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RESEARCH ARTICLE

Mapping the next forest generation reveals multiple regeneration gaps across German forests

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Abstract

1. In face of global change and increasing forest disturbances, forest regeneration is crucial for ensuring future generations of trees and resilient forest ecosystems. However, spatially explicit information on the current availability and climate suitability of trees in the seedling and sapling stage remains scarce.
2. We assessed the potential to predict species-specific forest regeneration densities at high spatial resolution (1 ha) by calibrating generalised additive models (GAMs) using regeneration data from the German National Forest Inventory (NFI) and 44 environmental predictors. Regional regeneration gaps were then identified based on three indicators: low total density (<1000 ha^{-1}), low species richness (≤2 species) and a high proportion (≥75%) of tree species projected to be climatically unsuitable in the future.
3. For 28 tree species, we obtained regeneration density models that performed well in spatially blocked cross-validation. We were therefore able to generate regeneration density and indicator maps that represent 82.5% of the regeneration.
4. The indicator maps revealed considerable regeneration gaps. 14.3% of Germany's forest area has low regeneration density, 30.4% has low species richness, and 15.4% of the Bavarian forest area lacks climate-adapted regeneration.
5. Our study demonstrates the potential of NFI regeneration data and its applicability for monitoring forest regeneration over large spatial scales. The regeneration indicator maps show that silvicultural interventions should prioritise increasing tree species richness and the proportion of species adapted to climate change. However, as regeneration gaps vary from region to region, management and political guidelines must be adapted accordingly to ensure future forest resilience.
6. *Synthesis and applications*. Our study provides the first nationwide, high-resolution assessment of forest regeneration, offering a valuable baseline for monitoring forest development. The regeneration density and indicator maps enable forest managers and policymakers to identify regeneration deficits, prioritise adaptive management interventions and contribute to the development of climate-resilient forests.

KEYWORDS
climate-adapted species, forest regeneration, future climatic suitability, generalised additive models GAMs, regeneration debt, sapling density, species distribution models SDMs, tree species richness

1 | INTRODUCTION

Forest ecosystems are increasingly affected by ongoing climate change. In Europe, repeated droughts have caused increased spread of pests and diseases, defoliation of trees (Potočić et al., 2021), reduced tree growth (Martinez del Castillo et al., 2022) and higher tree mortality (George et al., 2022; Senf et al., 2020). The consequences are more open canopies and larger, more frequent disturbances (Senf & Seidl, 2021). This dynamic constitutes a partial loss of a forest generation, making it necessary to consider the subsequent generation, the regenerating trees that are currently in the seedling and sapling stage.

Forest regeneration can ensure future forest resilience, even under increased disturbances and higher canopy mortality. A high density of regeneration can accelerate the regrowth of a closed canopy, avoid arrested succession (Royo & Carson, 2006) and serve as an advanced start of post-disturbance forest reorganisation (Seidl et al., 2024; Seidl & Turner, 2022). Furthermore, regeneration is key for the species composition and structure of future stands and thus is targeted by management to adapt forests to climate change (Fischer et al., 2016). While natural regeneration is the dominant regeneration type in many European forest systems, seeding, planting and cutting are selectively applied to ensure forest regeneration, increase the proportion of climate-adapted species and create mixed stands (Erdozain et al., 2024). To assess how well forest regeneration is adapted to future climates and where targeted forestry measures would be necessary, regional quantification of regeneration is needed.

One of the most important data sources on forests at large spatial scales are national forest inventories (NFIs). Besides statistically representative information on mature trees, most European NFIs also include assessments of forest regeneration. Regeneration is often measured as a local density by counting individuals below a threshold of diameter at breast height (dbh) per tree species within small sampling areas, for example from 12 to 79 m^2 (Gschwantner et al., 2024; McRoberts et al., 2011). The potential of such NFI regeneration data is largely untapped and underestimated. First, despite the intense collection of such regeneration data, NFI reports either provide no information on forest regeneration (Lackner et al., 2023) or only its dominant type, such as natural regeneration or planting, at the national level (e.g. BMEL, 2024; Rigling & Schaffer, 2015). NFI reports thus lack information on the quantity and quality of forest regeneration. Second, it is a widespread perception that inference on forest regeneration and its patterns along large gradients using NFI data is challenging or impossible due to high spatial heterogeneity, many interacting processes (Shoemaker et al., 2020) and the relatively small size of regeneration plots. Nevertheless, inventory data on forest regeneration have been used to identify drivers of regeneration (Martini et al., 2024; Vayreda et al., 2013) and calibrate empirical models of regeneration distributions (Hasenauer et al., 2000; Kolo et al., 2017). This suggests that NFI regeneration data may have potential to map the next generation of forests at large spatial scales.

A common approach to creating maps from NFI sample plot data is to use species distribution models (SDMs; Xu et al., 2025), which make use of a species' ecological niche. However, these attempts (e.g. Bonannella et al., 2022; Dyderski et al., 2018) focus on large trees above the dbh threshold. Although the drivers of regeneration are becoming better understood, empirical models have not been applied to predict regeneration in space. The advantages of such regeneration maps would be their ability to provide information at unobserved locations, allowing for regional assessment of the regeneration and potential gaps of its quantity and quality. Species-specific regeneration maps could be used for early detection of post-disturbance reorganisation (Seidl et al., 2024), initialisation of dynamic forest simulation models (Díaz-Yáñez et al., 2024) and deriving regeneration indicators to inform forest management (Fischer et al., 2016).

Important indicators for the ability of forest regeneration to contribute to a more resilient next forest generation are its total density, species richness and proportion of climate-adapted species (Cerioni et al., 2024; König et al., 2022). High total regeneration density maintains the ability to establish the next forest generation (Hanbury-Brown et al., 2022). High species richness can reduce losses of productivity and biomass under more extreme climatic conditions (Jactel et al., 2017; Sebald et al., 2021). A high proportion of climate-adapted species indicates better resilience of the future stand and higher economic value (Erdozain et al., 2024; Hanewinkel et al., 2013). Evaluation of these indicators at high spatial resolution is essential to assess whether regeneration can secure future forests and maintain their multifunctionality in a changing climate.

Here, we assess the potential of regeneration density models calibrated with NFI data to infer and evaluate the current quantity and quality of forest regeneration at high spatial resolution (Figure 1). We built flexible species-specific regeneration models using the untapped regeneration density data of the German NFI in combination with 44 environmental variables, describing the environmental preferences of tree species in early life stages. Subsequently, we used the regeneration models to predict the regeneration density per tree species for the German forest area at a resolution of 1 ha. We then assessed potential regeneration gaps by calculating the currently available total regeneration density as a measure for regeneration

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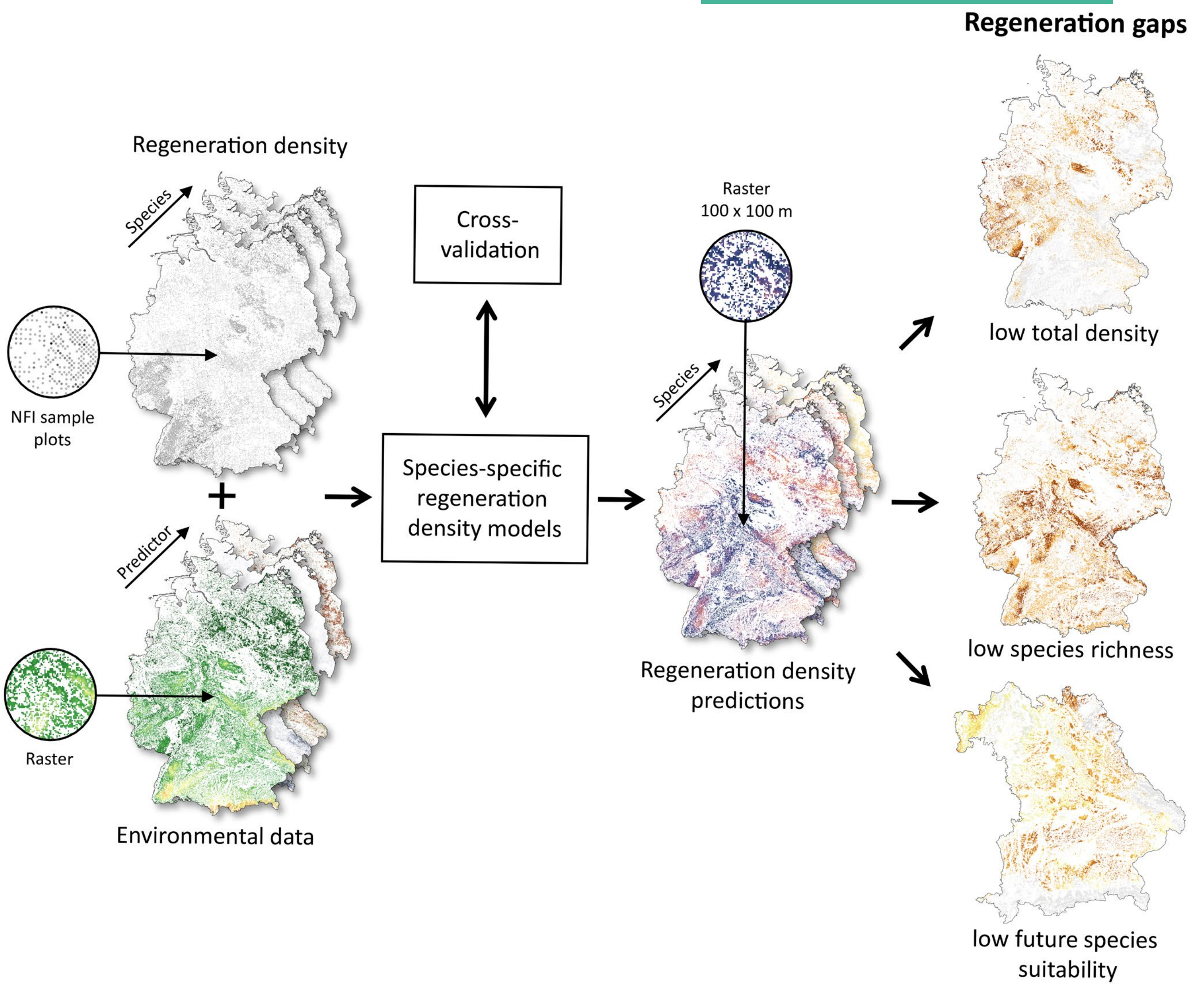

FIGURE 1 Workflow and indicators for the identification of potential regeneration gaps across German forests. To generate species-specific maps of current forest regeneration, we calibrated regeneration density models using data from the German National Forest Inventory (NFI). These maps allowed us to identify regions where forest regeneration has low total density, species richness or future tree species suitability.

quantity and two indicators for regeneration quality. For the latter, we derived species richness and the proportion of climatically suitable tree species in early life stages.

2 | MATERIALS AND METHODS

2.1 | Regeneration data

We used forest regeneration data from the German NFI conducted in 2011 and 2012 (Thünen-Institut, 2015). The German NFI is conducted every 10 years to assess tree and stand characteristics that are representative of the German forests. The sampling design is based on a regular grid, with each cluster consisting of four sample plots arranged in a square, 150 m apart (see Riedel et al., 2017, for survey design). One regeneration subplot of 2 m radius (12.57 m^2) is established 5 m north of the sample plot. Regeneration is assessed by counting trees between 50 cm height and 7 cm dbh. All individuals are counted, whether they are naturally regenerated, sown or planted. In total, our regeneration dataset covered information of 43 tree species at 59,848 NFI plot locations.

2.2 | Predictors of regeneration patterns

To calibrate predictive species distribution models, we used 44 environmental predictors related to topography, soil, macroclimate, microclimate, stand structure, space and time (Table S1). Besides previously used predictors for regeneration (e.g. Martini et al., 2024; Vayreda et al., 2013), we included the variables month and year of NFI measurement to account for seasonal differences in growing conditions and detection probability, plot coordinates to account for unobserved spatial predictors and federal state to account for potential management differences between states.

Environmental predictor information at each plot location was retrieved by the Thünen-Institute, as only anonymised plot locations on a 1×1 km grid are available (Hennig, 2022). Variables, including topography, NFI plot coordinates and the month and year of measurement, were obtained from the NFI (meta)data (Table S1). Since conspecific basal area, a crucial predictor of a species' forest regeneration, was unavailable for the entire German forest area, we used a flexible spatial regression to interpolate it (see Supporting Information S1).

The regeneration density and environmental datasets were then combined, and observations with missing predictor values were removed. The resulting dataset consisted of 48,228 NFI plot observations used for model calibration (Gass & Hülsmann, 2026a). For prediction, we used the raster layers of the same predictors (see Supporting Information S1).

2.3 | Model calibration

As predictive species-specific models of forest regeneration density, we calibrated generalised additive models (GAMs; Wood, 2017) with a negative binomial distribution and a log link function. We used GAMs with cubic regression splines (Wood et al., 2016) to allow for a broad spectrum of non-linear relationships between regeneration densities and our chosen environmental predictors (Table S1). Month and year of NFI measurement and federal state were included as random effects and plot coordinates as a tensor product smooth. GAM smoothness selection and estimation of the negative binomial functions theta value were performed using fast restricted maximum likelihood estimation. Basis dimensions of smoothing splines were kept at moderate complexity for environmental fixed effects ($k=10$) and were set to 25 and 50 in x and y direction, respectively. We allowed fixed effects to be shrunk to zero, serving as a variable selection technique (Wood, 2017), and used a ridge penalty for random effects.

Models were fitted with the function bam() suited for large data sets (Wood et al., 2015) from the R package mgcv (v.1.9.1, Wood, 2023).

2.4 | Model evaluation

Statistical assumptions of the regeneration models were assessed based on simulated residuals generated with the package DHARMa (v.0.4.6, Hartig, 2022). We visually evaluated distributional and residual assumptions as well as zero-inflation resulting in no critical violations (plots of simulated residuals can be found at Gass & Hülsmann, 2026a). To ensure that the observations are spatially independent, we tested for spatial autocorrelation within simulated residuals. We found a tendency towards spatial autocorrelation for the regeneration models of eight tree species (see Table S2). However, given the models' satisfactory performance in cross-validation (see subsequent paragraph), we assume that they generalise across space and likely capture meaningful spatial patterns.

Predictive model performance was assessed using 10-fold spatially blocked cross-validation implemented in the blockCV package (v.3.1.4; Valavi et al., 2019). Blocks were set up with hexagonal block shapes and block sizes corresponding to the spatial autocorrelation range of the regeneration densities. Where block sizes were found to be too large, resulting in less than 10 blocks for some species, we set the range to 300 km resulting in 11 blocks across Germany (Table S2). The mean absolute error (MAE) as an indicator for model performance (Chai & Draxler, 2014) and pseudo-R^2 (Cameron & Windmeijer, 1997) as an indicator of explanatory power were computed based on cluster means, that is averaged across the four sample plots, of observed and predicted regeneration densities for the test and training data of each fold. For MAE, we calculated the relative MAE from the test and training MAE $\left(\frac{MAE_{test}}{MAE_{train}}\right)$. The median was used to aggregate values of relative MAE and test pseudo-R^2 across all folds. We considered models where median relative MAE ≤2 and median pseudo-$R^2 \geq 0.1$.

2.5 | Predictions

After model evaluation, regeneration models for 28 tree species (Table 1) were available to be used for predicting regeneration densities across German forests. For creating regeneration maps, the variable month and year of NFI measurement was excluded to obtain predictions corresponding to average conditions. We converted the predicted regeneration counts per 2 m radius plot (approximately 12.6 m^2) to regeneration densities ha^{-1}. Uncertainty of predictions was calculated as the difference between upper and lower limit of 95% confidence intervals divided by the local prediction of regeneration densities (Figure S2).

2.6 | Regeneration indicators

Total regeneration density was calculated by summing up the densities for all 28 tree species per grid cell. Reported thresholds for sufficient regeneration density vary considerably, ranging from 1000 to 2500 ha^{-1} (Kolo et al., 2017; Miller & McGill, 2019; StMELF, 2023). Accordingly, we classified values <1000 ha^{-1} as insufficient and ≥2000 ha^{-1} as sufficient. These thresholds represent minimum rather than ideal conditions for regeneration indicators. To account for this and the variability of previously reported thresholds, we additionally chose a moderate class with total regeneration density of 1000–2000 ha^{-1}.

Tree species richness was calculated as the number of species with at least 5% of the total regeneration (BaySF, 2020). For Central European conditions, a species richness of three or four species has been proposed to be sufficient (BaySF, 2020; Lindner et al., 2025). Since our analyses included only 28 out of 43 species, we defined ≤2 species within the regeneration as insufficient, 3–4 species as moderate and ≥5 species as sufficient.

To more precisely assess how the current regeneration fits future climatic conditions, we used the federal state Bavaria as a case study.

TABLE 1 Evaluation and summary statistics of regeneration density models for 43 tree species.

Species	Model performance: Median relative MAE	Model performance: Median pseudo-R^2	Regeneration density map availability (Germany)	Regeneration density [#/ha]: Mean	Regeneration density [#/ha]: SD	Future suitability map availability (Bavaria)
Abies alba	1.02	0.53	●	72	300	●
Abies grandis	0.85	−0.13	○			●
Acer campestre	1.03	0.29	●	14	67	●
Acer platanoides	0.84	0.21	●	17	82	●
Acer pseudoplatanus	1.07	0.11	●	256	596	●
Alnus glutinosa	1.05	0.19	●	17	38	●
Alnus incana	1.12	0.40	●	19	479	○
Betula pendula	1.00	0.04	○			●
Betula pubescens	0.11	0.55	●	7	75	○
Carpinus betulus	1.03	0.08	○			●
Castanea sativa	0.52	0.62	●	<1	12	●
Fagus sylvatica	1.04	0.21	●	854	1335	●
Fraxinus excelsior	0.92	0.26	●	207	623	●
Larix decidua	1.09	0.05	○			●
Larix kaempferi	0.22	0.62	●	3	22	●
Malus sylvestris	0.77	0.16	●	<1	2	○
Picea abies	0.88	0.35	●	776	1332	●
Picea sitchensis	0.23	0.46	●	1	14	○
Pinus mugo	0.14	0.94	●	3	176	○
Pinus nigra	1.16	0.05	○			●
Pinus strobus	0.83	−0.18	○			○
Pinus sylvestris	0.96	0.49	●	230	747	●
Populus alba	0.44	−1.02	○			○
Populus nigra	0.58	−0.14	○			○
Populus tremula	0.94	0.22	●	33	90	○
Populus trichocarpa x maximoviczii	0.88	−0.37	○			○
Populus x canescens	1.23	−0.34	○			○
Prunus avium	0.91	0.25	●	12	30	●
Prunus padus	1.11	−0.36	○			○
Prunus serotina	1.03	0.29	●	197	1243	○
Pseudotsuga menziesii	1.01	0.16	●	16	25	●
Pyrus communis	0.83	0.01	○			●
Quercus petraea	0.95	0.25	●	54	103	●
Quercus robur	1.22	0.21	●	60	104	●
Quercus rubra	0.98	0.34	●	12	50	●
Robinia pseudoacacia	0.45	0.52	●	6	35	●
Salix spp.	1.05	−0.04	○			○
Sorbus aria	0.78	0.37	●	3	35	○
Sorbus aucuparia	1.00	−0.05	○			●
Sorbus torminalis	0.63	0.05	○			●
Taxus baccata	0.50	0.22	●	<1	<1	○
Tilia spp.	1.04	0.22	●	29	101	●
Ulmus spp.	0.94	0.28	●	13	92	●
All species *n* = 28				2912	2655	

Note: The availability of predicted regeneration density maps (Germany) and future tree species suitability maps (only Bavaria; Falk & Mellert, 2011; Thurm et al., 2018) is indicated by a dot (available) or a circle (not available). Regeneration density maps were predicted when the model performance criteria of median relative MAE ≤2 and median pseudo-R^2 ≥ 0.1 were met, as determined by 10-fold spatially blocked cross-validation.

We combined our species-specific regeneration density maps with future tree species suitability maps based on predicted occurrence probabilities of adult trees in the year 2100 (Falk & Mellert, 2011; Thurm et al., 2018). These were developed as a planning tool for forest practitioners throughout Bavaria and are actively used to select tree species considering climate projections and local site conditions. The maps categorise future suitability into five groups and are available for 32 tree species. Of these, 19 are also available as regeneration distribution maps (Table 1). For each grid cell, we calculated the percentage of regeneration density of low future suitability $R_{\text{low suitability}}$ as:

$$R_{\text{low suitability}}[\%] = \frac{N_{\text{low suitability}}}{N_{\text{total}}} * 100$$

Here, $N_{\text{low suitability}}$ is the regeneration density summed up over the species with the suitability categories *very low* and *low*, which relate to the original *very high risk* and *high risk* categories, and N_{total} the total regeneration density across all species of the grid cell. We defined $R_{\text{low suitability}} \geq 75\%$ as problematic. The analysis of future suitability of the regeneration could be done for 76.9% of the Bavarian forest area.

The full workflow of modelling and data analysis can be found at GitHub (https://github.com/LeonieCG/GermanRegenerationMaps2012) and Zenodo (Gass & Hülsmann, 2026b). All analyses were conducted using R v.4.4.1 (R Core Team, 2024).

3 | RESULTS

3.1 | Regeneration density models

From the 43 calibrated species-specific regeneration density models, 28 met the performance criteria of median pseudo-$R^2 \geq 0.1$ and median relative MAE ≤2 from cross-validation (Table 1). We used these models to predict the regeneration density for 78.5% (8,615,918 ha) of the German forest area. The 28 species represented 82.5% of the regeneration measured within the NFI. In predictions across Germany, the most common tree species within the regeneration were *Fagus sylvatica* L., *Picea abies* (L.) H.Karst and *Acer pseudoplatanus* L. with mean densities of 854, 776 and 256 individuals ha^{-1}, respectively (Table 1). Species with the lowest abundance in the regeneration throughout Germany were *Castanea sativa* Mill., *Malus sylvestris* Mill. and *Taxus baccata* L. with average densities of <1 individuals ha^{-1}.

Of all 43 calibrated regeneration models, 15 did not meet the performance criteria (Table 1). Out of these, 11 were rare tree species with total regeneration density <1% within the German NFI (Table S3). The other four were common tree species: *Sorbus aucuparia* L., *Carpinus betulus* L., *Betula pendula* Roth and *Prunus padus* L. (Table S3) that nevertheless could not be sufficiently modelled with our approach (Table 1). Median pseudo-R^2 was the primary factor to exclude models, as the median relative MAE criterion was consistently met.

3.2 | Species-specific regeneration maps for Germany

The predicted density maps showed distinct patterns in the availability of regeneration for each tree species (Figure 2, for all other tree species see Figure S1). For example, the regeneration of *Fagus sylvatica* was widely distributed with very high abundance in the centre of Germany and lower densities towards the east and the western lowlands (Figure 2). Similarly, the regeneration of *Picea abies* was widely abundant across Germany but showed lower densities towards the northeast. *Abies alba* Mill., a less common tree species, showed a clear north–south trend with no occurrence in the northern half of Germany and a gradual increase in regeneration towards southern low mountain ranges. All maps can be explored online at https://easi.users.earthengine.app/view/regeneration-maps.

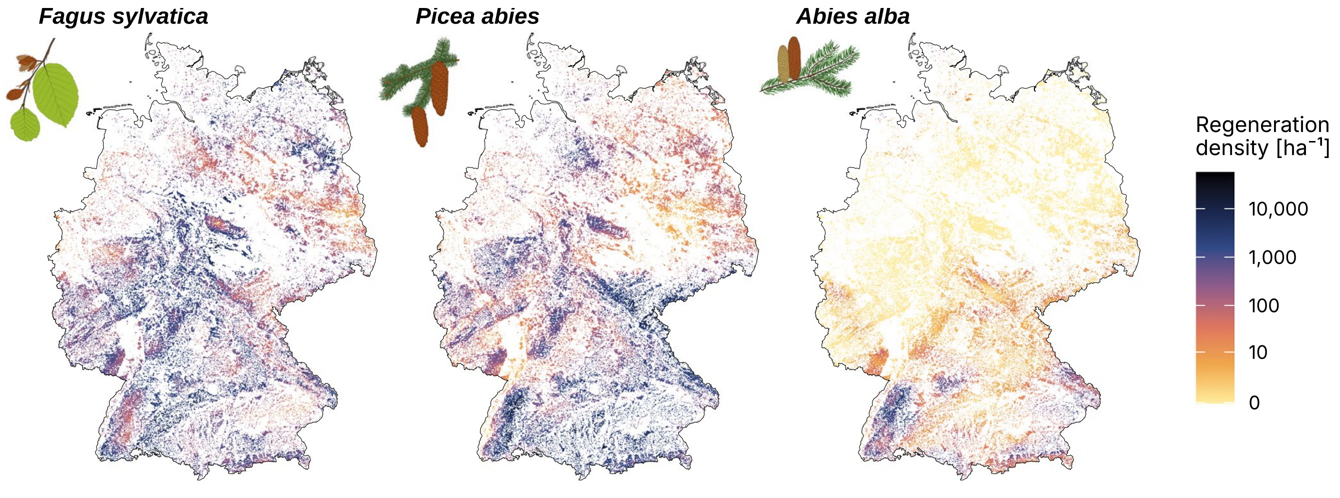

FIGURE 2 Regeneration densities shown for three important Central European tree species - *Fagus sylvatica*, *Picea abies* and *Abies alba* - in 1 ha grid cells for Germany (for remaining tree species maps see Figure S1 and for relative 95% confidence interval width maps see Figure S2). All maps are available for exploration at https://easi.users.earthengine.app/view/regeneration-maps and for download at Zenodo (Gass & Hülsmann, 2026a).

Journal of Applied Ecology

3.3 | Indicators of regeneration quantity and quality

The quantity of regeneration, evaluated as the total regeneration density based on 28 tree species, showed an average of 2912 individuals ha^{-1} (Table 1). We found a clear trend of insufficient (0–1000 ha^{-1}) and moderate (1000–2000 ha^{-1}) total regeneration densities in parts of Mid and North Germany (Figure 3, for continuous density scale see Figure S3), whereas the South and Northeast mainly displayed sufficient regeneration (≥2000 ha^{-1}). Overall, 53.6% of the predicted forest area had sufficient regeneration density, 32.1% had a moderate density, and 14.3% had an insufficient density.

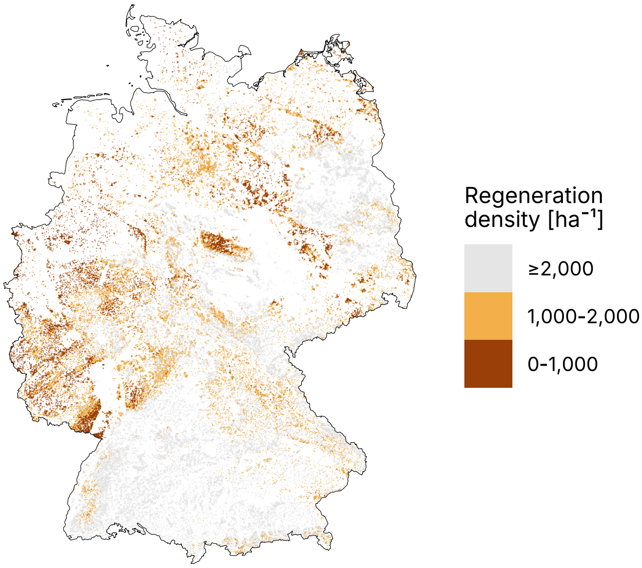

FIGURE 3 Spatial patterns of total regeneration density for the forest area of Germany based on 28 tree species. Colours indicate insufficient (0–1000 ha^{-1}), moderate (1000–2000 ha^{-1}) and sufficient (≥2000 ha^{-1}) total regeneration densities (for continuous scale see Figure S3). The map is available for exploration at https://easi.users.earthengine.app/view/regeneration-maps and for download at Zenodo (Gass & Hülsmann, 2026a).

As part of the quality assessment of the regeneration, we evaluated species richness (Figure 4, for continuous species richness scale see Figure S4), which was moderate with an average of 3.4 species ha^{-1} across Germany. A total of 30.4% of the predicted forest area had too few (≤2) tree species in the regeneration (Figure 4b), while 49.6% and 20.0% of the area contained a moderate (3–4) and sufficient number of species (≥5), respectively. Forests that were particularly species-rich in the regeneration were found towards the north and northeast (Figure 4a) but were otherwise restricted to local hotspots. Forests with a species richness of ≤2 were particularly common in low mountain ranges.

Regeneration quality was additionally assessed as the future suitability of tree species in the regeneration. We showcase this—and the identification of regeneration gaps and potential management strategies more generally—in Box 1.

4 | DISCUSSION

Our results demonstrate the potential to predict forest regeneration density at high spatial resolution from species-specific models calibrated with NFI regeneration data. Using the regeneration density maps predicted for Germany, we evaluated indicators of

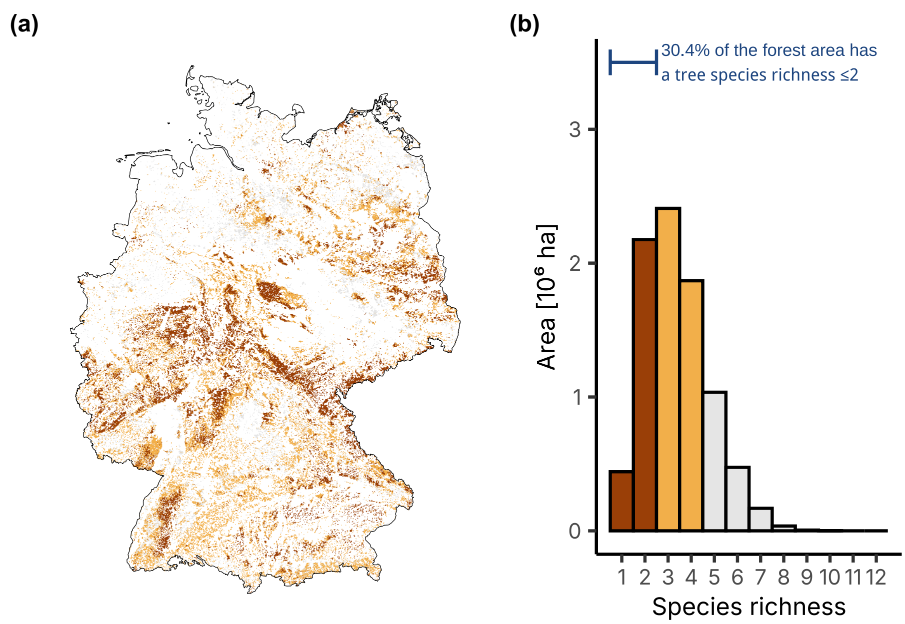

FIGURE 4 Tree species richness of regeneration for the forest area of Germany based on 28 tree species. The map (a) shows spatial patterns, the histogram (b) indicates the distribution of species richness values. Colours indicate insufficient (1–2), moderate (3–4) and sufficient (≥5) regeneration species richness (for continuous scale see Figure S4). We considered a species present in a 1 ha grid cell if its density was at least 5% of the total density. The map is available for exploration at https://easi.users.earthengine.app/view/regeneration-maps and for download at Zenodo (Gass & Hülsmann, 2026a).

BOX 1 Bavaria (Germany)—A case study for identifying and managing regeneration gaps.

Using Bavaria as an example, we demonstrate the potential use of regeneration indicator maps to identify regeneration gaps (Figure 5) and derive regional recommendations for silvicultural interventions. Bavaria, a federal state in the southeast of Germany, has recently been affected by severe summer droughts and subsequent bark beetle outbreaks, which have led to a loss of tree canopies, especially in Norway spruce (*Picea abies*) forests (Thonfeld et al., 2022). We chose Bavaria because detailed maps of the future suitability of many tree species are available. This allowed us to derive not only the total regeneration density and species richness but also the proportion of regeneration with low future suitability.

In Bavaria, only few regions, amounting to 1.3% of the forest area, showed a deficit of total regeneration density <1000 ha^{-1} (Figure 5a). Species richness of the regeneration was critically low (≤2 tree species; Figure 5b) in 30.6% of the Bavarian forest area, mainly found in the low mountain ranges. Regeneration of low future suitability (i.e. proportions ≥75%) dominated on 15.4% (299,225 ha; Figure 5d) of the forest area, for example, in the northeast (Figure 5c), which is mainly the result of *Picea abies*, responsible for 92.6% of unsuitable regeneration densities (Table S4). Half of the analysed forest area had a proportion of less than 30.8% of low future suitability (Figure 5d), with a considerable area of future suitable regeneration. All indicators showed high spatial heterogeneity (Figure 5).

Such spatially resolved results on the quantity and quality of forest regeneration indicate regeneration gaps and allow for targeted silvicultural measures and incentives that can significantly contribute to the adaptation of forests to climate change. Regions like the Frankenwald and the Bavarian Alps (Figure 5a) are climate impact and adaptation hotspots, with the Frankenwald facing large-scale disturbances (Viana-Soto & Senf, 2024) and the Alps being increasingly prone to rockfall (e.g. Hillebrand et al., 2023). Combining this with forest regeneration indicators helps to prioritize forest management: In the Frankenwald, where species richness and climate-adapted tree species are lacking (Figure 5b,c), selective thinning and planting of additional climate-adapted tree species should be promoted. In the Bavarian Alps, regeneration gaps are more moderate and exist with respect to total regeneration density (Figure 5a) and species richness (Figure 5b). They can be addressed by promoting natural regeneration and targeted planting. Overall, regions with severe regeneration gaps like the Frankenwald should be prioritized.

regeneration quantity and quality and identified regional gaps in forest regeneration.

4.1 | Predicting forest regeneration at large spatial scale

We successfully predicted forest regeneration density for a large part of the modelled tree species in Central Europe. This contrasts with previous models of forest regeneration. These included only a few species (Hasenauer et al., 2000; Kolo et al., 2017), covered only small environmental gradients (Hasenauer et al., 2000) and achieved low predictive accuracy at high spatial resolution (Zhu et al., 2014). Previous models were therefore not suited to reliably predict community composition and diversity across large environmental gradients.

Our modelling approach distinguishes itself by successfully cross-validating 28 of the 43 tree species models (Table 1). This is likely due to the large environmental gradient of the NFI data, the large number of environmental predictors ($n = 44$), partly at high spatial resolution (Table S1), and the flexibility of our modelling approach (GAMs). We conclude that even though forest regeneration is subject to a variety of stochastic processes (Shoemaker et al., 2020) and is measured on small sample plots (12.57 m^2), there is enough signal in local regeneration densities to successfully predict the regional availability of forest regeneration.

4.2 | Tree species coverage of the regeneration models

The predicted regeneration density maps (Figure 2 and Figure S1) cover a major part of the regeneration sampled within the German NFI. Therefore, our indicators derived from the regeneration maps provide reliable information about the dominant forest regeneration. Nevertheless, it would be desirable to expand the range of tree species modelled, especially since a large species pool and rare species will play a greater role as climate change progresses (Huth et al., 2025). Eleven species (Table 1) that could not be modelled occurred at average densities <1% in the German NFI regeneration dataset (Table S3) and are therefore not well represented by the small NFI sample plots. To better cover the environmental preferences of such rare tree species, future predictive regeneration models could be calibrated with regeneration data from further German NFI surveys, other European NFIs or local inventories.

We could also not reliably predict the regeneration density for more generalist species, such as *Carpinus betulus*, *Betula pendula*, *Sorbus aucuparia* and the *Salix* species group, which are found across large environmental gradients (BfN & NetPhyD, 2013; Caudullo et al., 2016). This may have made it difficult to relate the regeneration densities of these species to the environmental predictors available to us. Future models could include even more predictors to better reflect environmental niches.

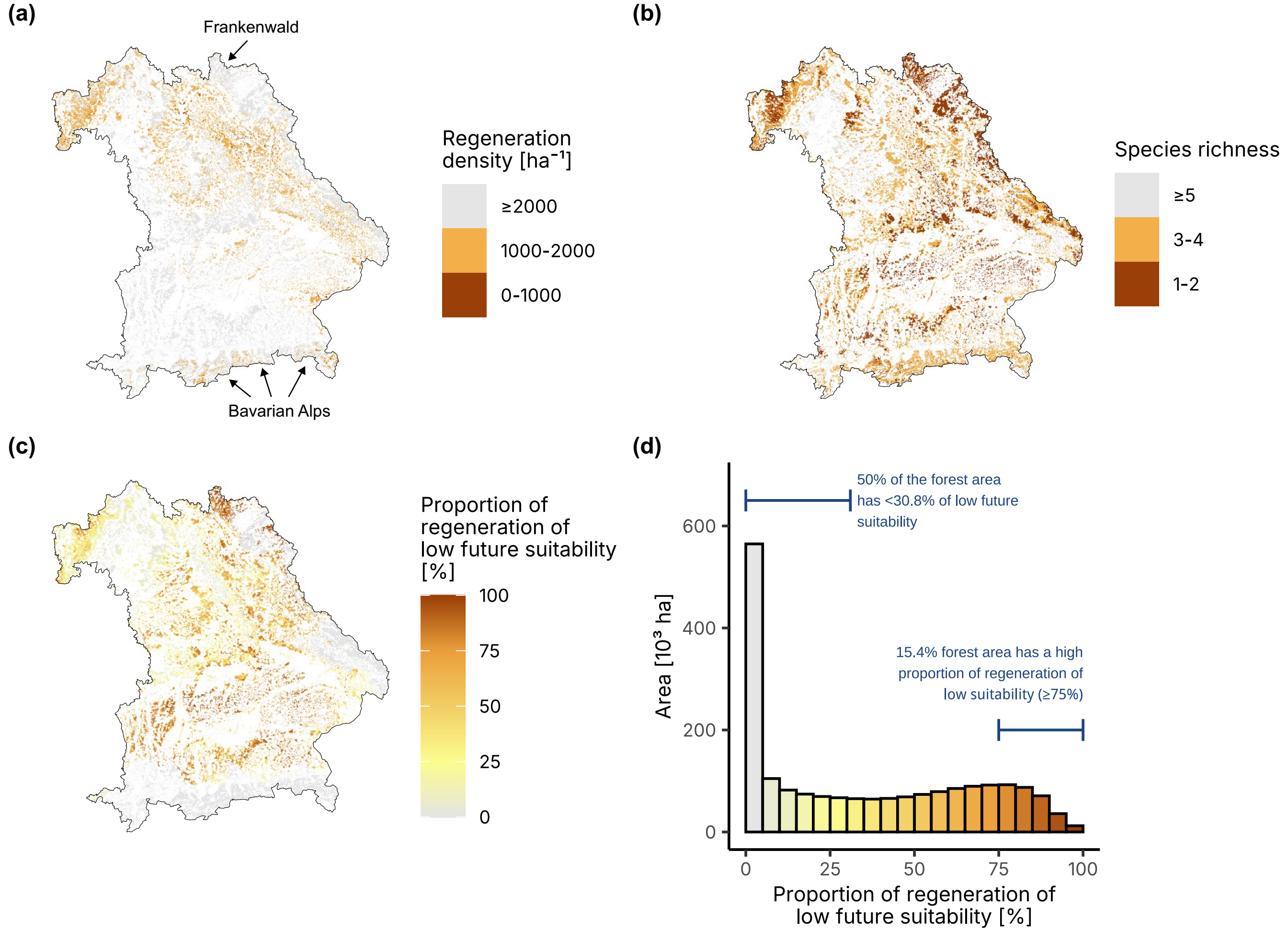

FIGURE 5 Maps of regeneration quantity and quality for Bavaria: (a) total density, (b) species richness and (c) proportion of regeneration of low future suitability. (d) shows the distribution of values in (c). (a) and (b) were derived from regeneration density maps of 28 tree species, (c) and (d) are based on 19 tree species. Maps are available for exploration at https://easi.users.earthengine.app/view/regeneration-maps and for download at Zenodo (Gass & Hülsmann, 2026a).

4.3 | Predictors of forest regeneration

The regeneration models were calibrated using 44 predictive variables describing the environment with respect to topography, soil, microclimate, macroclimate, stand structure and spatial patterns (Table S1). However, it has been shown that forest regeneration density is also related to other predictors such as browsing intensity (Martini et al., 2024; Vayreda et al., 2013), understory light availability (Harris et al., 2024; Martini et al., 2024), or silvicultural management and ownership (Kolo et al., 2017).

We could not include these additional predictors in our forest regeneration maps because they are not (yet) available as spatial datasets for the German forest area, only available at low spatial resolution or not homogenised across federal states. We consider it promising to evaluate how much these additional predictors can contribute to the predictability of forest regeneration and to invest accordingly in datasets for these predictors with better spatial coverage. Although our approach already allows for highly flexible effects (GAM), the complexity of environmental relationships could be further enhanced using machine learning (Pichler & Hartig, 2023).

4.4 | Application of regeneration density and indicator maps

Creating species-specific regeneration density maps was motivated by the need to assess the potential contribution of forest regeneration to a more resilient next forest generation (Miller & McGill, 2019). To this end, we used three indicators that are widely used in forest management and planning: total regeneration density, species richness and proportion of climate-adapted tree species (Cerioni et al., 2024; König et al., 2022). Typically, these indicators are assessed for individual stands by forest practitioners. Our results demonstrate the potential to monitor these indicators at national scales and to identify regional differences in forest regeneration.

For Germany, we found that regeneration gaps are small in terms of total density (Figure 3) but are of concern regarding species richness, with a deficit for almost one third of the German forest area (Figure 4). In addition, 15.5% of the forest area in Bavaria is affected by a lack of climate-adapted tree species (Figure 5d). While the forest regeneration indicator maps cannot replace a local, on-site assessment for stand level silvicultural decisions, they can provide an indication of potential regeneration gaps at the regional scale (cf. Box 1). Such knowledge can help forest policymakers identify potential priority areas to increase future suitability, species richness and regeneration density. These actions can be implemented through direct hands-on management or through incentives for silvicultural practices that promote regeneration of a diverse set of climate-adapted species (Huth et al., 2025).

Beyond practical applications, our species-specific regeneration maps can be used to increase the robustness of projections of future forest dynamics by incorporating comprehensive information on regeneration availability and species composition (e.g. Díaz-Yáñez et al., 2024). In turn, this also allows for the evaluation of different regeneration management strategies. Future research should also focus on developing ecosystem-specific indicator thresholds, for example using dynamic forest models. Such approaches would improve the identification of forest regeneration gaps. In addition, studies should investigate canopy and stand characteristics that are particularly associated with regeneration gaps.

5 | CONCLUSIONS

Currently available forest regeneration appears insufficient to secure future forests and maintain their multifunctionality in a changing climate. Furthermore, the nature of gaps in regeneration quantity and quality varies spatially. Here, we demonstrated this using the German NFI regeneration data as an example to build predictive models of species-specific regeneration densities. We strongly encourage the evaluation of regeneration patterns and the regional assessment of total regeneration density, species richness and climate-adapted species across other countries and at continental scales.

AUTHOR CONTRIBUTIONS

Leonie C. Gass: Conceptualisation (equal), data curation (lead), formal analysis (lead), methodology (equal), project administration (supporting), visualisation (lead), writing—original draft preparation (lead), writing—review and editing (equal). **Lisa Hülsmann**: Conceptualisation (equal), formal analysis (supporting), funding acquisition (lead), methodology (equal), project administration (lead), resources (lead), supervision (lead), visualisation (supporting), writing original draft preparation (supporting), writing—review and editing (equal). Our study was based on secondary rather than primary data. Therefore, no local data were collected. All of the authors are based in the country where the study was conducted. We discussed our research with local forest practitioners whenever possible to seek feedback related to our regeneration indicators.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

All code supporting the findings of this study is openly available at Zenodo https://doi.org/10.5281/ZENODO.18455023 (Gass & Hülsmann, 2026b) and GitHub (https://github.com/LeonieCG/GermanRegenerationMaps2012). Resulting maps of forest regeneration can be explored online at https://easi.users.earthengine.app/view/regeneration-maps. Data used to calibrate the regeneration models were compiled from the German national forest inventory together with metadata sources, originally collected by various institutions. As far as we were permitted, we have republished the data at Zenodo https://doi.org/10.5281/ZENODO.18455038 (Gass & Hülsmann, 2026a) and provided the code to work with the reduced set of environmental variables.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Additional Methods.

Supporting information S2. Additional Figures and Tables.

Table S1. Predictor variables used for the calibraon of species-specific regeneration density models.

Table S2. Spatial autocorrelation of each calibrated model and set up for partially blocked cross-validation.

Table S3. Forest regeneration densities per tree species from the German national forest inventory of 2012.

Table S4. Proportion of regeneration in Bavaria of low future suitability for 19 tree species.

Figure S1. Regeneration density maps of remaining tree species not displayed in Figure 2.

Figure S2. Relative 95% confidence interval width maps for all 28 regeneration tree species.

Figure S3. Spatial patterns of total regeneration density (ha^{-1}) for Germany based on 28 tree species.

Figure S4. Regeneration tree species richness for the forest area of Germany based on 28 tree species.

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