was measured. In order to examine factors influencing the dependent variable, various explanatory variables were used. These are divided into plot-specific variables, site variables and variables describing the surrounding. Plot-specific information for the overstory was obtained from two concentric plots (6 and 12 m radius). Information obtained from the plots are quadratic mean diameter (d_q), total basal area, tree species-specific basal areas, stand density index (*SDI*) and a spatially interpolated browsing percentage on rowan. For further information on the inventory design, please refer to Axer et al. (2021a). Since seed dispersal also extends the radius of the plot (Kurek & Dobrowolska 2016), remote sensing data were incorporated to determine distances to the nearest potential seed trees. Site variables that were considered for the analysis were altitude, nutrient content, moisture level and pH, and spatially interpolated C stocks and N stocks.

Modelling oak regeneration occurrence and density

Due to a spatial dependence of the regeneration data and a huge proportion of plots without oak regeneration, zero-altered negative binomial generalized linear models (ZANB) with spatial random effects were used (eqn. 1). The occurrence {0,1} and density of oak regeneration (OD_i – i = 1, …, n) at n observations in the plots depending on covariates can be examined and thus facilitate an ecological understanding. Following the example of Zuur et al. (2018), the model was fitted in a Bayesian framework using the integrated nested Laplace approximation of the package INLA (Lindgren & Rue 2015) in R (R Core Team 2018). The following formula describes the full ZANB model used to investigate the variables (eqn. 1 to eqn. 7):

$$OD_i \sim ZANB(\mu_i, \pi_i, k) \qquad (1)$$

$$E(OD_i) = \frac{\pi_i}{1-P_0} \cdot \mu_i \qquad (2)$$

$$var(OD_i) = \frac{\pi_i}{1-P_0} \cdot \left(\mu_i^2 + \mu_i + \frac{\mu_i^2}{k}\right) - \left(\frac{\pi_i}{1-P_0} \cdot \mu_i\right)^2 \qquad (3)$$

$$logit(\pi_i) = \gamma_o + z_{1i}\gamma_1 + \ldots + z_{ni}\gamma_n + v_i \qquad (4)$$

$$v = (v_i)_{i=1,\ldots,n} \sim N(0, \Sigma v) \qquad (5)$$

$$\log(\mu_i) = \beta_0 + x_{1i}\beta_1 + \ldots x_{mi}\beta_m + u_i \qquad (6)$$

$$u = (u_i)_{i=1,\ldots,n} \sim N(0, \Sigma u) \qquad (7)$$

where $P_0 = [k/(\mu_i+k)]^k$, π_i is the probability that oak regeneration occurs on the plot and is modelled *via* a Bernoulli GLM (General Linear Model). The γs represent the n coefficients of the Bernoulli model multiplied by each of the n chosen explanatory variables z_i. A negative binomial distribution with zero truncation is used for the non-zero frequencies μ_i. The *β*s represent the m coefficients of the count model multiplied by each of the m selected explanatory variables x_i. The zero-truncated negative binomial model estimated a hyperparameter k termed size that accounts for overdispersion. For the parameter estimation of the fixed effects, the default prior distributions of R-INLA (*i.e.*, normal distributions) were used.

The terms u_i and v_i are random intercepts, which are assumed to be spatially correlated in the occurrence and density part of the model with the mean value 0 and the covariance matrix ∑. It was assumed that u and v show Markovian behavior and follow a Gaussian Markov Random Field (GMRF). To quantify the associated covariance matrices of u and v, Matérn covariance functions were used and numerically approximated using SPDE (continuous domain stochastic partial differential equation). In this way, parameters are obtained that characterize the spatial random field.

A comparative analysis conducted previously suggests that those models containing only covariates and those models containing only a spatial random term had poorer model goodness of fit than the full model, which includes both covariates and spatial random effects. This result from the preliminary analysis suggests that the spatial relationship between plots contains valuable information that is not captured by the environmental covariates on their own. Therefore, the final ZANB model included spatial correlation in both the count and binary parts of the model. The fixed effects for regeneration occurrence and density are described separately below. Subsequently, the spatial random effects and the overall prediction by the model are presented.

Results and discussion

Occurrence of oak regeneration

For 83.4% of the plots, there was no oak regeneration in the size class investigated. However, oak regeneration occurred on 1005 plots. The most important variables for the occurrence of oak regeneration were oak quadratic mean diameter in the overstory of a plot and the distance to the nearest oak stand (Fig. 2, Tab. 1). These two variables indicate that both barochory and zoochory are decisive for the dispersal of acorns. In oak stands with d_q ≥ 40 cm, oak regeneration can be expected. With increasing distance to the nearest oak, the probability of oak regeneration occurrence decreases, but oak regeneration can be expected even at distances greater than 1 km (Axer et al. 2021b). Here, however, the establishment environment is crucial: while high total basal area and beech basal area have a negative effect on the occurrence

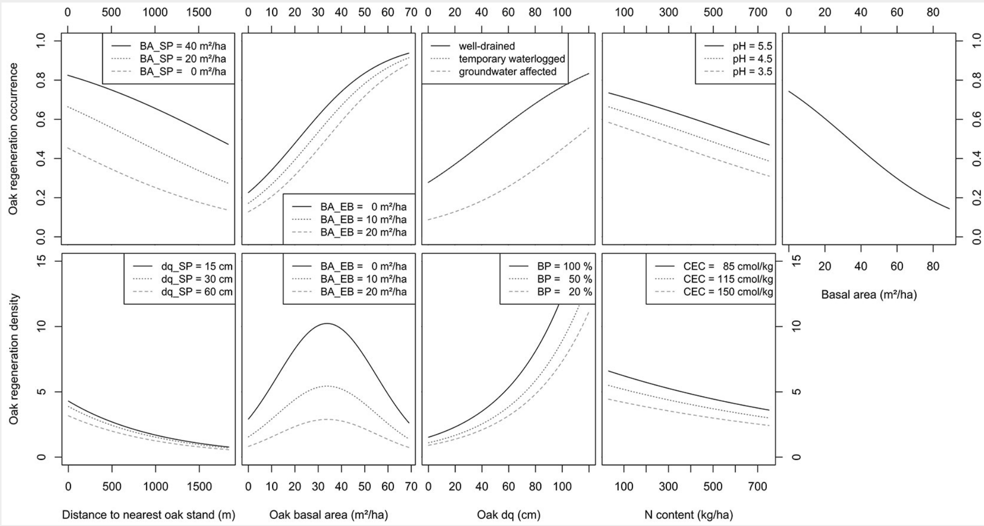

Fig. 2 - Predicted probability of the occurrence (above) and density (below) of natural regeneration of oak depending on distance to the nearest oak stand, oak basal area, oak quadratic mean diameter (dq), N content and total basal area with varying pine basal area (BA_SP), beech basal area (BA_EB), and pH for regeneration occurrence and with varying pine quadratic mean (dqSP), beech basal area, browsing percent and Cation exchange capacity (CEC) (all continuous variables are set to their mean; all factors are set to their most frequent factor level).

and reflect the light requirements of oak regeneration (Annighöfer et al. 2015, Modrow et al. 2020), the probability of oak regeneration increases with increasing pine basal area (Tab. 1). A preference of the Eurasian jay (*Garrulus glandarius* L.) for the dispersal of acorns into pine stands is clearly indicated (Gómez 2003, Kurek et al. 2019). Furthermore, the favourable conditions for the establishment of oak regeneration in pine stands are due to the comparatively high crown transparency, the low influence of abiotic and biotic damaging factors, the favourable stand climate, and a favourable flora composition (Mosandl & Kleinert 1998, Dobrowolska 2006, Mirschel et al. 2011, Onaindia et al. 2013, Kurek & Dobrowolska 2016, Kurek et al. 2019). An admixture with beech, on the other hand, often leads to problems with oak regeneration due to shading and interspecific competition within the regeneration (Ligot et al. 2013, Annighöfer et al. 2015). With a beech basal area of 20 m² ha⁻¹, the probability of oak regeneration is significantly reduced (Fig. 2).

While beech regeneration is less frequent on temporarily waterlogged sites (Axer et al. 2021a), no difference between well-drained sites and temporarily waterlogged sites can be demonstrated for oak regeneration (Tab. 1). Only on groundwater-affected locations oak regeneration probability is reduced (Leuschner & Ellenberg 2017). A negative influence of high nitrogen stocks was demonstrated (Fig. 2), which is in accordance with the investigations of Mirschel et al. (2011). Furthermore, a higher probability of oak regeneration occurrence was demonstrated at higher pH values. Both, nitrogen content and pH value characterise soil quality. Similar results with regard to soil enzyme activity were reported by Dobrowolska et al. (2021).

Humus cover and the type of ground vegetation are indirectly described by the nitrogen content of the topsoil. A negative influence of ground vegetation has also been demonstrated in previous studies (Collet & Frochot 1996, Mölder et al. 2019b).

Density of oak regeneration

On average, 4.5 oak saplings (3600 ind. ha^{-1}) were found in the 1005 colonised plots (16.5 % colonised). The distance to the nearest oak stand strongly influences the regeneration density (Axer et al. 2021b). At high dispersal distances, only low regeneration densities around 1000 trees per hectare were predicted (Fig. 2). These densi-

Tab. 1 - Fixed effects of the occurrence and density part of the ZANB models for oak natural regeneration. The optimised model with the lowest WAIC values are presented. In the table the output is shown with the posterior mean and the 95 % credible intervals (0.025 and 0.975). Interpreting the estimated values, it should be noted that the covariates have quite different ranges.

Model	Covariate	Mean	0.025 quant	0.975 quant
Occurrence	Intercept	-2.039	-3.179	-0.912
	Distance to oak stand	-0.001	-0.001	-0.001
	D_q oak	0.023	0.016	0.030
	D_q pine	0.007	0.001	0.014
	N content	-0.002	-0.003	-0.001
	pH value	0.001	0.001	0.004
	Basal area	-0.030	-0.056	-0.004
	Basal area beech	-0.053	-0.086	-0.023
	Basal area oak	0.054	0.039	0.070
	Basal area pine	0.036	0.021	0.051
	Stand density index	-0.001	-0.002	-0.001
	Canopy cover	0.819	0.231	1.406
	Groundwater-affected	-0.933	-1.653	-0.232
	Well-drained	0.407	-0.031	0.865
	Temporarily waterlogged	0.329	-0.122	0.797
Density	Intercept	0.812	0.432	1.182
	Distance to oak stand	-0.001	-0.002	-0.001
	D_q oak	0.021	0.016	0.027
	D_q pine	-0.009	-0.014	-0.004
	Basal area beech	-0.048	-0.083	-0.012
	Basal area oak	0.070	0.049	0.091
	I(Basal area oak)^2	-0.001	-0.001	-0.001
	Browsing percent rowan	0.009	0.004	0.014
	CEC	-0.006	-0.009	-0.003
	N content	-0.001	-0.002	-0.001

Tab. 2 - Random field hyperparameters for the ZANB model. The term *u* characterizes the spatial random field of the zero-truncated part of the model, while *v* characterizes the spatial random field for the Bernoulli part of the model.

Spatial random field	Hyper-parameter	Mean	0.025 quant	0.975 quant
u	θ_{u1}	8.367	5.231	12.397
	θ_{u2}	-5.508	-6.732	-3.557
v	θ_{v1}	6.845	5.625	8.232
	θ_{v2}	-6.900	-7.716	-6.176

ties are consistent with previous studies of jay induced natural oak regeneration (Mosandl & Kleinert 1998). The influence of pine d_q indicates that there seems to be a window of opportunity for oak regeneration. As the diameter of the pine stand increases, the predicted oak regeneration density of the investigated size class decreases (Tab. 1). This can be attributed to an increasing disruption of canopy closure due to thinning and the establishment of other competitive tree species and grasses at different successional phases (Eisenhauer 1996). This successional process within pine stands was also demonstrated by Onaindia et al. (2013).

Oak stands have a significant positive effect on oak regeneration density (Annighöfer et al. 2015). For plots within oak stands, an optimum relationship results with regard to the oak basal area (Tab. 1). As the oak basal area increases, the proportion of other tree species in the basal area decreases, so that light transmission improves in addition to seed quantity (Lüpke & Hauskeller-Bullerjahn 1999, Kamler et al. 2016). The highest regeneration densities were predicted at 30 m^2 ha^{-1} (Fig. 2). This is in line with Annighöfer et al. (2015), who were able to identify an oak basal area of 25 m^2 ha^{-1} as the optimum. The significant influence of the beech basal area also affects the oak regeneration density: with a higher beech basal area, the oak regeneration density is clearly reduced (Manso et al. 2019). In line with the oak basal area, the oak d_q also shows a positive influence on the regeneration density (Fig. 2). With increasing dbh, the number of seeds produced increases and the light transmission improves.

The browsing percentage on rowan showed a surprising effect. When the percentage of rowan browsing is high, the density of oak regeneration is higher (Tab. 1). Similar results could also be found by Mirschel et al. (2011) and Annighöfer et al. (2015). Due to the high browsing preference of rowan, it may happen that oak is protected by selective browsing (Motta 2003, Kupferschmid 2018). However, oaks are also preferentially browsed (Götmark et al. 2005). Nevertheless, recent studies suggest that short-term browsing mainly reduces the growth of oak seedlings rather than increasing its mortality (Bideau et al. 2016, Barrere et al. 2021). A significantly lower proportion of plots with larger oak regeneration in the study area supports this observation (> 50 cm and < 130 cm height: 5 %; height > 130 cm and dbh < 7 cm: 2.4 % colonised).

The variables describing soil conditions have a similar effect on the density as on the occurrence of oak regeneration (Mirschel et al. 2011). Vegetation cover indicating low-nitrogen sites, such as blueberry (*Vaccinium myrtillus* L.) and moss, has proven to be particularly favourable for high regeneration density (Stähr & Peters 2000, Mirschel et al. 2011, Drössler et al. 2017). The same effect is indicated for the cation exchange capacity. On sites with lower CEC, the predicted regeneration density is higher (Fig. 2). This has also been confirmed by the work of Annighöfer et al. (2015).

Model prediction

Maps for the presence and density of oak regeneration can be created based on the explanatory variables and random effects (Krainski et al. 2019). Spatial predictions for a given location are possible because the model provides an approximation of the entire random field (Lindgren & Rue 2015). The spatial random field was defined by the hyperparameters θ_1 and θ_2 which defined the spatial range and variance of the random field given in Tab. 2.

Fig. 3 shows the spatial predictions for a part of the study area. It also becomes apparent that in many areas there is a very good fit between observation and prediction. It becomes clear that natural regeneration occurs in many areas. However, the spatial random fields indicate that there was an obvious spatial pattern of unexplained variability where the fixed effects alone underestimate both presence and density. At the same time, there are areas where the fixed effects overestimate the occurrence probability and the regeneration density (Fig. 3). The precision of the overall prediction provided by the model can be seen both in Fig. S1 (Supplementary material) and in the CPO values (Tab. S1). The comparison of observed densities with predicted densities, root mean square error (RMSE) and bias estimate in the form of the mean prediction error (E), as well as the CPO values of the leave-one-out cross-validation indicated a quite good predic-

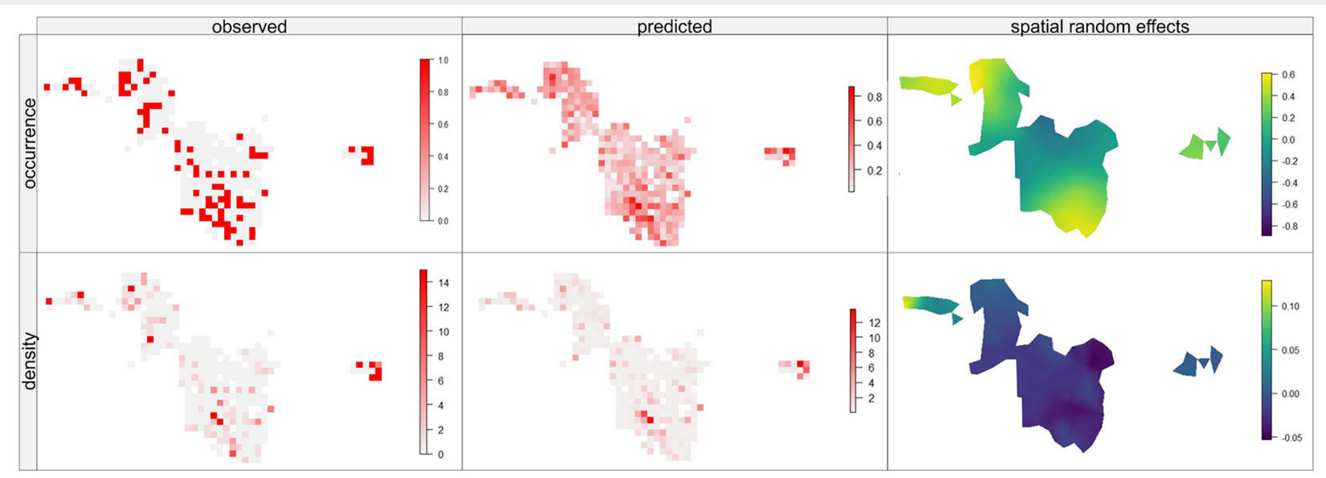

Fig. 3 - Example area within the study area with observed occurrence and density of oak regeneration (left), spatial prediction (centre) and spatial random field of the ZANB model for a part of the study area. Dark blue shaded areas have a lower probability of occurrence and high density of regeneration than predicted by the fixed effects. Yellow areas have a higher probability.

tion accuracy (Tab. S1 in Supplementary material).

Based on the spatial patterns of the random effects, unobserved processes responsible for these patterns can be deduced (Zuur et al. 2018). Influencing factors such as hunting intensity, areas avoided by deer due to forest visitors, small-scale differences in ground vegetation, or unrecorded seed sources could, for example, be the underlying factors for these patterns.

Conclusions

Geostatistical models offer the possibility to analyse regeneration data. Factors influencing the occurrence and density of oak regeneration can be studied separately. Considering spatial random effects assists in explaining more variation in the model and thus improves model prediction. In addition, the patterns of spatial random effects provide indications of unobserved processes. These predictions can be used to incorporate natural regeneration in decisions on forest conversion activities at the forest management level.

Oak regeneration can be used in the conversion of coniferous-dominated stands into climate-adapted mixed stands. Areas where artificial regeneration is necessary can also be identified using predictive models. This is of enormous importance for forest management in terms of cost reduction. The results suggest that there is a huge natural regeneration potential. The ingrowth of natural regeneration can be promoted by targeted measures such as thinning of the overstory, fencing or intensified hunting.

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Author Contributions

M.A. conceived the study and methodology, processed data, performed statistical analysis and validation, wrote the original draft, and visualised the published work. S.M. participated in conceptualisation and methodology of the study, contributed to data processing and validation, reviewing, and editing of the paper. R.S. assisted with statistical analysis and validation and, contributed to reviewing the paper. D.E. participated in conceptualisation of the study, provided resources, and contributed to validation and reviewing the paper. S.W. conceived the study, administered the project, provided resources and supervision, reviewed, and edited the paper, and acquired funding.

References

Annighöfer P, Beckschäfer P, Vor T, Ammer C (2015). Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. PloS One 10: 134935. - doi: 10.1371/journal.pone.0134935

Arvai M, Morgós A, Kern Z (2018). Growth-climate relations and the enhancement of drought signals in pedunculate oak (*Quercus robur* L.) tree-ring chronology in Eastern Hungary. iForest - Biogeosciences and Forestry 11: 267-274. - doi: 10.3832/ifor2348-011

Axer M, Martens S, Schlicht R, Wagner S (2021a). Modelling natural regeneration of European beech in Saxony, Germany: identifying factors influencing the occurrence and density of regeneration. European Journal of Forest Resaerch: 1-22. - doi: 10.1007/s10342-021-01377-w

Axer M, Schlicht R, Wagner S (2021b). 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. Forest Ecology and Management 482: 118802. - doi: 10.1016/j.foreco.2020.118802

Barrere J, Petersson LK, Boulanger V, Collet C, Felton AM, Löf M, Saïd S (2021). Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. Forest Ecology and Management 487: 118976. - doi: 10.1016/j.foreco.2021.118976

Bideau E, Maublanc M-L, Picot D, Hamard J-P, Ballon P, Gerard J-F (2016). Short-term browsing by roe deer has little effect on survival and growth of sessile oak seedlings. Scandinavian Journal of Forest Research 31: 40-45. - doi: 10.1080/02827581.2015.1054873

Brown PE (2015). Model-based geostatistics the easy way. Journal of Statistical Software 63: 1-24. - doi: 10.18637/jss.v063.i12

Caignard T, Kremer A, Firmat C, Nicolas M, Venner S, Delzon S (2017). Increasing spring temperatures favor oak seed production in temperate areas. Scientific Reports 7: 8555. - doi: 10.1038/s41598-017-09172-7

Chybicki IJ, Burczyk J (2010). Realized gene flow within mixed stands of *Quercus robur* L. and *Q. petraea* (Matt.) L. revealed at the stage of naturally established seedling. Molecular Ecology 19: 2137-2151. - doi: 10.1111/j.1365-294X.2010.04632.x

Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007). Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. The American Naturalist 170: 128-142. - doi: 10.1086/518565

Collet C, Frochot H (1996). Effects of interspecific competition on periodic shoot elongation in oak seedlings. Canadian Journal of Forest Research 26: 1934-1942. - doi: 10.1139/x26-218

Crawley MJ, Long CR (1995). Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. Journal of Ecology 83: 683. - doi: 10.2307/2261636

Demeter L, Molnár AP, Ollerer K, Csóka G, Kiš A, Vadász C, Horváth F, Molnár Z (2021). Rethinking the natural regeneration failure of pedunculate oak: the pathogen mildew hypothesis. Biological Conservation 253: 108928. - doi: 10.1016/j.biocon.2020.108928

Dobrowolska D (2006). Oak natural regeneration and conversion processes in mixed Scots pine stands. Forestry 79: 503-513. - doi: 10.1093/forestry/cpl034

Dobrowolska D, Kurek P, Olszowska G, Bolibok L (2021). Effects of stand features and soil enzyme activity on spontaneous pedunculate Oak regeneration in Scots pine dominated stands-implication for forest ecosystems. Research Square, art. no. rs-153974, pp. 33. [preprint] - doi: 10.21203/rs.3.rs-153974/v1

Drössler L, Fahlvik N, Wysocka N, Hjelm K, Kuehne C (2017). Natural regeneration in a multi-layered *Pinus sylvestris-Picea abies* forest after target diameter harvest and soil scarification. Forests 8: 35. - doi: 10.3390/f8020035

Eisenhauer D-R (1996). Einwanderung der Eichen in Kiefernbestände-Bedeutung für den Waldbau im nordostdeutschen Tiefland [Immigration of oaks into pine stands - Relevance for silviculture in the north-eastern German lowlands]. In: Proceedings of the Silviculture Section of the German Association of Forest Research Institutes, Schopfheim–Wiechs, Germani, pp. 30-43. [in German]

Fischer H, Huth F, Hagemann U, Wagner S (2016). Developing restoration strategies for temperate forests using natural regeneration processes. In: "Restoration of Boreal and Temperate Forests" (Stanturf JA ed). CRC Press, Boca Raton, FL, USA, pp. 103-164. [online] URL: http://books.google.com/books?id=D15ECgAAQBAJ

Gómez JM (2003). Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573-584. - doi: 10.1034/j.1600-0587.2003.03586.x

González-Rodríguez V, Navarro-Cerrillo RM, Villar R (2011). Artificial regeneration with *Quercus ilex* L. and *Quercus suber* L. by direct seeding and planting in southern Spain. Annals of Forest Science 68: 637-646. - doi: 10.1007/s13595-011-0057-3

Götmark F, Berglund A, Wiklander K (2005). Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scandinavian Journal of Forest Research 20: 223-234. - doi: 10.1080/02827580510008383

Hanley ME, Cook BI, Fenner M (2019). Climate variation, reproductive frequency and acorn yield in English Oaks. Journal of Plant Ecology 12: 542-549. - doi: 10.1093/jpe/rty046

Humphrey JW, Swaine MD (1997). Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. I. Competition from *Pteridium aquilinum*. Journal of applied Ecology 34: 577-584. - doi: 10.2307/2404908

Kaliszewski A (2017). Cost analysis of artificial and natural oak regeneration in selected forest districts. Forest Research Papers 78: 315-321. - doi: 10.1515/frp-2017-0035

Kamler J, Dobrovolny L, Drimaj J, Kadavy J, Kneifl M, Adamec Z, Knott R, Martiník A, Plhal R, Zeman J, Hrbek J (2016). The impact of seed predation and browsing on natural sessile oak regeneration under different light conditions in an over-aged coppice stand. iForest - Biogeosciences and Forestry 9: 569-576. - doi:

10.3832/ifor1835-009

Kohler M, Pyttel P, Kuehne C, Modrow T, Bauhus J (2020). On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests a literature review. Annals of Forest Science 77. - doi: 10.1007/s13595-020-00998-2

Krainski ET, Gómez-Rubio V, Bakka H, Lenzi A, Castro-Camilo D, Simpson D, Lindgren F, Rue H (2019). Advanced spatial modeling with stochastic partial differential equations using R and INLA. CRC Press, Taylor and Francis Group, Boca Raton, FL, USA, pp. 298. - doi: 10.1201/9780429031892

Kunz J, Löffler G, Bauhus J (2018). Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. Forest Ecology and Management 414: 15-27. - doi: 10.1016/j.foreco.2018.02.016

Kupferschmid AD (2018). Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type. Forest Ecology and Management 429: 317-326. - doi: 10.1016/j.foreco.2018.06.046

Kurek P, Dobrowolska D (2016). Acorns dispersal by jays *Garrulus glandarius* onto clear-cuts and under the forest canopy. Sylwan 160: 512-518. - doi: 10.26202/sylwan.2015143

Kurek P, Dobrowolska D, Wiatrowska B (2019). Dispersal distance and burial mode of acorns in Eurasian Jays *Garrulus glandarius* in European temperate forests. Acta Ornithologica 53: 155-162. - doi: 10.3161/00016454AO2018.53.2.005

Leuschner C, Ellenberg H (2017). Ecology of central European forests. In: "Vegetation Ecology of Central Europe (6th edn)", vol. 1. Springer International Publishing AG, Cham, Switzerland. [online] URL: https://link.springer.com/book/9783319507101

Ligot G, Balandier P, Fayolle A, Lejeune P, Claessens H (2013). Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. Forest Ecology and Management 304: 391-398. - doi: 10.1016/j.foreco.2013.05.050

Lindgren F, Rue H (2015). Bayesian spatial modelling with R-INLA. Journal of Statistical Software 63: 1-25. - doi: 10.18637/jss.v063.i19

Löf M, Brunet J, Filyushkina A, Lindbladh M, Skovsgaard JP, Felton A (2016). Management of oak forests: striking a balance between timber production, biodiversity and cultural services. International Journal of Biodiversity Science, Ecosystem Services and Management 12: 59-73. - doi: 10.1080/21513732.2015.1120780

Lüpke VB, Hauskeller-Bullerjahn K (1999). Production forestry without clear felling: will oak become marginalised? Forst und Holz 54 (18): 563-568.

Manso R, Ligot G, Fortin M (2019). A recruitment model for beech-oak pure and mixed stands in Belgium. Forestry 93: 124-132. - doi: 10.1093/foresj/cpz056

Mirschel F, Zerbe S, Jansen F (2011). Driving factors for natural tree rejuvenation in anthropogenic pine (*Pinus sylvestris* L.) forests of NE Germany. Forest Ecology and Management 261: 683-694. - doi: 10.1016/j.foreco.2010.11.025

Modrow T, Kuehne C, Saha S, Bauhus J, Pyttel PL (2020). Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. European Journal of Forest Research 139: 41-52. - doi: 10.1007/s10342-019-01238-7

Mölder A, Meyer P, Nagel R-V (2019a). Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur, Q. petraea*) forests: an overview. Forest Ecology and Management 437: 324-339. - doi: 10.1016/j.foreco.2019.01.006

Mölder A, Sennhenn-Reulen H, Fischer C, Rumpf H, Schönfelder E, Stockmann J, Nagel R-V (2019b). Success factors for high-quality oak forest (*Quercus robur, Q. petraea*) regeneration. Forest Ecosystems 6: 49. - doi: 10.1186/s40663-019-0206-y

Mosandl R, Kleinert A (1998). Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. Forest Ecology and Management 106: 35-44. - doi: 10.1016/S0378-1127(97)00237-5

Motta R (2003). Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. Forest Ecology and Management 181: 139-150. - doi: 10.1016/S0378-1127(03)00128-2

Myczko L, Dylewski L, Zduniak P, Sparks TH, Tryjanowski P (2014). Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe. Forest Ecology and Management 331: 35-39. - doi: 10.1016/j.foreco.2014.07.027

Nilsson U, Gemmel P, Lof M, Welander T (1996). Germination and early growth of sown *Quercus robur* L. in relation to soil preparation, sowing depths and prevention against predation. New Forest 12: 69-86. - doi: 10.1007/BF00029983

Onaindia M, Ametzaga-Arregi I, San Sebastián M, Mitxelena A, Rodríguez-Loinaz G, Peña L, Alday JG (2013). Can understorey native woodland plant species regenerate under exotic pine plantations using natural succession? Forest Ecology and Management 308: 136-144. - doi: 10.1016/j.foreco.2013.07.046

R Core Team (2018). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: http://www.R-project.org/

Schroder T (2002). On the geographic variation of *Ciboria batschiana* (Zopf) Buchwald, the main pathogenic fungus on acorns of *Quercus robur* and *Q. petraea* in Europe. Dendrobiology 47: 13-19. [online] URL: http://bibliotekanauki.pl/articles/41225.pdf

Shaw MW (1968). Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales: I. A preliminary study of acorn production, viability and losses. The Journal of Ecology: 565-583. - doi: 10.2307/2258251

Stähr F, Peters T (2000). Sowing by jays-quality and vitality of natural regenerated oak in North-eastern German lowland. AFZ/Der Wald, Allgemeine Forst Zeitschrift für Waldwirtschaft und Umweltvorsorge 55: 1231-1234. [online] URL: http://www.cabdirect.org/cabdirect/abstract/20013060165

Vrška T, Ponikelsky J, Pavlicová P, Janík D, Adam D (2016). Twenty years of conversion: from Scots pine plantations to oak dominated multifunctional forests. iForest - Biogeosciences and Forestry 10: 75-82. - doi: 10.3832/ifor1967-009

Watt AS (1919). On the causes of failure of natural regeneration in British oakwoods. The Journal of Ecology: 173-203. - doi: 10.2307/2255275

Ziegenhagen B, Kausch W (1995). Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. Forest Ecology and Management 72: 97-108. - doi: 10.1016/0378-1127(94)03482-C

Zimmermann J, Hauck M, Dulamsuren C, Leuschner C (2015). Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. Ecosystems 18: 560-572. - doi: 10.1007/s10021-015-9849-x

Zuur AF, Ieno EN, Saveliev AA (2018). Beginner's guide to spatial, temporal and spatial-temporal ecological data analysis with R-INLA. In: "GAM and Zero-Inflated Models", vol. 2. Highland Statistics Ltd, Newburgh, UK, pp. 357.

Supplementary Material

Fig. S1 – Results of the leave-one-out cross-validation served as another factor for model selection.

Tab. S1 - Presentation of the validation indicators for the different size classes.

Link: Axer_4064@suppl001.pdf