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RESEARCH ARTICLE

Ecological drivers of garden dormouse (*Eliomys quercinus*) occupancy in a human modified landscape in Germany

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Funding information

German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection; German Federal Agency for Nature Conservation; Friends of the Earth

Handling Editor: Danielle Hinchcliffe

Abstract

1. The garden dormouse (*Eliomys quercinus*) is an understudied mammal species endemic to Europe. Once distributed widely across the continent, its eastern populations have significantly declined, with the species now found in only 50% of its former range. In Germany, it also occurs in spruce forests in low mountain ranges. However, this habitat has recently been lost due to bark beetle infestation following a prolonged period of drought. In some places, not only the dead trees are removed, but also all the branches and topsoil.
2. We assessed habitat requirements of a garden dormouse population in such a changing habitat in the Harz Mountains, Germany. To assess garden dormouse occupancy, we conducted transect surveys using footprint tunnels during July and October 2022 for the presence of garden dormice. Additionally, we measured covariates such as coverage of tree, shrub and herb layers, as well as deadwood, soil characteristics and reforestation. Using single-season occupancy modelling, we evaluated the effects of these habitat covariates on the occupancy of the garden dormouse.
3. Our results indicated that garden dormouse occupancy was negatively affected by herb cover but positively associated with plant successional stages. Furthermore, occupancy of the garden dormouse was positively coupled with the occurrence of the hazel dormouse (*Muscardinus avellanarius*). Detection probability increased with higher weekly minimum temperatures.
4. Practical implications: For the conservation of garden dormice in low mountain ranges like the Harz, practical measures should include establishing interconnected forest edges and strips. Moreover, we suggest adopting a dynamic, mosaic approach to felling, avoiding topsoil removal and promoting regeneration that fosters semi-open successional habitats as essential strategies.

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KEYWORDS

ecological restructuring, forest strips, Gliridae, mammal conservation, successional habitats

1 | INTRODUCTION

The garden dormouse (*Eliomys quercinus*) is an understudied mammal species of the dormouse family (Gliridae) (Lang et al., 2022). It is endemic to Europe and was historically distributed across 26 countries from Portugal in the west to the Urals (Russia) in the east (Bertolino, 2017; Bertolino et al., 2008). However, garden dormouse populations in the eastern range have declined significantly, and the species now occurs in only 50% of its former range since the 1990s, making it the most severely declining rodent species in Europe (Bertolino, 2017; Temple & Terry, 2007). However, especially on a local scale, little is known about the factors driving the population decline (Bertolino, 2017; Erhardt et al., 2022; Meinig & Büchner, 2012). Germany holds >10% of its distribution range and therefore has a high responsibility to enhance the status of the declining rodent (Meinig, 2004). The garden dormouse is classified as 'critically endangered' in Germany's Red List of threatened species (Meinig et al., 2020), with the species being considered common only in the west of the river Rhine (Meinig & Büchner, 2012).

Garden dormice were commonly found in spruce dominated forests, yet its habitat requirements still remain largely unknown (Meinig & Büchner, 2012; Mori et al., 2020). In Germany and Central Europe, the species reaches its northernmost distribution in the Harz Mountains, where it also reportedly occurred mostly in spruce dominated forests (Meinig & Büchner, 2012). In recent years, many forests in the Harz region were managed in response to the large-scale spruce forest dieback (Schmidt et al., 2022), often resulting into large-scaled clear cuts. Furthermore, even the topsoil had been pushed off in those areas to remove the acidic needle litter and facilitate mechanical re-planting. As this forest landscape is also known for its garden dormouse population, it is of conservation importance to monitor the species, explore its habitat associations and determine appropriate forestry management practices. In this study, we aim to address the habitat requirements of that garden dormouse population as part of the German-wide project 'In Search of the Garden dormouse' (Büchner et al., 2024).

So far, it is known that fruits such as blackberries and elderberries serve as the primary plant-based food source of the garden dormouse (Kuipers et al., 2012; Schoppe, 1986). Being omnivorous, they also feed on invertebrates like millipedes, beetles and snails (Gil-Delgado et al., 2010; Kuipers et al., 2012; Storch, 1978), which are often associated with deadwood. Previous studies have reported that the garden dormouse is preferentially associated with stony and rocky environments with a well-developed shrub layer and a reduced herb cover (Bertolino, 2017; Capizzi & Filippucci, 2008; Le Louarn & Spitz, 1974; Meinig & Büchner, 2012). Also, shrubs serve as nesting sites during the summer and as hibernation sites during colder months (Bertolino & Di Cordero Montezemolo, 2007).

Therefore, we sought to examine the following hypotheses:

1. Garden dormice are more likely to be found in early successional stages characterised by a dense and species-rich shrub layer, and a lower percentage of herbaceous cover (Bertolino, 2017; Capizzi & Filippucci, 2008; Le Louarn & Spitz, 1974; Meinig & Büchner, 2012).
2. We hypothesised that garden dormice occupancy would be positively associated with the presence of hazel dormouse, because of comparable habitat requirements in woodlands (Capizzi et al., 2002; Goodwin et al., 2020).
3. We also hypothesised that the detection probability of garden dormice may vary with temperature, as higher temperatures can lead to increased activity, making dormice easier to detect, whereas extremely high or low temperatures might reduce detectability due to limited movement as temperature affects their activity patterns and behaviour (Ruf & Geiser, 2015; Torre et al., 2018).
4. We furthermore hypothesised that detection would vary with respect to seasonal change, with higher probabilities during peak activity periods, such as late spring and early autumn, when dormice are known to be more active (e.g. June–October; Burton et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was located in the western foothills of the Harz Mountains, near the Grane Dam in Lower Saxony, Germany (51°90'N, 10°34'E; Figure 1). It covered an area of 89 hectares at an altitude of 365m. The mean annual air temperature and mean annual precipitation were 9.43°C and 827.7mm (DWD Climate Data Center (CDC), 2022a, 2022b). The area would have been deciduous forests in its natural state, with mainly beech (*Fagus sylvatica*) forest dominating (Aßmann et al., 2016). Due to overexploitation by the mining industry in the 19th century, the developments during and after the second world war, as well as the 1972 storm 'Quimburga' the forested area has undergone multiple periods of deforestation and reforestation with spruce (*Picea abies*) (Niedersächsische Landesforsten, 2019, 2022). Since 1991, the ecological forest restructuring programme LÖWE has been implemented, resulting in a significant increase in deciduous trees (*Fagus sylvatica*, *Quercus robur*, *Acer* spp.; Niedersächsische Landesforsten, 2019). In turn, the spruce forest has decreased by 70% since the 1970s and currently comprises 30% to 40% of the area, a trend that is exacerbated by the more recent and consecutive drought events (W. Grope, pers. comm).

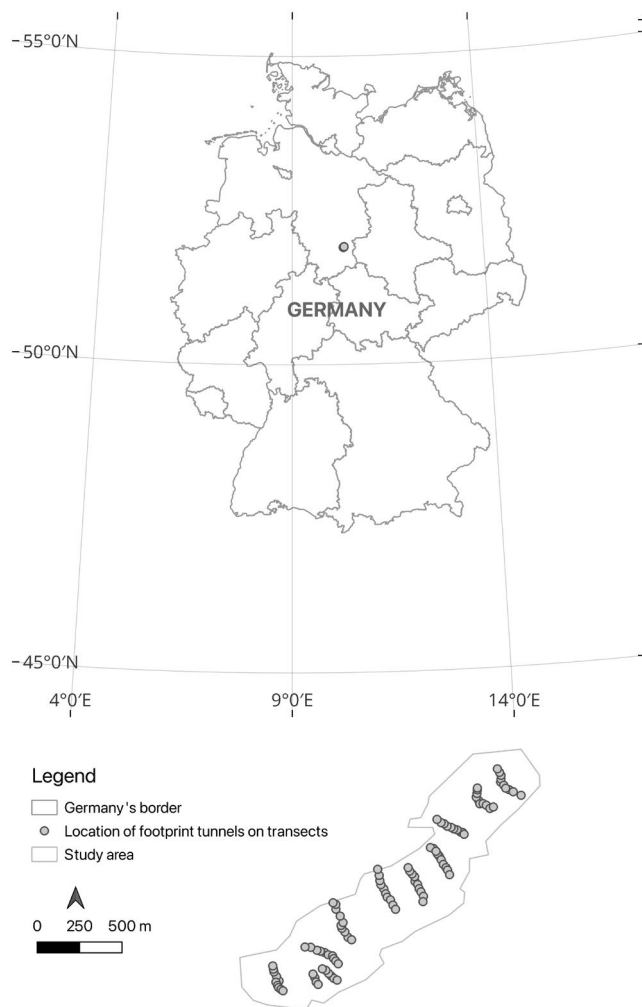


FIGURE 1 Germany, location of our study area in the northwestern Harz Mountains, and study design. Grey circles within the study area represent the footprint tunnels that were deployed along transects to detect the presence of the European garden dormouse.

December 2022). As a result of the forest restructuring, the study area exhibits distinct successional stages, including open habitats and several reforestation stages (Figures S2, S3 and S5). In contrast to the ecological forest conversion efforts, deforestation areas are managed in a way that also includes soil removal (Figure S3). Permission to enter the study site by car was granted by 'Revierförsterei Riesberg' from 27 June 2022 until 31 December 2022.

2.2 | Study design

The local occurrence of the Garden dormouse is known from 26 bird nest boxes that were yearly checked by the forester W. Grope since 2001. In July 2022, we installed 100 footprint tunnels in 10 transects positioned perpendicularly along the forest road (Figure 1). A transect comprising 10 footprint tunnels was established every 200m, with five tunnels on each side of the forest road. Three transects could not be completed due to fences or inaccessible terrain.

In such instances, we either conducted the transect on the opposite side of the road or initiated an additional transect further along the road (Figure 1). To adequately cover the activity range of the garden dormouse, we deployed the tunnels at regular intervals of 20m from each other (Büchner et al., 2024; Melcore et al., 2020). Of all the footprint tunnels, 7% were located in deforested areas, 13% in forest strips, 30% in areas with succession and 50% in reforested areas, of which 8% were classified as old-growth forest.

2.3 | Footprint tunnels

Each tunnel contained a cardboard sheet (21×6cm) and an ink pad infused with charcoal ink (Figure S6). For the ink pad, we used coarse, uncoated crepe tape. The charcoal ink was prepared by mixing ultra-fine powdered charcoal (40g) with sunflower oil (90g) and was then applied to the ink pad of each tunnel. The indication of quantity for the charcoal ink mixture varies by temperature; the consistency to spread the ink should be slightly more liquid than toothpaste. Tunnels were affixed to tree branches at a suitable distance from the tree trunk, thereby enabling garden dormice to access them via climbing. In localities where trees were unavailable, the tunnels were attached to shrubs or deadwood branches situated close to the ground (Figure S6).

To prevent overlapping of footprints and to ensure that the ink remained wet, we monitored the tunnels on a weekly basis from 13 July to 26 October 2022. If footprints were detected or if the sheet was soiled, we replaced it with a new blank sheet, and the original was labelled with the footprint tunnel number and the date. We applied fresh charcoal ink on each tunnel, and a total of 12 surveys were conducted over the sampling period. We identified the footprints of the garden dormouse and distinguished them from other animal traces (Büchner et al., 2024). Hazel dormouse records, as a fellow member of the Gliridae family (dormice), were collected as a covariate for the occupancy of the garden dormouse.

At each footprint tunnel location, the following covariates were surveyed within a 2.5m radius, sorted according to the occupancy hypotheses (Tables 1 and 2; Liesenfelder et al., 2025):

1. Shrub cover; shrub diversity; herb cover; successional stage ('succession')
2. Density, size, dispersion and abundance of fallen logs ('FL'); density and dispersion of deadwood ('DW'); Reforestation stage ('reforest'); tree dispersion and size of overstorey ('OS') and understorey ('US'); woody stem ('WS') density of overstorey and understorey; Soil surface exposure; Soil loss.

Furthermore, we divided the study area into the following five habitat types: reforestation, forest strip, deforestation, succession and old-growth forest. The forest was further classified as beech (*Fagus sylvatica*), spruce (*Picea abies*), mixed and open areas (i.e. no trees while containing grasses and shrubs). In this

TABLE 1 Definition of the predictor variables measured at each footprint tunnel location in a 2.5 m radius.

Predictor variable	Definition and units
Density	Average number of tree stump, fallen log, dead wood
Size	Average diameter (cm) of tree stump, fallen log
Dispersion	Average distance (cm) of tree stump, fallen log, dead wood
Abundance	Average total length (m) of fallen log
Diversity	Number of plant species (tree, shrub and herbaceous layer)
Cover	% covered by stratum (canopy, shrub and herb layer)
Exposure	% not covered by any vegetation
Reforestation	0: no reforestation 15: reforestation younger than 15 years 30: reforestation between 15 and 30 years 45: reforestation between 30 and 45 years 50: reforestation older than 45 years
Succession	0: no natural succession (includes areas where succession has not started yet: bare soil, fresh clear cut; areas already reached climax: grown forest; areas with reforestation) 1: young or adjoining (characterised by herbaceous layer, first shrubs emerge) 2: intermediate (shrub layer begins to dominate herb layer; no trees) 3: mature (characterised by pronounced shrub layer and appearance of birches)
Soil loss	0: no mechanical soil loss due to forest management 1: mechanical soil loss due to forest management
Hazel dormouse	0: no detection of hazel dormouse 1: detection of hazel dormouse

TABLE 2 Definition of vegetation layers.

Overstorey	Woody vegetation ≥ 17.5 cm DBH
Understorey	Woody vegetation > 2 m in height and < 17.5 cm DBH
Shrub level	Woody vegetation ≤ 2 m in height
Herb level	Herbaceous vegetation

study, the term 'no succession' refers to areas where natural succession is either discontinued by the forest management due to clear cuts and active soil removal, reforestations or mature forests where succession has already reached a state close to the climax (Table 1). Successional and reforestation stages were classified by their age. The selection of covariates was based on Bertolino (2007) (Table 1). The weekly minimum temperature value was obtained from the nearby meteorological station at Seesen (DWD Climate Data Center (CDC), 2023). Vegetation layers were defined as in Table 2.

2.4 | Statistical analyses

Prior to modelling, all the selected covariates were scaled (mean centred to 0, SD = 1). We then checked for multicollinearity of the predictor variables using the Spearman's correlation coefficients test with a cut-off point of $|\rho| > 0.7$ (Spearman, 1904). The covariates larger than the threshold were omitted. We applied single-season occupancy modelling (MacKenzie et al., 2002) to analyse the response of garden dormouse to different habitat characteristics using the 'unmarked' R package (Fiske & Chandler, 2011) in R version 4.2.1 (R Core Team, 2023). The occupancy model is a type of hierarchical model that takes the detection (1) and non-detection (0) data. It comprises two parameters: the detection (p) and occupancy (ψ) and jointly models the occupancy state of the target species. Thus, our response variable contained a sequence of (binary) 1s and 0s data of the garden dormouse traces collected across footprint tunnels during July and October 2022. We expected that the occupancy of the garden dormouse would be influenced by the *a priori* hypothesised covariates (Table 1). The detection probability of the garden dormouse was modelled as a function of temperature and Julian date (MacKenzie et al., 2006). In occupancy modelling, the Julian date, represented as a number between 1 and 365 or 366, is often used as a covariate to account for temporal variation in species detection or occupancy. This is particularly important in studies where detectability or occupancy may vary throughout the year, for example due to seasonal patterns (Bailey et al., 2014; MacKenzie et al., 2006).

2.4.1 | Modelling

Initially, we fitted a null model, which assumes that occupancy and detection probability are constant across time and sites (MacKenzie et al., 2002). To model the effect of the *a priori* hypothesised covariates, we included covariates first for the detection probability (p) and then for occupancy (ψ). After identifying the most suitable model for the detection parameter, the covariates associated with the probability of occupancy were jointly modelled (Kéry & Royle, 2016).

Our most complex model for both parameters (p , ψ) can be described as:

Detection sub-model (p)

$$y_{ij} \sim \text{Bernoulli}(z_i \times p_{ij})$$

$$\text{logit}(p_{ij}) = \alpha_0 = \alpha_1 \times X_{\text{temperature},ij} + \alpha_2 \times X_{\text{temperature}}^2_{,ij} + \alpha_3 \times X_{\text{Julian date},ij}$$

where y_{ij} is the binary observations (0s and 1s) of garden dormouse i at site j . z_i denotes a random variable with the Bernoulli distribution and p_{ij} is the detection probability of garden dormouse i being present at site j . α_p is the intercept that represents the log-odds of garden dormouse occurrence when temperature is zero, and α is the slope (alpha coefficient) that represents the change in detection probability for a unit increase in temperature and Julian date.

Occupancy sub-model (ψ)

To estimate the observed detection and non-detection data of the dormouse, we modelled the probability of true occurrence z of

the species in site i as a random variable drawn from Bernoulli's distribution with probability ψ :

$$z_i \sim \text{Bernoulli}(\psi_i)$$

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 \times X_{\text{successional stage},i} + \beta_2 \times X_{\text{herb cover},i} + \beta_3 \times X_{\text{hazel dormouse},i}$$

The effects of covariates on occupancy of garden dormouse were assessed through estimation of the intercept β_0 and slopes (or beta coefficients) β . The beta coefficients for each predictor variable indicate the direction and strength of the relationship between that variable and occupancy probability. The effects of covariates were judged as significant or statistically significant if their confidence interval (CI) did not cross 0, and as non-significant effect otherwise. We used the Akaike information criterion corrected for small sample size (AICc) for model ranking and regarded those with delta $\Delta\text{AICc} < 2$ as the best candidate models (Burnham & Anderson, 2002). We applied 'MuMIn' R package to examine possible combinations of the covariate effects (Bartón, 2022). We then performed the goodness-of-fit test for the best-fitting model using 'MacKenzie and Bailey' goodness-of-fit test (Chi-squared parametric bootstrapping) with 1000 iterations (MacKenzie et al., 2002).

3 | RESULTS

Among the 100 footprint tunnels, we detected traces of garden dormouse in 32 tunnels, as well as traces of hazel dormouse in 43 tunnels. Moreover, 18 tunnels exhibited evidence of both garden and hazel dormouse. We observed the presence of a hazel dormouse nest in two tunnels. We further found that the percentage of footprint tunnels per habitat type that contained garden dormouse tracks was 26% in reforestations, of which 8% were old forest, 28.6% in deforestations, 36.7% in successional areas and 38.5% in forest strips. The classification of forest habitat resulted in the following distribution of garden dormouse tracks relative to the total number

of footprint tunnels per habitat type: 23.5% in mixed, 25% in spruce, 27.8% in non-forested open areas and 36.4% in beech forests.

3.1 | Occupancy models

Our findings showed that the detection probability of garden dormouse was significantly and positively influenced by the linear effect of minimum temperature ($\beta_{\text{temperature}} = 1.24$, CI = 0.69 to 1.78), but the non-linear (quadratic) effect of temperature had a relatively lower but negative effect on dormouse occurrence ($\beta_{\text{temperature}^2} = -0.76$, CI = -1.19 to -0.34; Figure 2). With a uniform effort of 12 repetitions for each tunnel, the detection probability was not influenced by the level of effort. The detection probability of garden dormouse increased steadily and significantly ($\beta_{\text{julian date}} = 0.54$, CI = 0.07, 1.02) throughout the sampling period (Julian date), especially from August to October (Figure 3).

Occupancy of garden dormouse was negatively affected by the herb cover percentage ($\beta_{\text{herb cover}} = -0.61$, CI = -1.18 to -0.03; Figures 2 and 4) and positively by the successional stage ($\beta_{\text{successional stage}} = 0.56$, CI = 0.09 to 1.04; Figures 2 and 4). Furthermore, the occupancy of garden dormouse was positively correlated with the occurrence of the hazel dormouse ($\beta_{\text{hazel dormouse}} = 0.91$, CI = -0.01 to 1.87; Figures 2 and 4). The best-fitting model passed the MacKenzie–Bailey goodness-of-fit test ($c\text{-hat} = 1.07$, $p = 0.174$, $\chi^2 = 3314.64$), and the null model did not appear among the models; this suggests that the model fitted the data well (Table 3).

4 | DISCUSSION

4.1 | Habitat type

Our results indicate that the garden dormouse predominantly tends to inhabit successional semi-open habitats (36.7% of garden dormouse tracks) and forest strips (38.5% of garden dormouse

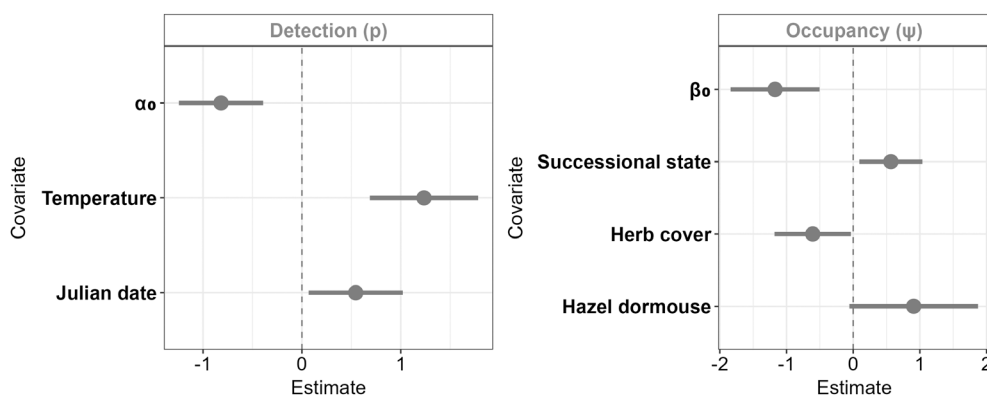


FIGURE 2 Alpha (intercept) and beta (or slope, β) coefficients of the best-fitting single-season occupancy model, along with their 95% confidence intervals estimated for the garden dormouse in the western Harz Mountains, Germany. The confidence intervals that do not include 0 indicate statistical significance. The left panel shows the detection probability estimates with beta coefficients for temperature and Julian date. The right panel shows the occupancy probability estimates with beta coefficients for succession, herb cover and hazel dormouse.

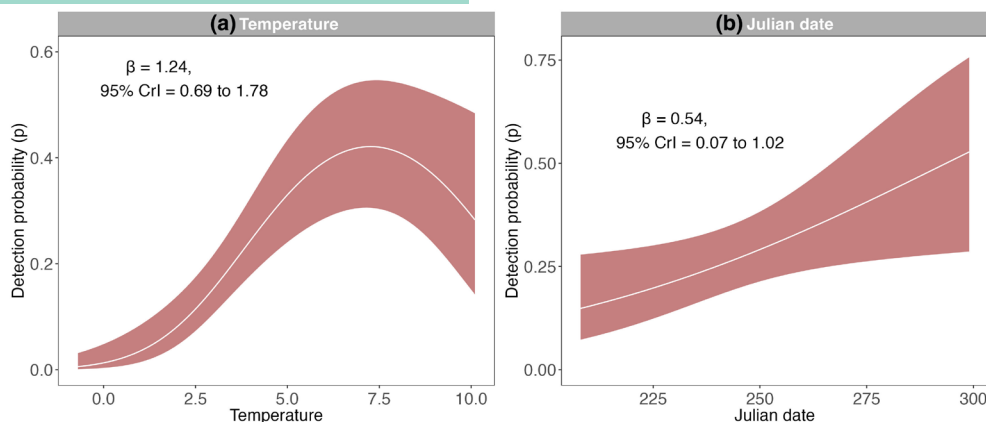


FIGURE 3 Estimated detection probability (p) in relation to covariates (beta coefficients, β) of the best-fitting model for the garden dormouse in the western Harz Mountains. Panel (a) shows the estimated detection probability in relation to temperature, and panel (b) shows the estimated detection probability in association with the Julian date (July–October 2022).

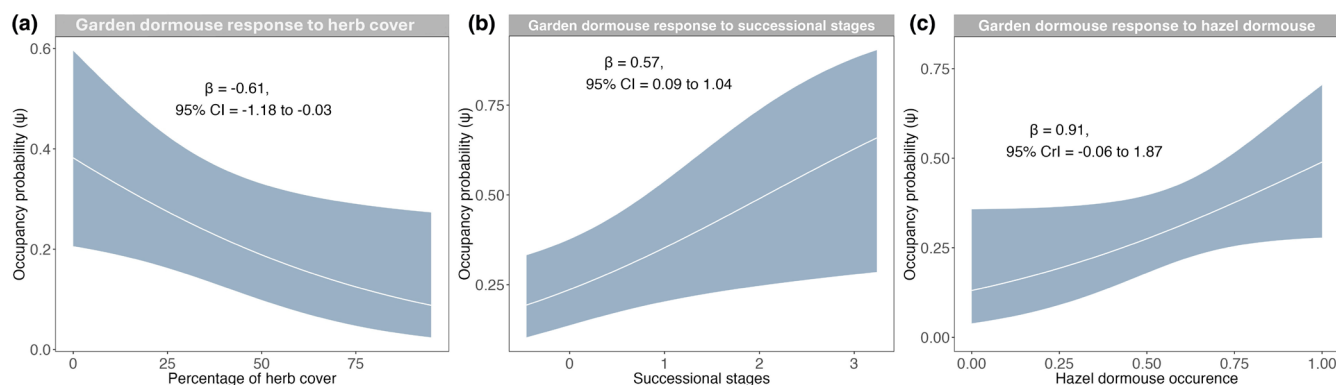


FIGURE 4 Estimated occupancy probability (ψ) against covariates (beta coefficients, β) of the best-fitting model for the garden dormouse in the western Harz Mountains. Panel (a) shows the estimated occupancy probability against the percentages of the herb cover. Panel (b) presents the estimated occupancy probability of dormice across plant successional stages, where 0 indicates no natural succession; Stage 1 represents the young stage, characterised by a herbaceous layer with the first shrubs emerging; Stage 2 represents the intermediate stage, where the shrub layer begins to dominate the herb layer, but trees have not yet appeared; and Stage 3 indicates a mature successional stage, characterised by a dominant shrub layer and the appearance of birches (see Table 1). Panel (c) displays the occupancy probability in relation to Hazel Dormouse occurrence.

tracks), but it was also present in deforested (28%) and reforested (26%) areas. Moreover, we observed its occurrence in mixed, spruce and beech forests. This observation suggests an ability to adapt to different habitat types, including beech and mixed forests, which are likely to dominate the study area in the near future. In these forests, the garden dormouse may also feed on beech nuts (Brosset & de Heim Balsac, 1967) and acorns (Kuipers et al., 2012). Yet, the establishment of the studied population in these areas remains uncertain. This uncertainty is particularly crucial considering the ongoing alterations in the Harz Mountains. The study area is anticipated to undergo continued habitat changes, with new open areas emerging due to deforestation, older reforestations evolving into denser forests and open areas becoming overgrown, reforested or dominated by natural regeneration (Niedersächsische Landesforsten, 2022). Our research indicates that successional areas and forest strips are likely to be important habitats during this transformation process.

4.1.1 | Successional habitats and forest strips

Our findings further show that garden dormouse occurrence in the western Harz Mountains is negatively affected by herb cover and positively affected by a well-advanced young successional stage of woody plants (Figures 2 and 4). In the study area, young successional stages are characterised by the prevalence of shrubs, particularly berry bushes such as blackberry (*Rubus sect. Rubus*) and raspberry (*Rubus idaeus*). As shrub cover becomes denser, the herb cover is reduced due to a reduction in light availability, resulting in less herb growth. Garden dormice were predominantly found in relatively young, but not in the earliest, initial, successional stages. These are characterised by advancing trees (birch and spruce) and a more complex and pronounced shrub layer, dominating over the herb layer (Figures S1 and S5). It seems, therefore, that it may take some time after the last clearing until garden dormice settle in those areas that are typically not reforested. Results also suggest that it is important

TABLE 3 Results of the three best candidate single-season occupancy models (i.e. $\Delta\text{AICc} < 2$) for the Garden Dormouse during July–October 2022 in Harz National Park, Germany.

Occupancy parameters					β -coefficients (95% confidence intervals)			
Model rank	k	logLik	ΔAICc	AICw (%)	$\beta_{\text{intercept}}$	$\beta_{\text{hazel dormouse}}$	$\beta_{\text{herb cover}}$	$\beta_{\text{successional stage}}$
m1	8	−237.25	0.00	0.99	−1.17 (−1.84 to −0.51)	0.91 (−0.06 to 1.87)	−0.61 (−1.18 to 0.03)	0.57 (0.09 to 1.04)
m2	7	−244.21	11.56	0.00	−1.17 (−1.84 to −0.50)	0.91 (−0.06 to 1.88)	−0.61 (−1.18 to −0.03)	0.57 (0.09 to 1.04)
m3	6	−245.95	12.72	0.00	−0.77 (−1.26 to −0.28)		−0.69 (−1.23 to −0.15)	0.55 (0.08 to 1.02)
Detection parameters					β -coefficients (95% confidence intervals)			
Model rank	df	logLik	ΔAICc	AICw (%)	$\beta_{\text{intercept}}$	$\beta_{\text{temperature}}$	$\beta_{\text{temperature}^2}$	$\beta_{\text{julian date}}$
m1	8	−237.25	0.00	0.99	−0.82 (−1.24 to −0.39)	1.24 (0.69 to 1.78)	−0.76 (−1.19 to −0.34)	0.54 (0.07 to 1.02)
m2	7	−244.21	11.56	0.00	−1.45 (−1.73 to −1.16)	0.73 (0.28 to 1.18)	—	0.19 (−0.26 to 0.64)
m3	6	−245.95	12.72	0.00	−1.45 (−1.73 to −1.16)	0.73 (0.26 to 1.18)	—	0.19 (−0.26 to 0.64)

Note: logLik indicates the log-likelihood, and ' ΔAICc ' represents the delta Akaike information criterion corrected for small sample size, and k is the number of model parameters. The table also provides separate beta (β) coefficient and 95% confidence intervals for both occupancy and detection parameters.

to spare out from management areas where succession can occur, providing suitable habitat for the species. Those successional stages with a higher shrub and lower herb cover are obviously preferred by the garden dormouse, eventually also being beneficial as they provide shelter from potential predators and food, especially in late summer (Bertolino et al., 2003; Büchner et al., 2022). Besides the successional areas that emerge after deforestation, the study area's forest strips possess these features as well and additionally facilitate connectivity and movement between different habitats. Maintaining a complex vertical structure of forest vegetation is crucial to providing arboreal movement corridors and nesting sites for dormice (Fedyń et al., 2021). Furthermore, the reduced herb layer could facilitate movement on the ground, which is also consistent with the initial colonisation of spruce forests in the Harz Mountains and previous observations of habitat requirements (Capizzi & Filippucci, 2008; Le Louarn & Spitz, 1974; Meinig & Büchner, 2012). However, varying stages of succession also enable the fulfilment of the changing needs of dormice throughout the season. Bertolino (2017) found that garden dormice move to areas with higher herb cover later in the year, likely to find more insects to increase weight for hibernation. To preserve the garden dormouse while enabling forest use, implementing a diverse shrub layer at forest edges can offer a practical solution. This is further supported by the findings of telemetry studies conducted on garden dormice in the Harz National Park. These studies revealed that forest edges with fringe structures and fruit-bearing shrubs present the preferred habitat in the Harz National Park (Battermann, 2022; Wuttke, 2022).

4.1.2 | Hazel dormouse

We obtained first evidence of the hazel dormouse being present in the study area and showed that garden and hazel dormouse

co-occur. The association between both species suggests that they have similar habitat requirements, and that the presence of the hazel dormouse may be an indicator of suitable habitat conditions for the garden dormouse. By implementing measures to protect the hazel dormouse, which is listed in Annex IV of the European Union's Habitat Directive (Sundseth, 2018) and as 'Near Threatened' in the German Red List (Meinig et al., 2020), suitable nesting sites, food and shelter could be ensured for both species, directly benefiting the occupancy and conservation of the garden dormouse. It is important to note that the conservation measures aimed at supporting the garden dormouse population should prove beneficial to the protected hazel dormouse. However, competition for the same resources, such as nesting sites and food, may also arise between the two species. The presence of the garden dormouse may impact the availability of resting sites for the hazel dormouse, as the latter species is primarily influenced by competition when selecting such sites (Lang et al., 2022). Ensuring an adequate provision of resources is of fundamental importance, enabling co-occurrence and benefiting both species in the long term.

5 | CONCLUSIONS

The diversity of habitats where the garden dormouse was found indicates that the species occupies different natural structures. The predominant occurrence of the species in successional areas and forest strips raises the question of whether those areas function as transition habitats during forest conversion or provide suitable habitats in the long term so that the garden dormouse can establish and maintain its population. As the future forest will mainly consist of beech and mixed forests, with pure successional areas possibly disappearing over time and being replaced by forested areas, it is of paramount importance to continue to maintain the preferred

structures in well-developed forest edges. The establishment of diverse forest edges along remaining spruce forests may also act as refuges for garden dormice in the event of further rapid habitat change. A continuous garden dormouse monitoring in the study area is strongly recommended to be able to react to changes if necessary.

Given the forest conversion and subsequent loss of habitats for the garden dormouse, it is crucial to adjust forest management practices to align with the species' requirements. Based on the findings of this study, our results suggest implementing the following effective forestry management practices for spruce-dominated forests in low mountain ranges in Germany:

1. The establishment of interconnected forest edges and strips.
2. The implementation of a dynamic and mosaic approach to felling and regeneration creates semi-open successional habitats with a dense and species-rich shrub layer and reduced herb cover.
3. In clear cuts of dying or dead spruce stands, avoid the total removal of the wood remnants and the upper soil layer, as this destroys all forest structures.

To maintain the garden dormouse population in the western Harz Mountains, those measurements should be accompanied by a reduction or prohibition of the use of rodenticides and pesticides, which have recently been identified as one of the main causes of mortality of garden dormice (Famira-Parcsetich et al., 2022). In the Harz National Park, deadwood piles were identified as day-time shelters, and the home ranges also encompassed deadwood forests (Battermann, 2022; Wuttke, 2022). We, therefore, recommend leaving deadwood and deadwood structures such as stacks of deadwood in the forest (Figure S4). Additionally, disturbances and killing of dormice during forestry operations should be minimised, especially avoiding large clear felling and driving over the whole area with heavy machinery. By adopting these practices, one can help to maintain a healthy and diverse ecosystem that supports the survival of the garden dormouse and other species.

AUTHOR CONTRIBUTIONS

Sven Büchner, Matthias Waltert and Holger Uwe Meinig conceived the ideas and designed the methodology. Hanna Liesenfelder collected the data. Hanna Liesenfelder and Mahmood Soofi analysed the data. Hanna Liesenfelder drafted the manuscript. Mahmood Soofi led the statistical analyses and writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

First, we would like to thank Nora Albers and Andrea Krug from the Friends of the Earth Germany for initiating the project and their material support, advice and checking of nest boxes. We would also like to extend our thanks to Willi Grope for his work in checking nest boxes and providing essential information about the study site. Lastly, we would like to express our gratitude to Vanessa Betker for the collaboration during fieldwork. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

This project is partly being funded by the German Federal Agency for Nature Conservation with resources from the German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection. It is included in the Federal Programme for Biological Diversity.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6t1g1jx94> (Liesenfelder et al., 2025).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: [Forest strips](#), [Mammal conservation](#).

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SUPPORTING INFORMATION

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

Figure S1. Typical habitats of the garden dormouse in the study area in the western Harz Mountains (Photos by Hanna Liesenfelder).

Figure S2. Representative areas of deforestation in the study area in the western Harz Mountains (Photos by Hanna Liesenfelder).

Figure S3. Areas with soil removal in the study area in the western Harz Mountains (Photos by Hanna Liesenfelder).

Figure S4. Deadwood structures in the study area in the western Harz Mountains (Photos by Hanna Liesenfelder).

Figure S5. Successional stages in the study area in the western Harz Mountains (Photos by Hanna Liesenfelder).

Figure S6. Build-up of a footprint tunnel with cardboard and ink pad with charcoal ink (top left and right) and the placement of footprint tunnels on trees (middle left), in shrubby vegetation (middle right) and on available branches (down left and right) (Photos by Hanna Liesenfelder).

Figure S7. A typical footprint of Garden dormouse (on top) and hazel dormouse (below) (Photos by Hanna Liesenfelder).

How to cite this article: Liesenfelder, H., Büchner, S., Waltert, M., Meinig, H. U., & Soofi, M. (2025). Ecological drivers of garden dormouse (*Eliomys quercinus*) occupancy in a human modified landscape in Germany. *Ecological Solutions and Evidence*, 6, e70023. <https://doi.org/10.1002/2688-8319.70023>